HABITAT USE DECISIONS BY BOTTLENOSE DOLPHINS (*TURSIOPS ADUNCUS*) AND TIGER SHARKS (*GALEOCERDO CUVIER*) IN A SUBTROPICAL SEAGRASS ECOSYSTEM

by

Michael R. Heithaus

B.A., Oberlin College, 1995

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

in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY
March 2001

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

0-612-61648-7

Canada

ABSTRACT

Understanding the factors that determine the spatial distribution of animals is critical to making predictions about how animals will respond to environmental change. Despite this, few studies have attempted to identify factors influencing habitat use decisions of animals in complex natural communities. In this thesis, I use behavioral ecological theory to make specific predictions about how bottlenose dolphins (*Tursiops aduncus*) should respond to natural variation in food availability and the risk of predation from tiger sharks (*Galeocerdo cuvier*). I begin by reviewing shark-dolphin interactions worldwide and show that in some regions sharks and dolphins are intraguild predators. Because there is no theoretical basis for making predictions about the spatial distribution of intraguild predators, I created a game theoretical model of intraguild predation. This model shows that the community context of interactions can influence the predicted distributions of predators and their prey. During field studies in Shark Bay, Western Australia, I found that tiger sharks are the greatest threat to dolphins, and over 74% of dolphins bear scars from unsuccessful attacks. However, dolphins are a minor component of tiger shark diets, which are composed mainly of dugongs (*Dugong dugon*), sea snakes, and sea turtles. Tiger shark catch rates were high in warm months and low in cold months and appear to be influenced by both water temperature and seasonal changes in primary prey density. When present, tiger sharks are found most often in shallow habitats where prey density is highest. Dolphins were found to trade-off food and safety. When sharks were absent, dolphins matched the distribution of their food, but when tiger sharks were present, dolphins foraged in productive shallow habitats less than expected by food availability alone. However, juvenile male dolphins foraged in dangerous habitats more often than other age/sex classes. Interestingly, dolphin habitat use may be influenced indirectly by habitat use decisions of other tiger shark prey species because of their influence on sharks. This thesis shows that behavioral ecological theory can be used in natural communities to understand the factors influencing habitat use decisions and that future research will benefit from considering the community context of behavioral decisions.

ACKNOWLEDGEMENTS

The work in this thesis was made possible thanks to the help and support of many people, businesses and organizations that are acknowledged at the end of specific chapters. However, there are a number of individuals who deserve special thanks.

First, I thank Larry Dill, my senior supervisor, for his guidance, encouragement, support, and assistance throughout every phase of this project. I also thank the members of my committee, the Behavioral Ecology Research Group at Simon Fraser University, and the Dill lab for their suggestions and stimulating discussions throughout my time at SFU.

Thanks also go to Alex Fraser (SFU), Ron Swann (University of Western Australia), Colin Simpfendorfer and Rory McAuley (Fiseries Western Australia), and Brad Barton and David Charles (Department of Conservation and Land Management) for providing equipment and logistical support that made it possible to carry out extended field seasons. I would also like to give extra thanks to Justin McLash, Jenny Burhardt, Patrick Greene, and Hugh Finn who all put in extended seasons as field assistants.

I owe a debt of gratitude to Greg Marshall and Birgit Buhleier at National Geographic Special Projects. Their logistical, financial, and moral support and the loans of Crittercam systems allowed me to conduct studies of shark behavior and habitat use that would not have been possible otherwise.

I thank my parents for instilling in me a curiosity about the natural world and providing me with opportunities to pursue my goals, even if it involved sending me into "shark-infested waters." I made it out alive, mom! Finally, I thank my wife, Linda, for her support, encouragement, and countless emails both while I was in the field and completing this dissertation.

Table of Contents

List of Tables and Appendices

List of Figures

CHAPTER 1

General Introduction

Identifying the factors that influence the spatial distributions of animals is critical for making predictions of how animals will respond to environmental changes. Furthermore, understanding how these factors influence individuals' habitat use decisions can provide a mechanistic basis for understanding interspecific interactions within communities (Werner 1992). Both the spatial distribution of food and habitat differences in predation risk may be important in determining animal habitat use (see Lima and Dill 1990 for a review of foraging decisions made under the risk of predation). Of particular interest are situations in which the habitats that have high food availability are also the most dangerous, causing animals to have to trade-off food and safety when selecting a habitat to occupy.

In recent years there has been a proliferation of both theoretical and empirical studies aimed at understanding how food availability and predation risk influence habitat use. Fretwell and Lucas (1970) developed the most basic model, the ideal free distribution (IFD). This model predicts that when foraging success is density-dependent, food is the only factor influencing fitness, animals have perfect knowledge of food distribution, and are free to move among habitats then the proportion of animals in each habitat will be equal to the proportion of food available there. Modifications have been made to this basic IFD model to incorporate predation risk, and predict that animals should often be willing to accept lower energetic returns in order to forage in safer habitats (e.g. McNamara and Houston 1990) or even respond solely to the relative safety of habitats (e.g. Hugie and Dill 1994, Sih 1998). Although some laboratory (e.g. guppies, *Poecilia reticulata*, Abrahams and Dill 1989) and simple field systems (e.g. creek chub, *Semotilus atromaculatus*, Gilliam and Fraser 1987; armored catfish, *Ancistrus spinosus*, Oksanen et al. 1995) conform to the predictions of these IFD-based models, the application of these theories to gain an understanding of behavioral decisions made by animals in field situations in relatively complex communities, has been minimal. However, behavioral ecological theory has the potential to provide a framework for elucidating the influences of food availability and predation risk in natural communities.

Food availability and predation risk have been hypothesized to be important in influencing habitat use and group size of bottlenose dolphins (Wells et al. 1980, 1987), but no studies have tested these hypotheses. The population of bottlenose dolphins

(*Tursiops aduncus*) in Shark Bay, Western Australia provides an excellent field system for studying food – safety tradeoffs. The dolphins in this area are long-lived and are year-round residents within relatively restricted home ranges that encompass numerous habitat patches. Therefore, more than many species, dolphin individuals will have good knowledge of the food availability in various habitats. Also, because dolphins have low locomotion costs (Williams et al. 1992) and there is no obvious aggression during foraging (personal observation) they are likely able to move freely between habitats as ecological parameters vary. Finally, the dolphins in Shark Bay appear to face a substantial risk of predation, especially from tiger sharks (*Galeocerdo cuvier*). An additional benefit of working in Shark Bay is the availability of data on the age/sex class of most dolphins in the study area, allowing analysis of age/sex differences in habitat use. In this thesis, I investigate the influence of prey availability and predation risk on bottlenose dolphin habitat use in Shark Bay.

To understand the influence of food availability and predation risk on bottlenose dolphin habitat use, it is important to determine the possible interactions between dolphins and their predators. As well, a basic understanding of the biology, foraging behavior, habitat use, and movements of their main predators is necessary. Thus, this thesis also investigates the behavior and biology of tiger sharks in Shark Bay.

I begin, in Chapter 2, with a review of both predator-prey and competitive interactions between sharks and odontocete cetaceans and show that both interactions sometimes occur simultaneously, a situation referred to as intraguild predation (IGP, Polis et al. 1989). No theoretical investigations of habitat use under conditions of IGP have been conducted so it is unclear how animals should distribute themselves across habitats when predator and prey are also competitors. Therefore, I developed a game theoretical model of habitat selection of predators and prey engaged in asymmetrical intraguild predation (Chapter 3) to allow such predictions. In Chapter 3, I also investigate how community structure can influence habitat use decisions by both predators and prey in such a senario.

Tiger sharks were thought to be the major predation threat to dolphins in Shark Bay, but little was known about the frequency of tiger shark attacks. Chapter 4 investigates shark attacks on dolphins and identifies shark species and size classes that appear to pose the greatest threat. Chapter 5 summarizes a basic study of tiger shark biology that describes the size distribution of tiger sharks in the study area as well as their seasonal abundance. This chapter also investigates whether tiger shark seasonal movements are influenced by changes in the availability of their prey.

In Chapters 6 and 7, I investigate tiger shark habitat use and foraging behavior. Chapter 6 describes the techniques used to study sharks with an animal-borne video camera ("Crittercam") and investigates the influence of these instruments on sharks. Chapter 7 investigates tiger shark foraging behavior and habitat use in relation to food availability and introduces new Monte Carlo methods for analyzing tracking data.

Chapter 8 presents data on spatial and temporal variation in Shark Bay's fish communities, upon which dolphins rely for food. In Chapter 9, I use the basic framework of behavioral ecological theory to investigate the influence of food availability and predation risk on dolphin habitat use and group size. Finally, I discuss how indirect behavioral effects ("behaviorally mediated indirect interactions") may be an important feature of communities and provide empirical evidence to support theoretical arguments (Chapter 3) that studies of animal habitat use must consider the community context in which behavioral decisions are made.

1.1 LITERATURE CITED

Abrahams, M.V. and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999-1007.

Fretwell, S. D. and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16-36.

Gilliam, J. F. and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856-1862.

Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45 (Suppl. A): 151-169.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

McNamara, J. M. and A. I. Houston. 1990. State-dependent ideal free distributions. Evolutionary Ecology 4: 298-311.

Oksanen, T., M. E. Power, and L. Oksanen. 1995. Ideal free habitat selection and consumer-resource dynamics. American Naturalist 146: 565-585.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330.

Sih, A. 1998. Game theory and predator-prey response races. Pages 221-238 in L. A. Dugatkin and H. K. Reeve, editors. Game Theory and Animal Behavior. Oxford University Press: Oxford.

Wells, R. S., A. B. Irvine, and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pages 263-317 in L. M. Herman, editor. Cetacean Behavior: Mechanisms and Functions. Wiley: New York.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 in H. H. Genoways, editor. Current Mammalogy, Volume 1. Plenum Press: New York.

Werner, E. E. 1992. Individual behavior and higher-order interactions. American Naturalist 140: S5-S32.

Williams, T. M., A. W. Friedl, M. L. Fong, R. M. Yamada, P. Sedivy, and J. E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355: 821-823.

CHAPTER 2

Predator-Prey and Competitive Interactions Between Sharks and Dolphins: a Review*

*A version of this chapter appears as Heithaus, M. R. 2001. Predator-prey and competitive interactions between sharks (Order Selachii) and dolphins (suborder Odontoceti): a review. Journal of Zoology 253: 53-68. Reprinted with permission from the Zoological Society of London.

2.1 ABSTRACT

The importance of interactions between sharks and cetaceans has been a subject of much conjecture, but few studies have addressed these interactions. Sharks have been hypothesised to be important predators on dolphins and porpoises, but there are often few data to back up claims that certain shark species are a major threat to small odontocete cetaceans. To help identify potential shark predators in specific locations, available data on interactions with odontocetes for all shark species that may include cetaceans in their diet are reviewed. Shark species are categorized into groups based on predatory interactions with dolphins and porpoises (regular predators, occasional predators, potential predators, ectoparasites, and insufficient data). Several shark species that have been overlooked in the cetacean literature are identified as potentially important predators while others that have been suspected to be important predators are probably at most occasional predators. I discuss how shark predation can influence dolphin populations, habitat use, group size, and behaviour. I also consider how the risk of shark predation can vary with habitat attributes in both nearshore and pelagic waters. Although predator-prey interactions have been the focus of most studies of shark-dolphin interaction, competitive interactions may also occur. A quantitative analysis of both shark and dolphin diets from South Africa shows significant dietary overlap between common dolphins and several species of sharks, including species that prey upon these dolphins.

2.2 INTRODUCTION

Predation risk is a primary factor that can influence group composition, group size, and habitat use (e.g. Betram 1978, van Schaik and van Noordwijk 1985, Lima and Dill 1990), and has been suggested as the selective pressure leading to the evolution of sociality in many taxa (e.g. Terborgh 1983, van Schaik and van Hoff 1983, van Schaik and van Noordwijk 1985), including odontocete cetaceans (toothed whales) (Norris 1994). Most studies of predation on odontocetes are based largely on wounds and scars on living individuals and chance observations of predation events (e.g. Corkeron, et al. 1987, Paterson et al. 1993, Mann and Barnett 1999). Other studies merely invoke predation to explain the patterns of grouping and habitat use that are observed without quantifying these relationships. Killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), polar bears (*Ursus maritimus*), and a variety of sharks have been identified as natural predators of odontocetes. In a brief review of shark predation on cetaceans, Long and Jones (1996) listed only a handful of shark species as cetacean predators including the white (*Carcharodon carcharius*), tiger (*Galeocerdo cuvier*), dusky (*Carcharinus obscurus*), bull (*Carcharinus leucas*), oceanic whitetip (*Carcharinus longimanus*), and shortfin mako sharks (*Isurus oxyrinchus*). Unfortunately, the criteria for these listings were unclear.

Interactions among sharks and odontocetes are not limited to predator-prey interactions. Many sharks and odontocetes feed largely on teleost fishes and cephalopods and there is a possibility for competitive interactions. For example, tiger sharks in Hawaii and northeastern Australia, small (<2.2m) white sharks in the Atlantic and Pacific, and sandbar sharks (*Carcharhinus plumbeus*) off South Africa feed on a variety of teleost fish, as do many dolphins and porpoises in these areas (Carey et al. 1982, Tricas and McCosker 1984, Cliff et al. 1988, Simpfendorfer 1992, Lowe et al. 1996). Also, there are observations of sharks and dolphins feeding from the same school of fish (e.g. Leatherwood 1977), and whaler sharks (*Carcharhinus* sp.) have been seen feeding with dolphins behind trawlers in Australia (Corkeron et al. 1987). Off the Farallon Islands, competition with killer whales over pinneped prey, may have been responsible for the displacement of white sharks from a traditional foraging area (Pyle et al. 1999).

Competitive interactions help determine animal group size, habitat use, and ranging patterns. Therefore, it is important to determine whether shark and odontocete diets may overlap significantly. Quantitative analysis of the potential for shark-odontocete competition is difficult, and competition has never been measured.

The primary goal of this Chapter is to compile the largely scattered literature on shark-odontocete interactions and shark feeding to provide a background for formulating testable hypotheses about shark-odontocete predator-prey and competitive interactions. This review investigates 1) the species of sharks that are odontocete predators world wide, 2) odontocete predation on sharks, 3) competition between dolphins and sharks in South Africa, and 4) the likely influences of sharks on dolphin and porpoise populations and behaviour.

2.3 MATERIALS AND METHODS

2.3.1 Classifying shark predator-prey interactions with odontocetes

It is not always apparent which species of sharks are predators on dolphins and porpoises and which are likely to only scavenge odontocete carcasses, and a variety of methods have been used to determine whether a particular shark species is a predator on dolphins and porpoises when direct observations are lacking. In this review, I only consider a shark to be a predator on odontocetes if it takes free-swimming animals. I do not consider killing a terminally ill, severely wounded, or stranded animal a predation event. Although scavenging of cetacean carcasses may be an important source of food for many shark species (e.g. Long and Jones 1996, Carey et al. 1982), scavenging is not treated in this review since it will not influence the behaviour or population dynamics of odontocetes.

There are several ways to determine if shark bites from unwitnessed attacks were predatory or the result of scavenging. Live-strandings of cetaceans with fresh shark-inflicted wounds are usually the result of a predation attempt, but this may not always be so (e.g. Ridgway and Daily 1972, see below). It is sometimes possible to determine predation events from dead strandings by analysis of the wounds (e.g. Long and Jones

1996) and to determine the species and approximate size of the shark responsible for the bites from the characteristics of the wounds and any teeth that are recovered.

When trying to determine if a shark species is a potential predator, the stomach contents of a large number of sharks must be examined to make an educated guess about a species' status as a predator or scavenger. In general, if odontocetes appear in a large proportion of sharks' stomachs or constitute a major portion of the diet (e.g. percent of prey mass or number), the species is probably a predator since it is unlikely that there would be an opportunity to scavenge such a large number of odontocete carcasses. Looking at the sharks' other prey species can strengthen this argument. If a shark species is known to prey upon large, fast-swimming prey, it is possible that it is also capable of capturing an odontocete.

The above approach is only useful for identifying regular predators on odontocetes. Low frequencies of occurrence in sharks' stomachs might indicate that a species is only a scavenger, or only an occasional predator. One important consideration is the size distribution of sharks being examined. Many shark species show ontogenetic shifts in diet (see below) and odontocetes may only be taken by the largest size classes. Therefore, if the diet analysis includes primarily small individuals, the importance of odontocetes in the diet of large sharks may be overlooked.

Determining whether individual stomach contents are from predation or scavenging is difficult. Shark predation might be inferred by the presence of flukes or vertebrae in a shark's stomach (Cockcroft et al. 1989) because scavenging sharks would be expected to consume only the fat-rich portions of a carcass, not bony material (e.g. Carey et al. 1982, Klimley 1994). Also, many shark attacks on odontocetes appear to be directed at the tail flukes (Arnold 1972, Cockcroft 1991, Long and Jones 1996). Studies on white sharks in South Africa provide evidence that this method is probably an underestimate of the actual predation rate. From 1978-1982, 24.2% of white sharks contained cetacean remains, and 20.7% had cetacean remains in their stomachs between 1983-1988 (Cliff et al. 1989). This is significantly higher than the 1% incidence of dolphin flukes and vertebrae that were found in white sharks from 1983-1987 by Cockcroft et al. (1989). The discrepancy between these results may be due to a high frequency of scavenging or sharks not necessarily consuming flukes and vertebrae in the process of a predatory attack. Although the fluke-and-vertebrae method probably underestimates the actual predation rate, it is still a useful technique for identifying odontocete predators.

Most studies on the diets of sharks do not provide enough detail for analyses using the fluke-and-vertebrae method. In section 2.4.1, I place shark species into several categories (regular predator, occasional predator, suspected predator, ectoparasite, and insufficient data) using a combination of the above techniques. This analysis is meant to help guide future research as there is still a critical lack of data for many species, and it is not possible to be certain of some classifications. The rationale for each species' listing and brief descriptions of each shark species' diet and behaviour should aid research into the influences of these species on many odontocetes. When considering the data below, it is important to keep in mind that many shark species are opportunistic foragers. Thus, it is possible that interactions between particular shark species and cetaceans may vary geographically depending on resources available to both sharks and dolphins.

2.3.2 Competition

Dietary data were available for three dolphin species and eight shark species caught off the coast of South Africa. Niche breadth was calculated using Levins' index (Ellis et al. 1996):

$$B = \frac{1}{\sum p_i^2} \qquad (1)$$

where p_i is the proportion of each prey group in the diet (based on % mass of the prey in stomachs containing a type of prey or % number for humpback dolphins). Levins' niche breadth index ranges from 1 (specific diet) to the total number of prey groups (broadest diet).

Dietary overlap was calculated with the MacArthur-Levins' index (Ellis et al. 1996). Two calculations are made for each pair of species to determine asymmetrical overlap.

$$M_{jk} = \frac{\sum p_{ij} p_{ik}}{\sum p_{ij}^2} \qquad (2)$$

$$M_{kj} = \frac{\sum p_{ik} p_{ij}}{\sum p_{ik}^2} \qquad (3)$$

where M_{jk} and M_{kj} are the degree to which species *k* overlaps species *j*'s diet and vice versa. P_{ij} and P_{ik} are the proportions that each prey type *i* contributes to the diet of species *j* and *k* respectively. Comparisons are all based on % mass of prey except those with humpback dolphins which are all based on % number. A value greater than 0.7 is considered significant (Macpherson 1981, Ellis et al. 1996).

Both niche breadth and dietary overlap were calculated for the South African data with family-level prey groups. Some ray families were lumped, but these always had similar ecologies (e.g. bottom-dwelling vs. free swimming), and this is unlikely to influence comparisons significantly, especially shark-dolphin comparisons. Indices for genus-level, and more highly lumped prey groups were calculated when possible. Basic results are the same except where discussed below, so these data are not presented.

2.4 RESULTS

2.4.1 Shark predators of dolphins and porpoises

2.4.1.1 Regular predators

White (*Carcharodon carcharius*), bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), sixgill (*Hexanchus griseus*), and sevengill sharks (*Notorynchus cepidianus*) are all relatively frequent predators on dolphins and porpoises in at least some parts of their range (Table 2.1, Table 2.2). White sharks show a marked shift in diet with size: young sharks feed primarily on fishes, but larger sharks switch to a diet of marine mammals (Tricas and McCosker 1984, Klimley 1985). White sharks have been recorded as predators of many cetaceans, including species as large as beaked whales (Long and Jones 1996). White sharks are a major predator on harbour porpoises (*Phocena phocena)* along the east and west coasts of North America (Arnold 1972, Long and Jones 1996), and odontocetes may be the most important part of the white sharks' diet in some areas of the world. In South Africa, Cliff et al. (1989) found that marine mammals were the most important prey of large juvenile white sharks (no mature individuals were captured) from 1983 to 1988, with dolphins making up the majority of the marine mammal prey (Table 2.3). Dolphins are the primary prey of large white sharks off South Australia, with 44%

of stomachs containing dolphin remains (Bruce 1992). Habitat use by white sharks in this location may be determined by dolphin abundance as white sharks were sighted in locations where pinnipeds are rare but dolphins are common. Scavenging of cetacean carcasses may also be an important component of white shark diets in both the Atlantic and Pacific Oceans as a shark can survive for over a month on a single meal scavenged from a carcass (Carey et al. 1982, Long and Jones 1996).

White sharks have generally been studied in temperate waters, but they may be a threat to odontocetes in subtropical waters as well. In Moreton Bay, Australia, Corkeron et al. (1987) attributed bites on free-swimming bottlenose dolphins (*Tursiops truncatus*) to white shark attack. Although predation has not been documented on all small odontocetes sharing the white shark's range, this shark is almost certainly a predation threat to any small odontocete that it encounters.

The bull shark starts taking large prey at a relatively small size, and is one of the only sharks that will attack prey larger than itself (Caldwell et al. 1965, Cockcroft et al. 1989, Long and Jones 1996). Scars and wounds on bottlenose dolphins indicate that bull sharks begin attacking dolphins at a smaller shark size than do white, tiger, or dusky sharks (Cockcroft et al. 1989). Wells (1991) and Irvine et al. (1973) have identified the bull shark as a predator of dolphins in the northeast Gulf of Mexico, and bull sharks off South Africa preyed upon bottlenose dolphins more often than did white, tiger or dusky sharks (Cockcroft et al. 1989); dolphin flukes and vertebrae were found in 2.2% of sharks over 1.8 m. In an earlier study in South Africa, cetacean remains were found in 12 of 99 (12.1%) bull sharks examined (Bass et al. 1973), but a large portion of this may have been scavenged from whale carcasses being towed to a whaling station. In a post-whaling study, cetacean remains were found in 5.7% of stomachs, but the predation rate may have been as low as 1.6% based on the fluke-and-vertebrae method (Cliff and Dudley 1991a). The bull shark may be one of the few predators on some river dolphins as it has been found almost 4000 km from the sea in the Amazon River system, and in many river systems in northern Australia, North America, Asia, and Africa (Last and Stevens 1994).

Table 2.1. Shark species with cetacean remains found in stomach contents, grouped into categories of possibility for predation on living cetaceans. Sharks were placed into categories based on frequency of odontocetes in stomachs, observations of attacks, and wounds on living cetaceans. Tt= *Tursiops truncatus*, Dd = *Delphinus delphis*, Pp = *Phocena phocena*, Sp = *Sousa plumbea*, Gg = *Grampus griseus*, Pd = *Phocenoides dalli*, Kb = *Kogia breveceps*, Ks = *Kogia simus*, Lo = *Lagenorhynchus obliquidens*, Lb = *Lagenorhynchus obscurus*, Ms = *Mesoplodon stejnegeri*, Zc = *Ziphia cavirostris*, Sa = *Stenella attenuata*, Pb = *Pontoporia blanvilli*, Ch = *Cephalorhynchus hectori*, Lp = *Lissodelphis peronii*, Mm = *Monodon monoceros*, Dl = *Delphinapterus leucas*, Sl = *Stenella longirostrus*, Sb = *Steno bredanensis*, Pc = *Pseudorca crassidens*, Fa = *Feresa attenuata*, Md = *Mesoplodon densirostris*, Pm = *Physter macrocephalus*, Us = *Stenella* sp., Ud = Unidentified Delphinidae, Uc = Unidentified cetacean

Species	Scientific Name	TL[1]	Cetaceans in Diet	References
Regular Predators				
White shark	*Carcharodon carcharias*	6.4[2]	Tt, Dd, Pp, Sp, Gg, Pd, Kb, Ks, Lo, Lb, Ms, Zc	Arnold (1972), Randall (1973) Carey et al. (1982), Cliff et al. (1989), Cockcroft et al. (1989), Bruce (1992), Last and Stevens (1994), Cliff et al. (1996), Fergusson (1996), Long and Jones (1996)
Tiger shark	*Galeocerdo cuvier*	6.0	Tt, Sa	Bell and Nichols (1921), McBride and Hebb (1948), Irvine et al. (1973), Compagno (1984b), Stevens (1984), Cockcroft et al. (1989), Stevens and McLoughlin (1991) Wells (1991), Randall (1992), Last and Stevens (1994)
Bull Shark	*Carcharhinus leucas*	3.4	Tt, Dd	Bell and Nichols (1921), Bass et al. (1973), Irvine et al. (1973), Compagno (1984b), Cockcroft et al. (1989), Cliff and Dudley (1991a), Last and Stevens (1994)
Sixgill shark	*Hexanchus griseus*	5.5[3]	Tt, Ud	Ebert (1986, 1994), Clark and Kristof (1990)
Sevengill shark	*Notorynchus cepedianus*	3.0	Pb, Ch, Lb	Brownell (1975), Compagno (1984a), Cawthorn (1988), Ebert (1991a, b)
Occasional Predators				
Dusky shark	*Carcharhinus obscurus*	4.0[4]	Tt	Irvine et al. (1973), Compagno (1984b), Cockcroft et al. (1989), Last and Stevens (1994)
Oceanic whitetip shark	*Carcharhinus longimanus*	3.9[5]	Us	Leatherwood et al. (1973), Bass et al. (1973), Compagno

				(1984b), Stevens (1984), Long and Jones (1996)
Suspected Predators				
Shortfin mako shark	*Isurus oxyrinchus*	3.9	Us, Dd	Ridgway and Dailey (1972), Leatherwood et al. (1973), Stillwell and Kohler (1982), Stevens (1984), Cliff et al. (1990), Last and Stevens (1994)
Pacific sleeper shark	*Somniosus pacificus*	6.0	Lp	Crovetto et al. (1992), Last and Stevens (1994)
Greenland shark	*Somniosus microcephalus*	6.4[4]	Mm, Dl	Williamson (1963), Beck and Mansfield (1969)
Ectoparasites				
Cookie-cutter shark	*Isistius brasiliensis*	0.5	Sl, Sb, Pc, Fa, Md	Jones (1971), Paterson et al. (1993), Last and Stevens (1994), Norris (1994)
Portugueese dogfish	*Centroscymnus coelolphis*	1.2	Pm, Uc	Clarke and Merrett (1972), Mauchline and Gordon (1983), Ebert et al. (1992), Last and Stevens (1994)
Insufficient Data				
Java shark	*Carcharhinus amboinensis*	2.8	Uc	Bass et al. (1973), Compagno (1984b), Cliff and Dudley (1991b)
Copper shark	*Carcharhinus brachyurus*	3.0	Dd	Cliff and Dudley (1992), Compagno (1984b)
Sandbar shark	*Carcharhinus plumbeus*	2.4	Uc	Stillwell and Kohler (1992), Compagno (1984b), Cliff et al. (1988)
Blacktip shark	*Carcharhinus limbatus*	2.5	Uc	Compagno (1984b), Dudley and Cliff (1993)
Galapagos shark	*Carcharhinus galapagensis*	3.0	Uc	Wetherbee et al. (1994)
Blue shark	*Prionace glauca*	3.8	Uc	Stevens (1973), Compagno (1984b), Stevens (1984)
Hammerhead shark	*Sphyra* sp	6.0	Dd	Leatherwood et al. (1973)

---

[1] Maximum reported total length (m). All measurements from Last and Stevens (1994) except where noted.

[2] This figure is the largest reliably measured white shark, but bite scars on whale carcasses suggest that individuals of 7.5-8.0m may exist (Randall 1973).

[3] This is the size of a single female described by Clark and Kristof (1990), and may not represent a maximum length.

[4] Compagno (1984b)

[5] Compagno (1984b), but most individuals < 3.0m

Table 2.2. Distribution and habitats of sharks thought to be predators on cetaceans. Data are based on references sighted in text and from Last and Stevens (1994). C = coastal, P = pelagic (including continental shelves and open ocean), F = fresh water, S = surface (generally <50m), D = deep ocean (generally >200m), Tr = tropical, CTr = cold tropical, Tp = temperate, WTp = warm temperate, CTp = cold temperate, Ar = arctic. Codes in parentheses indicate occasional only.

Species	Habitat	Depth	Latitude
White Shark	C	S	Tp, CTr, (Tr)
Tiger Shark	C, P	S, (D)	Tr, WTp
Bull Shark	C, F	S	Tp, WTp
Sixgill Shark	C, P	D, (S)	Tp, Tr
Sevengill Shark	C	S	Tp, Tr
Dusky Shark	C, P	S, (D)	Tr, WTp
Oceanic Whitetip Shark	P	S	Tr, WTp
Shortfin Mako Shark	P	S	Tp, Tr
Pacific Sleeper Shark	C, P	D	Tp
Greenland Shark	C, P	D, (S)	CTp, Ar
Cookie-Cutter Shark	P	D	Tp, Tr
Portugese Dogfish	P	D	Tp, Tr

The bull shark seems to be a highly adaptable forager, and its diet and interactions with odontocetes may vary considerably among locations.

Tiger sharks are another predator on small odontocetes, but they migrate into higher latitudes as water temperature rises, so may only pose a seasonal threat to small odontocetes in some areas. Like white sharks, tiger sharks change their diet as they grow. Small sharks appear to feed near the bottom at night, while large individuals (>3m) diversify their diet to feed on large-bodied prey and feed throughout the water column diurnally as well as at night (Simpfendorfer 1992, Lowe et al. 1996). The broad, heavily calcified jaws and nearly terminal mouth, combined with robust, serrated teeth enable the tiger shark to take and handle large prey like turtles and marine mammals (Randall 1992). Tiger sharks show considerable geographic variation in their diet (e.g. Simpfendorfer et al. 2001), and their propensity to attack cetaceans will probably be dependent on the abundance of other prey in a given location.

Tiger sharks generally swim slowly, which, combined with cryptic colouration, may make them difficult for prey to detect in some habitats. Despite their sluggish appearance, tiger sharks are one of the strongest swimmers of the carcharhinid sharks (Baughman and Springer 1950, Compagno, 1984b). Once the shark has come close, a speed burst allows it to reach the intended prey before it can escape.

Bottlenose dolphin calves have been killed by tiger sharks in Sarasota, Florida and Shark Bay, Western Australia (Wells 1991, Mann and Barnett 1999), and dolphins have been found in the stomachs of tiger sharks in both locations (Irvine et al. 1973, Simpfendorfer et al. in press). Seven of 36 (19.4%) tiger sharks caught in gill nets off North Carolina contained dolphin remains, but there is a chance that up to six of these had scavenged dolphins caught in the same net (Bell and Nichols 1921). In Hawaii, dolphins were found in 7% of 135 stomachs from large sharks (> 3.0m) and 2% of 118 stomachs from medium-sized sharks (2.0-3.0m) (Lowe et al. 1996). Only 1.3% of 558 tiger sharks caught in northeastern Australia had consumed dolphins (Simpfendorfer 1992), but if all dolphin remains came from large sharks (>3.0m), the frequency of occurrence for this size class would be 9%. Finally, 1.9% of tiger sharks off South Africa had dolphin flukes or vertebrae in their stomach contents (Cockcroft et al. 1989).

The sixgill shark has not previously been identified as a major odontocete predator in the cetacean literature, and is perhaps one of the most overlooked predators on odontocetes. They are large deep-water sharks and are the dominant predators along the outer continental shelves and upper continental slopes (Clark and Kristof 1990, Ebert 1990). Sixgill sharks are active hunters and the "... sixgill shark's large size, relatively broad mouth and huge cutting teeth ... is indicative of a predator with a voracious appetite and one that must have a substantial impact on the prey organisms within its area of distribution" (Ebert 1994).

Large (> 2.0 m) sixgill sharks off South Africa take many dolphins (Ebert 1994, Table 2.3). Dolphins occurred in 18.2% of stomachs, and were one of the most important components of the diet based on an index of relative importance. These sharks were caught by longline and trawler, so they would not have scavenged dolphin carcasses in nets. Despite this, the frequency of occurrence of odontocete remains in sharks over 2.0 m is similar to that of known dolphin predators in South Africa, including white and bull sharks. The frequency of dolphin occurrence in shark stomachs suggests that the sixgill shark is an active odontocete predator (Ebert 1994). Other evidence for the sixgill shark being capable of attacking free-swimming odontocetes comes from observations of sixgill sharks attacking large, fast swimming prey such as swordfish and other billfish (Ebert 1990), and a high occurrence of South African fur seals (*Arctocephalus pusillus*) in the diet of large sixgill sharks (Ebert 1994).

As with the sixgill shark, there are no direct observations of sevengill shark predation on odontocetes, but there is indirect evidence that suggests that this shark may be an important predator on coastal odontocetes in some areas. This shark feeds on a variety of prey including teleosts, cephalopods, sharks, rays, pinnipeds, and cetaceans (Brownell 1975, Ebert 1991a, Cawthorn 1988), but there is a high degree of geographic variation in the diet (Ebert 1991a). Two predatory tactics have been suggested which would facilitate the capture of large, actively swimming prey by this relatively small (3m) shark. Some sharks have been observed "gliding" up to the surface to attack South African fur seals lying there (Ebert 1991b), and it has been suggested that minimizing swimming movement might be a form of stealth so the intended prey would not see the predator before escape became unlikely. A preference for turbid water would further reduce the probability of detection, and aid in the capture of large, fast swimming prey like small cetaceans (Ebert 1991b).

Sevengill sharks also hunt in groups. Ebert (1991b) found that sevengill sharks hunt socially when they attack South African fur seals, which grow up to 350 kg. During this behaviour, a group circles around the intended prey until one or several sharks rush in to bite it. The rest of the group quickly follows them. These groups may travel together through a shared home range which would facilitate taking other large prey like dolphins (Ebert 1991b).

Ebert (1991a, b) noted that the frequency of occurrence of marine mammals in the diet of sevengill sharks appeared to be too high to be attributed exclusively to scavenging. The sharks were angler-caught, so were unlikely to have scavenged dolphins drowned in nets. The best evidence for predation on odontocetes comes from the Eastern Cape of South Africa where 12.5% of sevengill sharks contained dolphin remains (Ebert 1991a). In these sharks, dolphins constituted 29.3% of prey mass, which is much higher than most dolphin predators in Natal, where scavenging opportunities from shark nets are higher. Other sevengill populations in southern Africa also consume dolphins, but at a lower frequency (Ebert 1991a).

2.4.1.2 Occasional predators

The dusky (*Carcharhinus obscurus*) and oceanic whitetip (*Carcharhinus longimanus*) sharks are best classified as occasional predators (Table 2.1). These species are known to attack living odontocetes, but probably only rarely. In South Africa, only 0.2% of dusky sharks (most likely a single individual) were implicated as predators on bottlenose dolphins using the fluke-and-vertebrae method (Cockcroft et al. 1989), and another study off the eastern Cape of South Africa found no cetacean remains in 7 dusky sharks over 2m (Smale 1991). This is not surprising since dusky sharks primarily feed on bony fish and other elasmobranchs (Smale 1991, C. Simpfendorfer, Mote Marine Laboratory, pers. comm.) and only the largest dusky sharks are likely to pose a threat to small odontocetes. Compagno (1984b) commented on the relative rarity of mammalian remains (including carrion) in this species compared to tiger and bull sharks, but whale meat (probably scavenged) was found in 3 of 118 sharks off the east coast of southern Africa (Bass et al. 1973).

Oceanic whitetip sharks are common scavengers, and during whaling years, they were responsible for most of the damage to whale carcasses off Durban, South Africa (Compagno 1984b). In the eastern tropical Pacific, oceanic whitetip sharks are the most common shark found in association with dolphin and tuna schools (Au 1991), and an oceanic whitetip shark was implicated in killing a dolphin encircled by a purse seine (Leatherwood et al. 1973). While these sharks probably feed on the same prey as the dolphins (teleosts and cephalopods; Last and Stevens 1994) they may also be a threat to dolphins, especially calves, that stray too far from pelagic dolphin schools.

2.4.1.3 Suspected predators

Suspected predators on cetaceans include the shortfin mako shark (*Isurus oxyrinchus*), Pacific sleeper shark (*Somniosus pacificus*), and Greenland (sleeper) shark (*Somniosus microcephalus)* (Table 2.1). An adult common dolphin (*Delphinus delphis*) stranded alive with fresh mako shark bite wounds, but the dolphin was highly parasitized by liver flukes and had trematodes in its brain (Ridgway and Dailey 1972). Since this dolphin may have been incapacitated at the time of the attack this cannot be treated as a definitive predation event. Stomach content analyses of mako sharks in the northwest Atlantic Ocean, off South Africa, and southeast Australia do not implicate this shark as a regular predator of small odontocetes: dolphin remains were found in 3 of 273, 1 of 88, and 1 of 63 mako sharks respectively (Stillwell and Kohler 1982, Stevens 1984, Cliff et al. 1990). All these odontocete remains were thought to have been scavenged. In South Africa, mako sharks primarily feed on other elasmobranchs and teleosts (Cliff et al. 1990), and prey size was 23%-35% of the attacking shark's body length. The above studies did not contain many large sharks, and this may bias the view of mako shark predation on odontocetes. Last and Stevens (1994) commented that large mako sharks (>3.0m) might take small cetaceans, but only female makos reach this size and very few of these were examined in the above studies.

The Pacific sleeper shark is a dogfish that is large enough to be an odonotcete predator. This shark does not possess dentition that is designed for taking large prey and it is generally considered to be a sluggish bottom dweller (Compagno 1984a, Ebert et al. 1987, Last and Stevens 1994), so it would not seem to pose a threat to cetaceans. However, sleeper sharks may be very cryptic and able to closely approach unwary fast-swimming prey; albacore, tuna, billfish, and harbour seals (*Phoca vitulina*) have all been found in their stomachs (Bright 1959, Compagno 1984a, Ebert et al. 1987). A 3.6 m shark caught on a longline off Valdivia, Chile, contained the genital area of an adult female southern right whale dolphin (*Lissodelphis peronii*) and a complete 87 cm foetus (Crovetto et al. 1992). Due to the lack of decomposition of the foetus and genital region recovered from the stomach, the authors suggested that the shark had attacked a living pregnant female. Southern right whale dolphins feed at considerable depth (Baker 1981), and it is possible that the shark attacked the dolphin while it was feeding (Crovetto et al. 1992).

The Greenland shark is the Atlantic equivalent of the Pacific sleeper shark. This shark is primarily a fish eater, but is capable of taking large, active prey (Compagno 1984a). Seals are common in the diet and small cetaceans are also found (Compagno 1984a). Williamson (1963) reported a 79 cm harbour porpoise calf in the stomach of a 4.15m Greenland shark off Newfoundland, but suggested that the calf was either stillborn or only a few hours old when it was taken. Greenland sharks have been recorded feeding on narwhals (*Monodon monoceros*) and a beluga whale (*Delphinapterus leucas*) caught in nets (Beck and Mansfiled 1969). Sharks in this study were only reported as scavengers, but like the Pacific sleeper shark, they may be capable of attacking free-swimming cetaceans.

2.4.1.4 Ectoparasites

The cookie cutter shark (*Isistius brasiliensis*), and Portuguese dogfish (*Centroscymmus coelolphis*) are cetacean ectoparasites. Cookie-cutter sharks are found in deep water (> 1000 m), during the day and migrate toward the surface with the deep scattering layer at night (Jones 1971, Norris and Dohl 1980a, Last and Stevens 1994).

The shark is neutrally buoyant, with a bioluminescent body, and it may mimic squid (Jones 1971, Last and Stevens 1994). It probably remains motionless and the luminescence could lure cetaceans toward it (Jones 1971, Norris and Dohl 1980a, Last and Stevens 1994). The shark attaches itself to the cetacean with suctorial lips and modified pharynx, then spins and cuts out a crater of flesh with its lower teeth. The plug is then pulled out using the tongue and lips to create a vacuum (Clark and Kristof 1990). Almost every adult spinner dolphin (*Stenella longirostrus*) off Hawaii shows scars caused by this shark with bites found all over the dolphins' bodies except the appendages (Norris and Dohl 1980a). Cookie-cutter sharks are likely to attack any cetaceans that feed on deep scattering layer organisms, especially squid feeders.

It is unclear whether the Portuguese dogfish represents an ectoparasitic threat to odontocetes. Three studies on this shark have found whale remains in their stomachs. Clarke and Merrett (1972) found sperm whale (*Physter macrocephalus*) remains in the stomachs of 3 of 12 sharks they collected from the Northeast Atlantic. The skin and blubber in the sharks may have been scavenged but the authors suggest that living whales may have been attacked when diving. Mauchline and Gordon (1983) also reported that 6 of 24 (35%) sharks in the same area had eaten whale meat, and Ebert et al. (1992) found that unidentified cetaceans constituted 12.6% of the food mass in 71 stomachs examined.

2.4.1.5 Insufficient data

There are several species of sharks that either scavenge cetaceans or rarely take living individuals. With current data, these species cannot be considered odontocete predators, but future studies may change this conclusion.

The sandbar shark (*Carcharhinus plumbeus*) has been studied in South African waters and off the northeast coast of the US. This shark is almost certainly only a scavenger as it doesn't attack large prey (Stillwell and Kohler 1992) and even young dolphins and porpoises probably have a refuge in size. In Atlantic Ocean sharks, cetacean remains were present in only 1 out of a sample of 415 stomachs (Stillwell and Kohler, 1992), and in South Africa, cetacean remains were found in 1 of 178 stomachs (Cliff et al. 1988).

Although Java (pigeye) sharks (*Carcharhinus amboinensis*) may attain sizes of 2.8m, Cliff and Dudley (1991b) only examined sharks under 1.8m, and most were under 1.5m. Cetacean remains were found in only 1 of 72 sharks. It is unclear whether large individuals pose a predation threat to small odontocetes.

Despite their relatively large size, copper sharks (bronze whalers, *Carcharhinus brachyurus*) have a narrow diet and feed on small fish prey (Cliff and Dudley 1992). Only 1.4% of the sharks caught in South African shark nets contained cetacean remains, including common dolphins, but Cliff and Dudley (1992) concluded that they were scavenged from carcasses of dolphins caught in the nets or elsewhere.

Less than 1% of 442 blacktip sharks (*Carcharhinus limbatus*) caught off South Africa contained dolphin remains (Dudley and Cliff 1993), and none of 85 sharks with food in their stomachs off the southeastern US had consumed cetacean flesh (Castro 1996). Most of this shark's prey is small (Dudley and Cliff 1993, Castro 1996), so it is unlikely that even large blacktip sharks attack living cetaceans.

A single Galapagos shark (*Carcharhinus galapagensis*), of 65 examined in Hawaii, contained cetacean remains (Weatherbee et al. 1994), and this species is probably a scavenger of cetaceans.

Blue sharks (*Prionace glauca*) from the northeast Atlantic ate mainly teleosts, with cetacean remains (probably scavenged) found in only 2 of 98 stomachs (Stevens 1973). Only 1 of 31 sharks caught off the coast of New South Wales had small odontocete remains in its stomach (Stevens 1984).

Hammerhead sharks (*Sphyrna* spp.) attain sizes that may be capable of taking small odontocetes, but feed primarily on bottom fishes, including teleosts, small sharks and rays, as well as cephalopods and crustaceans (Last and Stevens 1994, Cliff 1995). Two studies on hammerhead feeding in South Africa found no cetacean remains (Smale 1991, Cliff 1995). Furthermore, no prey larger than 1m in length were reported, suggesting that hammerheads are unlikely to be a major threat to most cetaceans. However, a hammerhead shark may have been responsible for a lethal attack on a bottlenose dolphin in Florida (Wood et al. 1970), and these sharks have been seen scavenging odontocete carcasses (Leatherwood et al. 1973).

2.4.2 Odontocete predation on sharks

In general, sharks appear to be of little importance in the diet of most odontocetes but predation occasionally occurs (e.g. Wood et al. 1970). Bottlenose dolphins are known to consume elasmobranchs, including sharks, in South Africa, the Atlantic Ocean, and the Gulf of Mexico (Gunter 1942, Cockcroft and Ross 1990, Mead and Potter 1990). In South Africa, 1.3% of bottlenose dolphin prey mass was unidentified elasmobranch, but it is unclear what proportion of this prey was from small sharks (Cockcroft and Ross 1990). Most sharks found in bottlenose dolphin stomachs have been unidentified, and small hammerhead sharks are the only group positively identified. Bottlenose whales (*Hyperoodon ampullatus*) have been recorded consuming piked dogfish (*Squalus acanthias*) off the coast of Labrador, but squid and teleost fish are much more common prey (Benjaminsen and Christensen 1979). Pilot whales (*Globicephala* sp.) and harbour porpoises have also been recorded consuming small sharks (Wood et al. 1970).

While small odontocetes may occasionally consume small sharks, killer whales are the only cetacean species currently recorded attacking and killing large sharks, and sharks may be taken relatively often (Fertl et al. 1996). Killer whales have been recorded feeding upon a number of carcharhinid sharks as well as larger sharks, including basking (*Cetorhinus maximus*) and whale (*Rhiniodon typus*) sharks (Fertl et al. 1996). Off the Farallon Islands, California, killer whales were observed attacking and killing a 3-4m white shark (Pyle et al. 1999).

2.4.3 Competition

There were 21 significant dietary overlaps at the family-level and 10 of these were between sharks and dolphins (Tables 2.3, 2.4). Although there are several significant overlaps between humpback dolphins (*Sousa plumbea*) and sharks at the family level, these overlaps are the result of prey category lumping. The frequency of clupeid fishes is the primary factor in all of these interactions, and a detailed look at diets of these species shows that they feed on different prey genera within this family. The clupeid fish taken by humpback dolphins are primarily *Thryssa* while the sharks consume *Sardinops*.

The diets of common dolphins significantly overlapped with the diet of white (1989-1993) and small dusky sharks while those of small dusky and copper sharks overlapped significantly with the common dolphin's diet (Table 2.4). The largest overlap recorded was that of copper sharks on common dolphins. Unlike overlaps between sharks and humpback dolphins, all overlaps between sharks and common dolphins were upheld by analysis at the species level except for that with white sharks which consume *Sardinops sagax*. Overlaps with other shark species were primarily driven by competition for South African pilchards (*Sardinops ocellatus*). There was also overlap between dolphins and small dusky sharks for Sparidae and Teuthoidea.

The blacktip shark has the greatest overlap with bottlenose dolphins, but this is not a significant interaction (Table 2.4). This does not mean that there is no competitive interaction. When only the fish portion of the diet was analysed, the overlap is significant in both directions. Differentiation occurs because bottlenose dolphins round out their diet with squid while the sharks take elasmobranchs.

Table 2.3. Diets of three species of dolphins and eight species of sharks off South Africa. Figures are % mass of each prey family. Data for humpback dolphins are based on % number of prey items. Data are based on animals captured in protective shark nets off the Natal coast, except sixgill sharks which were caught on longlines, rod and reel, or trawls and dusky sharks which were captured by longlines and shore- and boat-based fishermen. Only families that constituted at least 0.5% of at least one species' diet were included. An x denotes that a prey species was found in trace amounts (<0.1% mass) and was not included in the analysis. [a] Niche breadth and prey groups for *Sousa* are underestimates as only prey groups constituting more than 1.3% were included in Ross et al. (1994). [b] Only juvenile white sharks were examined from 1983-1988, and the 1989-1993 sample was mostly juveniles. BOT = bottlenose dolphin, HUM = humpback dolphin, COM = common dolphin, BUL = bull shark, DUS = small dusky shark (<2.0m), DUL = large dusky shark (>2.0m), MAK = mako shark, BLA = blacktip shark, W83 = white sharks (1983-1988), W89 = white sharks (1989-1993), COP = copper shark, JAV = java shark, SIS = small sixgill shark (<1.2m), SIM = medium sixgill shark (1.2m – 2.0m), SIL = large sixgill shark (>2.0m).

	BOT[1]	HUM[2]	COM[3]	BUL[4]	DUS[5]	DUL[5]	MAK[6]	BLA[7]	W83[8b]	W89[9b]	COP[10]	JAV[11]	SIS[12]	SIM[12]	SIL[12]
Number of stomachs examined	127	84	297	247	67	7	59	442	58	33	262	72	39	48	12
Levins' niche breadth	5.8	4.0[a]	3.5	7.8	3.9	2.9	3.3	9.3	4.2	4.1	1.1	6.8	2.6	7.2	3.6
No. Prey Groups	18	7[a]	8	25	13	4	7	24	13	8	6	16	5	11	6
Prey Species															
Teleosts															
Congridae (conger eels)	7.6								0.1						
Clupiedae (herring)	1.1	27.1	48.9	6.0	48.1	16.7		7.6		33.4	92.5		2.4		
Engraulidae - (anchovies)			x	x		4.2		0.2						1.7	
Ariidae (seacatfish)	0.8			1.0	x			1.4	0.1	x		3.4			
Plotosidae (eel catfish)				0.2				1.1							
Exocoetidae (flyingfish)	1.2		3.1												
Serranidae (rockcods)	0.8			0.7				0.9				2.5			
Priacanthidae (bigeyes)	2.7														
Pomatomidae (elf)	2.0		8.7	0.5				2.0			x	0.8			
Haemulidae (grunters)	13.7	19.7	x	1.7	2.2		0.1	10.6		5.5	x	2.3			
Sparidae (seabream)	8.8	2.5	9.4	2.3	5.5			10.6	0.5	0.1		x			
Scorpididae (stonebreams)								0.6							
Sciaenidae (kobs)	1.3	15.9	x	4.0	1.7		5.9	1.3	11.2			9.5			
Mugilidae (mullets)	3.6	x	x	0.6	2.8			0.2			x	x			
Trichiuridae (frostfish)	0.7	4.2	x		0.9			0.2				0.8			
Scombridae (mackerel)	5.2		13.5	0.9	1.2		3.2	7.1	0.9		x	11.1		2.2	

Bothidae (flounders)	0.8														
Carangidae (kingfish)	4.9		3.5	x			2.4	17.7			0.1	0.1			
Oplegnathidae (knifejaws)								0.9				1.5			
Cichlidae (cichlids)				1.7				4.4							
Drepanidae (sicklefishes)				0.9											
Merlucciidae (hake)			x										22.0	17.0	9.9
Myctophidae (lanternfish)		0.3											3.3		
Scorpaenidae (rockfishes)															32.3
Macrouridae (rattails)														1.2	
Crustacea					0.4										
Cephalopods															
Sepia spp (cuttlefish)	32.7		1.1	0.1	2.1			1.0	0.2	0.1		0.3			
Teuthoidea (squid)	3.5	6.5	10.1	x	24.3	35.9		x	x	x			47.7	10.4	2.9
Octopus	1.3			0.6	2.3			1.7				0.2			
Elasmobranchs															
Rhinobatidae	x			17.8	3.9			1.0	1.4			5.7			
Orectolobidae				1.0											
Callorhynchidae														1.8	6.7
Scyliorhinidae				0.1			x	0.1			x	0.6	12.4		
Squalidae							x		2.4		0.9			16.4	
Caracharhinidae				13.3			35.6	10.7	22.9	16.0		19.2		3.2	
Lamnidae				3.9											
Sphyrnidae				3.3			10.5	1.0	2.8	9.1		7.2			
Squantidae				0.2							0.8	x			
Odontaspididae				0.3					1.7						
Skates and bottom rays				1.7	3.9	42.5		2.5	x					17.9	
Manta and eagle rays				1.7			20.3		x		0.2	17.8			
Marine Mammals															
Cetacea				5.1			x	1.7	31.2	4.2	1.9	x		4.6	9.4
Pinnipeds									9.6	19.2				9.7	38.8

---

[1] Cockcroft and Ross (1990), [2] Ross, Heinsohn, and Cockcroft (1994) and Barros and Cockcroft (1999), [3] Young and Cockcroft (1994), [5] Smale (1991), [4] Cliff and Dudley (1991a), [6] Cliff et al. (1990), [7] Dudley and Cliff (1993), [8] Cliff et al. (1989), [9] Cliff et al. (1996), [10] Cliff and Dudley (1992), [11] Cliff and Dudley (1991b), [12] Ebert (1994)

Table 2.4. MacArthur-Levins' dietary overlaps based on proportion of prey groups in the diets of three species of dolphins and eight species of sharks found off the coast of South Africa. Dietary overlap is asymmetrical and is expressed as the overlap of the species along the top row on the diet of the species in the left hand column. Overlaps are based on %mass for all comparisons except those with humpback dolphins which are all based on % number (Table 2.3). Values of > 0.7 are considered significant and are in bold. BOT = bottlenose dolphin, HUM = humpback dolphin, COM = common dolphin, BUL = bull shark, DUS = small dusky shark (<2.0m), DUL = large dusky shark (>2.0m), MAK = mako shark, BLA = blacktip shark, W83 = white sharks (1983-1988), W89 = white sharks (1989-1993), COP = copper shark, JAV = java shark, SIS = small sixgill shark (<1.2m), SIM = medium sixgill shark (1.2m – 2.0m), SIL = large sixgill shark(>2.0m).

	BOT	HUM	COM	BUL	DUS	DUL	MAK	BLA	W83	W89	COP	JAV	SIS	SIM	SIL
BOT	-	0.53	0.17	0.06	0.14	0.01	0.03	0.30	0.02	0.08	0.07	0.09	0.12	0.04	0.01
HUM	0.57	-	**0.72**	0.64	**0.77**	0.24	0.07	0.47	0.06	**1.35**	**1.39**	0.37	0.32	0.17	0.01
COM	0.10	0.64	-	0.17	**0.90**	0.29	0.02	0.24	0.01	0.67	**1.68**	0.07	0.05	0.01	0.00
BUL	0.08	**0.77**	0.38	-	0.46	0.20	**0.82**	0.37	**0.72**	0.61	0.66	0.63	0.02	0.13	0.05
DUS	0.09	**0.74**	**0.99**	0.23	-	0.48	0.01	0.22	0.01	**0.74**	**1.80**	0.03	0.05	0.03	0.00
DUL	0.01	0.28	0.40	0.18	0.39	-	0.00	0.13	0.00	0.30	**0.76**	0.00	0.02	0.42	0.00
MAK	0.02	0.05	0.02	0.35	0.01	0.00	-	0.23	0.46	0.32	0.00	0.62	0.00	0.05	0.00
BLA	0.48	**0.73**	0.64	0.44	0.53	0.25	0.64	-	0.35	0.60	**0.79**	0.45	0.02	0.12	0.00
W83	0.02	0.20	0.01	0.38	0.01	0.00	0.57	0.16	-	0.32	0.00	0.34	0.00	0.07	0.18
W89	0.06	0.38	**0.78**	0.32	**0.78**	0.26	0.40	0.27	0.32	-	**1.50**	0.05	0.00	0.05	0.00
COP	0.01	0.37	0.52	0.09	0.51	0.18	0.00	0.09	0.00	0.40	-	0.00	0.03	0.00	0.00
JAV	0.10	0.50	0.13	0.55	0.05	0.00	**1.28**	0.33	0.56	0.05	0.00	-	0.01	0.08	0.00
SIS	0.06	0.14	0.04	0.01	0.04	0.61	0.00	0.01	0.00	0.00	0.07	0.00	-	0.30	0.11
SIM	0.04	0.15	0.03	0.12	0.06	0.64	0.13	0.09	0.11	0.05	0.01	0.09	**0.83**	-	0.18
SIL	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.14	0.09	-

2.5 DISCUSSION

2.5.1 Predation pressure on odontocete populations

Very little is known about the influence of predation on odontocete populations. The frequency of shark bite scars on odontocetes has been used as an indication of predation rate, but there are several problems with this approach. As many authors have pointed out, shark bite scars and wounds represent failed predation attempts. There may be a correlation between successful predation and failed attempts, but there are several confounding factors. The ratio between attacks and kills may vary from one shark species to another, or with shark length. For example, large sharks are probably more successful predators than smaller sharks. Second, the size (i.e. age or species) of attacked odontocete will bias this ratio as smaller individuals, or species, will be taken more often and scarred less frequently than large species or individuals. Therefore, a lack of scars on odontocetes in a population does not necessarily indicate a low predation rate. For example, offshore dolphins appear to have lower scarring frequencies than nearshore dolphins (Wood et al. 1970, Leatherwood et al. 1973). This could indicate a lower predation rate, if large groups of pelagic dolphins are more likely to detect and avoid predators or shark density is lower offshore. However, a predation attempt in such an open environment may be more likely to lead to death. Groups of sharks appear to follow pelagic dolphin schools (Leatherwood 1977, Au 1991) and once a single shark has made an attack, others are likely to converge as well. A dolphin, which may have evaded a single shark with just a wound, is likely to be killed if several sharks are involved in an attack. Despite the potential drawbacks of using shark-scarred individuals to assess shark predation, it is still useful for comparisons among relatively similar habitats and species of similar size.

At least 36.6% of the bottlenose dolphins surveyed (both photographically and with field observations) in Moreton Bay, Queensland exhibit shark bite scars. A number of scars that may have been healed bites were not scored, so an even greater scarring frequency is probable (Corkeron et al. 1987). A higher scarring frequency is also probable because observations were made of free-swimming animals, and photographs of free-swimming animals document only a fraction of dolphins with scars (Urian et al. 1998).

The frequency of shark bite scars is lower in Sarasota, Florida, where 31% of 151 bottlenose dolphins examined during captures showed signs of healed shark bites or fresh wounds (Urian et al. 1998). Overall, 23% had single scars and 8% had multiple scars.

Shark scarring frequency suggests that there is very little predation pressure on bottlenose dolphins in the Adriatic Sea. No unambiguous shark-inflicted scars were found on over 200 dolphins observed, although several individuals bore wounds that may have been shark-inflicted (Bearzi et al. 1997). Conversely, predation pressure on bottlenose dolphins in Shark Bay, Western Australia is probably quite high. Of 128 non-calves surveyed 95 (74.2%) had at least one shark bite scar and 40 (42.1% of attacked individuals) had multiple scars. Based on the accumulation of fresh bites, 11-13% of the Shark Bay population may be attacked each year (Chapter 4, Heithaus in press).

Shark bite scars or recent wounds that were not attributable to scavenging were found on 10 of 36 (28%) humpback dolphins caught in shark nets off Natal, South Africa (Cockcroft 1991). Five of these animals had received multiple bites, and some had obviously been attacked on more than one occasion. This frequency of scarring is greater than that of bottlenose dolphins in the same area (see below) and indicates that the two species are subjected to different predation pressures (Cockcroft 1991).

Scars and wounds that fit all criteria for nonscavenging shark bites were found on 10.3% (15 of 145) of bottlenose dolphins caught in Natal shark nets. However, the incidence of shark bites may be a high as 19.3% since 13 additional dolphins had scars that may have been inflicted by sharks (Cockcroft et al. 1989). Seven of the 15 animals had multiple shark bite scars. Based on stomach contents of predatory sharks, Cockcroft et al. (1989) concluded that shark predation may be a significant mortality factor for bottlenose dolphins off the coast of Natal, with up to 2.2% of the population taken annually. If there is a positive relationship between scarring frequency and predation rate, even higher shark mortality would be expected in Shark Bay, Moreton Bay and Sarasota.

Disappearance rates of odontocete calves may also provide insight into predation pressure on populations. In Sarasota, between 1980 and 1984, two dependent bottlenose dolphin calves disappeared while 16 survived beyond three years (11% disappearance; Wells et al. 1987). A much higher disappearance rate is found in Shark Bay where approximately 31% (of 83 newborns) of calves disappear in the first year and 49% have disappeared by age 4 (Richards 1993). Both calf mortality and scarring frequency seem to indicate higher shark predation risk in Shark Bay than in Sarasota.

2.5.2 Odontocete behavioural responses to shark predation risk

Animals employ many tactics to reduce predation risk and there is a large body of literature on how animals minimize predation risk and make tradeoffs between this need and others such as energy intake and reproduction (see Lima and Dill 1990 for a review of behavioural decisions made under the risk of predation). Predation attempts do not have to occur frequently or always be successful to have a major influence on the behaviour of prey species (e.g. shifts in habitat use or activity budgets; Lima 1998). Unsuccessful predation attempts may have a significant detrimental effect on individual prey. Pinnipeds that survive white shark attacks incur a significant reduction in reproductive success. Most injured female elephant seals (*Mirounga angustirostris*) at Año Nuevo, California, do not succeed in pupping (Le Boeuf et al. 1982). Furthermore, none of the shark-bitten females was observed to copulate before returning to sea. Therefore, a shark bite resulted in a loss of two years of reproduction. A similar pattern was found at the Farallon Islands, where only about 10% of shark-injured mother elephant seals were able to wean their pups, and these individuals did not copulate (Ainley et al. 1981). A similar cost would probably be incurred by odontocetes that survive shark attacks. Shark-attacked individuals would have to devote energy to recuperation and wound healing, and wounded females would not be able to invest as much in their calves. Males might also incur reproductive losses if they are wounded, especially in odontocete species with high male-male competition for females. Therefore, odontocetes should employ strategies to reduce shark encounters even if sharks are successful predators only occasionally.

Dolphin behavioural responses provide evidence that they view sharks as a risk. Responses of dolphins to an encounter with sharks will be dependent on factors such as the species and size of the shark they encounter. Dolphins show species-specific reactions to sharks, and appear to distinguish between predatory species and those that pose no threat. For example, a captive bottlenose dolphin that was trained to repel large sharks harassed sharks that were not predation threats. When bull sharks were introduced, the dolphin became agitated, avoided the sharks, and refused to respond to commands (Irvine et al. 1973).

Close encounters between dolphins and predatory sharks often result in an evasive response by the dolphins. Bottlenose and humpback dolphins have been observed passively avoiding hammerhead (*Sphyrna zygaena*), white, and either a bull or dusky shark (Tayler and Saayman 1972, Saayman and Tayler 1979, Corkeron et al. 1987). An extreme evasive response was observed when resting bottlenose dolphins were startled by the approach of a white shark (Connor and Heithaus 1996).

Not all encoutnters between predatory sharks and dolphins result in avoidance, and predator mobbing of sharks has been observed several times. In one case, a school of common dolphins sought refuge next to a fisheries research vessel while sharks were attacking the group. The young dolphins were herded next to the boat while adults appeared to chase sharks away whenever one approached (AIBS 1967). In another observation, humpback dolphins were seen chasing a large white shark (4.0-5.0m) (Saayman and Tayler 1979).

Group formation is one way animals can reduce predation risk, but groups may form for other reasons (e.g. food acquisition, reproduction; see Bertram 1978 for detailed discussion of the benefits of group living, with examples). There are numerous examples of group formation successfully reducing predation in the terrestrial environment, and predation has been suggested as an important determinant of group size in some odontocetes (e.g. Norris and Dohl 1980b, Wells et al. 1980, Wells et al. 1987).

Another way to reduce predation risk is to avoid encounters with predators, and many species select habitats where predation risk is relatively low. Predation risk is determined by more than the number of predators in a location. The ability of predators and prey to detect each other and the probability of capture after detection can be influenced by habitat attributes such as substrate colour, water clarity, water depth, and light level (intrinsic habitat risk, e.g. Gotceitas and Colgan 1989, Hugie and Dill 1994, Miner and Stein 1996). In some predator-prey interactions, intrinsic habitat risk can be a primary determinant of habitat selection of prey species (Hugie and Dill 1994). As with group size, habitat use is influenced by factors other than predation risk (e.g. food distribution and abundance, social considerations) and many animals make tradeoffs between safety and energy intake (e.g. desert baboons, *Papio cynocephalus ursinus*, Cowlishaw 1997 and African hunting dogs, *Lycaon pictus*, Mills and Gorman 1997).

Fission-fusion societies allow individuals or subgroups to select their habitat and group size based on ecological conditions and their current activity. This social organisation allows individuals to balance conflicting demands like energy intake, safety, and reproduction. The size and habitat use of primate subgroups are responsive to food availability, predation risk and current activity (e.g. macaques, van Schaik and van Noordwijk 1985; desert baboons, Cowlishaw 1997). Some dolphin fission-fusion societies are probably influenced mainly by reproductive and foraging considerations (e.g. in the Adriatic Sea), but both food resources and predation risk probably drive other odontocete fission-fusion dynamics. Relationships between group size and habitat use of bottlenose dolphins in Sarasota appear to be a tactic for coping with predation pressure (mainly from bull sharks) balanced with prey availability (Wells et al. 1980, Wells et al. 1987, Wells 1991). However, no studies have tested the hypothesis that dolphin group size and habitat use is influenced by food availability and predation risk.

The activity state of odontocetes should influence their responsiveness to food distribution and risk of predation. Foraging is the activity most likely to be seen in dangerous habitats as the energetic benefits may counterbalance predation risk (e.g. desert baboons, Cowlishaw 1997). Conversely, dolphins would be expected to select safe habitats during resting since the energetic cost of moving to safe habitats is low (Williams et al. 1992) and the benefit of spending time in low-risk habitats can be high. Comparing the habitat use and group sizes of dolphins engaged in resting relative to foraging may provide an index of habitat-specific predation risk. To test this, information about shark habitat use should be collected concurrently with data on activity specific habitat use of odontocetes.

Social considerations may complicate studies of odontocete habitat selection and group size as individuals of different age/sex classes may respond differently to predation risk, resource distribution, and reproductive concerns. For example, male dolphins may be more willing to risk shark predation than females. In Sarasota, male bottlenose dolphins had a significantly higher frequency of scarring than did females, and males seemed to take risks more consistently throughout their lives as they accumulated scars as they matured while females did not (Urian et al. 1998).

To understand group sizes and habitat use of dolphins it is important to understand the relative risk to an individual odontocete from predators, particularly sharks, in different habitats. It is difficult to compare vastly different habitats because many factors can influence risk. One habitat attribute that will affect predation risk is water depth, but there is probably not a simple relationship between depth and intrinsic risk making comparisons between nearshore and pelagic waters difficult.

In nearshore waters the shark species present, shark density, water depth, water clarity, and substrate colour will influence predation risk. White, tiger, bull, and sevengill sharks are probably the major predators on nearshore cetaceans, but dusky sharks may also represent a risk (Table 2.2). The risk nearshore cetaceans face from sharks will vary with location. For example, the risk of shark predation is probably higher in tropical waters than in higher latitudes because of the diversity and abundance of large, predatory sharks in warm waters (Table 2.2). Turbidity and substrate colour also contribute to habitat risk. Tiger sharks and white sharks are well camouflaged against dark backgrounds, and some sharks (e.g. sevengill sharks; Ebert 1991b) prefer turbid waters. This may be one reason that odontocetes in some areas avoid turbid waters and dark substrates (e.g. Hawaiian spinner dolphins; Norris and Dohl 1980a, Würsig et al. 1994; bottlenose dolphins, Ross 1977).

In the open ocean, a primary tactic for reducing predation risk is to form groups, and pelagic dolphins consistently form much larger groups than their coastal counterparts (e.g. Saayman et al. 1972). One interesting possibility in the pelagic environment is for predation risk to be vertically stratified because of changes in light level and vertical stratification of shark species. In the upper water layers dolphins would be at risk from oceanic whitetip and mako sharks, and occasionally tiger, dusky, and white sharks. (Table 2.2). Deep diving cetaceans would face a different suite of sharks while at their foraging depth (Table 2.2), including ectoparasitic sharks. Large deep water sharks (e.g. sleeper and sixgill sharks) would pose a much greater threat. These sharks, which grow to well over 4m, are capable of killing adult odontocetes and the primary depths at which Ebert (1986) found sixgill sharks (100-200m) coincides with the feeding depth of many pelagic dolphin species (e.g. Fitch and Brownell 1968, Crovetto et al. 1992).

2.5.3 Competition

Most data on feeding habits of odontocetes and sharks have been collected in different manners and may have different biases associated with them. The protective shark nets of South Africa provide concrete data on the feeding habits of dolphins and sharks in the same area. Because most species were caught in the same manner (incidental entanglement), biases among species should be minimized and comparisons meaningful. Analyses of dietary overlap showed significant competition between several shark species and common dolphins. This level of overlap suggests that interspecific competition among these species could be an important factor determining group size, habitat use, and ranging patterns. In addition to interactions between common dolphins and sharks, moderate levels of overlap were found between sharks and both humpback and bottlenose dolphins. Little is known about how species with a moderate overlap might influence each other, but it seems unlikely that there is no interaction at all, and interactions may become significant at times when certain prey species are scarce.

These above results are only instructive for South Africa. Due to the dietary flexibility of both dolphins and sharks, competitive interactions are likely to be highly variable geographically. Further investigations into competition between sharks and dolphins in other areas of the world will provide insights into the generality of these results.

Resource competition among sharks and odontocetes is likely to be non-aggressive. On four occasions, Leatherwood (1977) witnessed groups of bottlenose dolphins and sharks feeding from the same school of fish with no aggressive interactions, and sharks and dolphins feed together behind trawlers in Australia (Corkeron et al. 1987). The lack of aggression is not surprising given that the time spent defending resources would significantly decrease the feeding times of defending individuals, and individuals that did not participate in resource defence would gain an advantage over those that did. Since individuals would not benefit from resource defence, it should not occur. Aggression or avoidance was probably not observed in the above cases because sharks were not a predatory threat, given that abundant and more easily captured teleost prey were available to them.

Seasonal variation in food resources may influence shark-odontocete interactions. There may be a large overlap in shark and odontocete prey species, but, if resources are abundant, competition will be unimportant and coexistence may be expected. However, when resources are limiting, increased competition may lead to niche divergence or nontolerant interactions. During these times, some shark species may switch to preying upon dolphins. If this were the case, dolphins should not show a reaction to the presence of sharks when other shark food resources are abundant, but change their habitat use or show strong evasive responses to the presence of predatory sharks during food-limited seasons.

One interesting possibility raised by the competition analyses is that shark and dolphin species that engage in predator-prey interactions may also compete for food (intraguild predation). Intraguild predation among dolphins and sharks also occurs between killer whales and white sharks (e.g. Pyle et al. 1999). In this situation, both species consume pinniped prey, and killer whales prey upon white sharks. Intraguild predation is a common feature of many communities and may have a major influence on habitat use of both species even when dietary overlap is not high (e.g. Holt and Polis 1997, Chapter 3). It is possible that intraguild predation may be responsible for the displacement of white sharks, by killer whales, in the Farallon Islands.

2.5.4 Size dependent interactions

Both competitive and predator-prey interactions between sharks and cetaceans will be influenced by the body size of both sharks and odontocetes. White (Tricas and McCosker 1984, Klimley 1985, Cliff et al. 1989), tiger (Simpfendorfer 1992, Lowe et al. 1996), sixgill (Ebert 1994), and bull sharks (Cliff and Dudley 1991a) all show marked changes in diet with increasing size. Small sharks of each species tend to feed on teleost fishes, but as shark size increases, so does the number of prey groups and size of prey.

Once sharks are able to capture larger prey, it can be energetically more efficient to capture a small number of large, high energy prey items rather than many small prey items. Odontocets represent a high-energy food source, and once sharks are large enough to capture them, they should include dolphins and porpoises in their diet at least opportunistically. Large tiger, bull, white, and sixgill sharks increase their predation rate on odontocetes as predator size increases (Cliff et al. 1989, Cliff and Dudley 1991a, Ebert 1994, Lowe et al. 1996). However, relatively small sharks are still capable of taking young calves and sick individuals (e.g. Mann and Barnett 1999).

Ontogenetic shifts in diet lead to size-structured interactions among species (see Werner and Gilliam 1984 for a review), and shark competition with odontocetes will be size-structured. South African feeding data for dusky sharks show that dietary overlap with all three dolphin species changed with shark size (Table 2.4). Small dusky sharks always showed a higher overlap with dolphins than did large dusky sharks. Unfortunately, most data that have been collected have been lumped for sharks of all size classes, but if a pattern like that of dusky sharks occurred with other shark species then there should be greater dietary overlap between odontocetes and small to medium shark size classes.

2.6 FUTURE DIRECTIONS

This review of shark-dolphin interactions reveals that there is a lack of quantitative data on the potential influences of shark predation and competition on odontocete populations, habitat use, and behaviour. However, several methods have been suggested that will enhance future investigations. If these methods are applied in future studies, a much greater understanding of shark - odontocete interactions will emerge. Although difficult, a significant step toward understanding the nature of these interactions will involve attempts to quantify predation risk and prey availability. Researchers should make use of data available from sport fishing and net catches of sharks to understand the possibility for size-structured competition, predation, and intraguild predation. Data on habitat use of predatory sharks must be collected and integrated with habitat characteristics to provide an index of habitat-specific predation risk. By incorporating these data into long-term research projects, it will be possible to investigate more detailed questions about how individual dolphins make decisions about habitat use and group size as well as the fitness consequences of these decisions. Finally, understanding the influences of shark predation on current cetacean populations may enhance our understanding of the pressures leading to the evolution of odontocete group living and sociality.

2.7 ACKNOWLEDGEMENTS

I would like to thank L. Dill, I. Hamilton, R. Connor, R. Heithaus, L. Barre, H. Finn, V. Janik, the late K. Norris, B. Würsig, V. Cockcroft, M. Abrahams, J. Clutton-Brock, and an anonymous reviewer for helpful comments on previous versions of this manuscript. Thanks also go to I. Hamilton who helped me obtain necessary papers. Support was provided by NSERC Canada grant A6869.

2.8 LITERATURE CITED

Ainley, D. G., C. S. Strong, H. R. Huber, T. J. Lewis, and S. H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. Fishery Bulletin US 78: 941-945.

AIBS. 1967. Conference on the shark-porpoise relationship. American Institute of Biological Sciences, Symposium Proceedings, Washington D.C.

Arnold, P. W. 1972. Predation on harbour porpoise, Phocena phocena, by a white shark, *Carcharodon carcharias*. Journal Fishery Research Board Canada 29: 1213-1214.

Au, D. W. 1991. Polyspecific nature of tuna schools: shark, dolphin, and seabird associates. Fishery Bulletin US 89 89: 343-354.

Baker, A. N. 1981. The southern right whale dolphin *Lissodelphis peronii* (Lacepede) in Australasian waters. Natural History Museum of New Zealand Records 2: 17-34.

Barros, N. B. and V. G. Cockcroft. 1999. Prey resource partitioning between Indo-Pacific hump-backed dolphins (*Sousa chinensis*) and bottlenose dolphins (*Tursiops truncatus*) off South Africa – competitive exclusion or mutual tolerance? Abstracts, Thirteenth Biennial Meeting of the Society for Marine Mammalogy, Maui, HI. 28 November – 3 December.

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. 1973. Sharks of the east coast of southern Africa. 1. The genus Carcharhinus (Carcharhinidae). Investigative Reports of the Oceanographic Research Institute, Durban, South Africa 33: 1-168.

Baughman, J. L. and S. Springer. 1950. Biological and economic notes on the sharks of the Gulf of Mexico, with esecial reference to those of Texas, and with a key for their identification. American Midland Naturalist 44: 96-152.

Beck, B. and A. W. Mansfield. 1969. Observations on the Greenland shark, *Somniosus microcephalus*, in northern Baffin Island. Journal of the Fisheries Research Board, Canada 26: 143-145.

Benjaminsen, T. and I. Christensen. 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Forster). In *Behaviour of Marine Animals, Volume 3, Cetaceans*: 143-164. Winn, H. E. and B. A. Olla. (Eds.). Plenum Press, New York.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 64-96 *in* J. R. Krebs and N. B. Davies, editors. Behavioural Ecology: An Evolutionary Approach, Fourth Edition. Blackwell, Oxford.

Bell, J. C. and J. T. Nichols. 1921. Notes on the food of Carolina sharks. Copeia 92: 17-20.

Bearzi, G., G. Notarbartolo-di-Sciara, E. Politi. 1997. Social ecology of bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). Marine Mammal Science 13: 650-668.

Bright, D. B. 1959. The occurrence and food of the sleeper shark, *Somniosus pacificus*, in a central Alaskan Bay. Copeia 1959: 76-77.

Brownell, R. L. Jr. 1975. Progress report on the biology of the Franciscana dolphin, *Pontoporia blainvillei*, in Uruguayan waters. Journal of the Fisheries Research Board, Canada 32: 1073-1078.

Bruce, B. D. 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.

Caldwell, M. C., D. K. Caldwell, and J. B. Siebenaler. 1965. Observations on captive and wild Atlantic bottlenose dolphins, *Tursiops truncatus*, in the northeastern Gulf of Mexico. Los Angeles County Museum of Natural History, Contributions to Science 91: 3-10.

Carey, F. G., J. W. Kanwisher, O. Brazier, G. Gabrielson, J. G. Casey, and H. L. Pratt Jr. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982: 254-260.

Castro, J. I. 1996. Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. Bulletin of Marine Science 59: 508-522.

Cawthorn, M. W. 1988. Recent observations of Hector's dolphin *Cephalorhynchus hectori*, in New Zealand. Report of the International Whaling Commision., Special Issue 9: 303-314.

Clark, E. and E. Kristof. 1990. Deep sea elasmobranchs observed from submersibles off Bermuda, Grand Cayman, and Freeport Bahamas. Pages 269-284 *in* H. L. Pratt, S. H. Gruber, and T. Taniuchi, editors. Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries. NOAA Technical Report to NMFS 90: 269-284.

Clarke, M. R. and N. Merrett. 1972. The significance of squid, whale and other remains from the stomachs of bottom-dwelling deep-sea fish. Journal of the Marine Biological Assocociation, U.K. 52: 599-603.

Cliff, G. 1995. Sharks caught in the protective gill nets off Kwazulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rüppell). South African Journal of Marine Science 15: 105-114.

Cliff, G. and S. F. J. Dudley. 1991b. Sharks caught in the protective gill nets off Natal, South Africa. 5. The Java shark *Carcharhinus amboinensis* (Muller and Henle). South African Journal of Marine Science 11: 443-453.

Cliff, G. and S. F. J. Dudley. 1992. Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Gunther). South African Journal of Marine Science 12: 663-674.

Cliff, G., S. F. J. Dudley, and B. Davis. 1988. Sharks caught in the protective gill nets off Natal, South Africa. 1. The sandbar shark *Carcharhinus plumbeus* (Nardo). South African Journal of Marine Science 7: 255-265.

Cliff, G., S. F. J. Dudley, and B. Davis. 1989. Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). South African Journal of Marine Science 8: 131-144.

Cliff, G., S. F. J. Dudley, and B. Davis. 1990. Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). South African Journal of Marine Science 9: 115-126.

Cliff, G. and S. F. J. Dudley. 1991a. Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* (Valenciennes). South African Journal of Marine Science 10: 253-270.

Cliff, G., S. F. J. Dudley, and M. R. Jury. 1996. Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. Pages 351-362 *in* Great White Sharks: The Biology of Carcharodon carcharias. A. P. Klimley and D. G. Ainley, editors. Academic Press, New York.

Cockcroft, V. G. 1991. Incidence of shark bites on Indian Ocean hump-backed dolphins (*Sousa plumbea*) off Natal, South Africa. Report of the International Whaling Commission, Special Issue 12: 277-282.

Cockcroft, V. G., G. Cliff, and G. J. B. Ross. 1989. Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. South African Journal of Zoology 24: 305-310.

Cockcroft, V. G. and G. J. B. Ross. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. Pages 295-308 *in* The Bottlenose Dolphin. S. Leatherwood and R. R. Reeves, editors. Academic Press, New York.

Compagno, L. J. V. 1984a. FAO species catalogue. Vol 4. Sharks of the world. Part 1 - Hexanchiformes to Lamniformes: FAO Fisheries Synopsis. 125: 1-249.

Compagno, L. J. V. 1984b. FAO species catalogue. Vol 4. Sharks of the world. Part 2 - Carchariniformes: FAO Fisheries Synopsis. 125: 250-655.

Connor, R. C. and M. R. Heithaus. 1996. Great white shark approach elicits flight response in bottlenose dolphins. Marine Mammal Science 12: 602-606.

Corkeron, P. J., R. J. Morris, and M. M. Bryden. 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. Aquatic Mammals 13: 109-113.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour 53: 667-686.

Crovetto, A., J. Lamilla, and G. Pequeno. 1992. *Lissodelphis peronii* Lacepede 1804 (Delphinidae, Cetacea) within the stomach contents of a sleeping shark, *Somniosus* cf. *Pacificus*, Bigelow and Schroeder 1944, in Chilean waters. Marine Mammal Science 8: 312-314.

Dudley S. F. J. and G. Cliff. 1993. Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). South African Journal of Marine Science 13: 237-254.

Ebert, D. A. 1986. Biological aspects of the sixgill shark, *Hexanchus griseus*. Copeia 1986: 131-135.

Ebert, D. A. 1990. *The taxonomy, biogeography,* and *biology of cow* and *frilled sharks (Chondrichthyes: Hexanchiformes).* Ph.D. thesis, Rhodes University: 308 pp.

Ebert, D. A. 1991a. Diet of the sevengill shark *Notorynchus cepedianus* in the temperate coastal waters of southern Africa. South African Journal of Marine Science 11: 565-572.

Ebert, D. A. 1991b. Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. South African Journal of Marine Science 11: 455-465.

Ebert, D. A. 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. South African Journal Marine Science 14: 213-218.

Ebert, D. A., L. J. V. Compagno, and P. D. Cowley. 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of Southern Africa. South African Journal of Marine Science 12: 601-609.

Ebert, D. A., L. J. V. Compagno, and L. J. Natanson. 1987. Biological notes on the Pacific sleeper shark, *Somniosus pacificus* (Condrichthyes: Squalidae). California Fish and Game 73: 117-123.

Ellis, J. R., M. G. Pawson, and S. E. Shackley. 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. Journal of the Marine Biological Association, U.K. 76: 89-106.

Fergusson, I. K. 1996. Distribution and autoecology of the white shark in the eastern north Atlantic Ocean and the Mediterranean Sea. Pages 321-345 *in* Great White Sharks: The Biology of Carcharodon carcharias. A. P. Klimley and D. G. Ainley, editors. Academic Press, New York.

Fertl, D., A. Acevedo-Guiterrez, and F. L. Darby. 1996. A report of killer whales (*Orcinus orca*) feeding on a carcharhinid shark in Costa Rica. Marine Mammal Science 12: 606-611.

Fitch, J. E. and R. L. Brownell, Jr. 1968. Fish otoliths and their importance in interperating feeding habits. Journal of the Fisheries Research Board, Canada 25: 2561-2574.

Gotceitas, V. and P. Colgan. 1989. Predator foraging success and habitat complexity: quantiative test of the threshold hypothesis. Oecologia 80: 158-160.

Gunter, G. 1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montagu), on the Texas coast, with particular reference to food habits. Journal of Mammalogy 23: 267-276.

Heithaus, M. R. in press. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. Marine Mammal Science 17.

Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149: 745-764.

Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45 (Suppl. A): 151-169.

Irvine, A. B., R. S. Wells, and P. W. Gilbert. 1973. Conditioning an Atlantic bottlenosed dolphin to repel various species of sharks. Journal of Mammalogy 54: 503-505.

Jones, E. C. 1971. *Isistius brasiliensis*, a squaliod shark, the probable cause of crater wounds on fishes and cetaceans. Fishery Bulletin US 69: 791-798.

Klimley, A. P. 1985. The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. Memoirs of the Southern California Academy of Sciences 9: 15-40.

Klimley, A. P. 1994. The predatory behavior of the white shark. American Scientist 82: 122-133.

Last, P. R. and J. D. Stevens. 1994. *Sharks* and *Rays of Australia*. CSIRO: Australia.

Leatherwood, S. 1977. Some preliminary impressions of the numbers and social behavior of free-swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northeastern Gulf of Mexico. Pages 143-167 *in* Breeding dolphins: present status, suggestions for the future. S. H. Ridgway, editor. Report to the US Marine Mammal Commission MM6AC009.

Leatherwood, S., W. F. Perrin, R. Garvie, and J. LaGrange. 1973. Observations of sharks attacking porpoises (*Stenella* spp. and *Delphinus* cf. *D. delphis*) Naval Undersea Center Technical Note 908: 1-7.

Le Boef, B. J., M. Reidman, and R. S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. Fishery Bulletin US 80: 891-895.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48: 25-34.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Long, D. J. and R. E. Jones. 1996. White shark predation and scavenging on cetaceans in the eastern north Pacific Ocean. Pages 293-307 *in* Great White Sharks: The Biology of Carcharodon carcharias. A. P. Klimley and D. G. Ainley, editors. Academic Press, New York.

Lowe, C. G., B. M. Wetherbee, G. L. Crow, and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes 47: 203-211.

Macpherson, E. 1981. Resource partitioning in a Mediterranean demersal fish community. Marine Ecology Progress Series 4: 183-193.

Mann, J. and H. Barnett. 1999. Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: defense and reactions by the mother. Marine Mammal Science 15: 568-575.

Mauchline, J. and J. D. M. Gordon. 1983. Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology 75: 269-278.

Mead, G. M. and C. W. Potter 1990. Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pages 165-195 *in* The Bottlenose Dolphin. S. Leatherwood and R. R. Reeves, editors. Academic Press, New York

McBride, A. F. and D. O. Hebb. 1948. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. Journal of Comparative Physiology and Psychology 41: 111-123

Mills, M. G. and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11: 1397-1406.

Miner, J. G. and R. A. Stein. 1996. Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. Transactions of the American Fisheries Society 125: 97-103.

Norris, K. S. 1994. Predators, parasites, and multispecies aggregations. Pages 287-300 *in* The Hawaiian Spinner Dolphin. K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, editors. University of California Press, Berkeley.

Norris, K. S. and T. P. Dohl. 1980a. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin US 77: 821-849.

Norris, K. S. and T. P. Dohl. 1980b. The structure and function of cetacean schools. Pages 211-261 *in* Cetacean Behavior: Mechanisms and Functions. L. M. Herman, editor. Wiley: New York.

Paterson, R. A., C. J. Quayle, and S. M. Van Dyck. 1993. A humpback whale calf and two subadult dense-beaked whales recently stranded in southern Queensland. Memoirs of the Queensland Museum 33: 291-297.

Pyle, P., M. J. Schramm, C. Keiper, and S. D. Anderson. 1999. Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. Marine Mammal Science 15: 563-568.

Randall, J. E. 1973. Size of the great white shark. Science 181: 169-170.

Randall, J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Australian Journal of Marine and Freshwater Research 43: 21-31.

Richards, A. F. 1993. Reproductive parameters of bottlenose dolphins in Shark Bay, Western Australia. Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, TX, Abstracts: 91.

Ridgeway, S. H. and M. D. Dailey. 1972. Cerebral and cerebellar involvement of trematode parasites in dolphins and their possible role in stranding. Journal of Wildlife Disease 8: 33-43.

Ross, J. G. B. 1977. The taxonomy of bottlenose dolphins, *Tursiops* species in South African waters, with notes on their biology. Annals of the Cape Provincial Museum (Natural History) 11: 135-194.

Ross, G. J. B., G. E. Heinsohn, and V. G. Cockcroft. 1994. Humpback dolphins *Sousa chinensis* (Osbeck 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii* (Kukenthal 1892). Pages 23-42 *in* Handbook of Marine Mammals: Volume 5: The First Book of Dolphins. S. H. Ridgway and R. Harrison, editors. Academic Press, New York.

Saayman, G. S., D. Bower, and C. K. Tayler. 1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. Koedoe 15: 1-24.

Saayman, G. S. and C. K. Tayler. 1979. The socioecology of humpback dolphins (*Sousa* sp). Pages 165-226 *in* Behaviour of Marine Animals, Volume 3, Cetaceans. H. E. Winn and B. A. Olla, editors. Plenum Press, New York.

Schaik, C. P. van and J. A. R. M. van Hoff. 1983. On the ultimate causes of primate social systems. Behaviour 85: 91-117.

Schaik, C. P. van and M. A. van Noordwijk. 1985. Evolutionary effects of the absence of felids on the social organization of the macaques on the island of Simeulue (*Macaca fasicularis fusca*, Miller 1903). Folia Primatologia 44:138-147.

Scott, M. D. and K. L. Cattanach. 1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. Marine Mammal Science 14: 401-428.

Simpfendorfer, C. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. Australian Journal of Marine and Freshwater Research 43: 33-43.

Simpfendorfer, C. A., A. B. Goodreid and R. B. McAuley. 2001. Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes: in press.

Smale, M. J. 1991. Occurrence and feeding of three shark species, *Charcharhinus brachyurus*, *C. obscurus*, and *Sphyrna zygaena*, on the eastern Cape coast of South Africa. South African Journal MarineScience 11: 31-42.

Stevens, J. D. 1973. Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. Journal of the Marine Biological Association, U. K. 53: 357-361.

Stevens, J. D. 1984. Biological observations on sharks caught by sport fishermen off New South Wales. Australian Journal of Marine and Freshwater Research 35: 573-590.

Stevens, J. D. and K. J. McLoughlin. 1991. Distribution, size, and sex composition, reproductive biology and diet of sharks from northern Australia. Australian Journal of Marine and Freshwater Research 42: 151-199.

Stillwell, C. E. and N. E. Kohler. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Canadian Jounal of Fisheries and Aquatic Science 39: 407-414.

Stillwell, C. E. and N. E. Kohler. 1992. Food habits of the sandbar shark *Carcharhinus plumbeus* off the US northeast coast, with estimates of daily ration. Fishery Bulletin US 91: 138-150.

Tayler, C. K. and G. S. Saayman. 1972. The social organization and behavior of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Annals of the Cape Provincial Museum (Natural History) 9: 11-49.

Terborgh, J. W. 1983. Five New World Primate: A Study in Comparative Ecology. Princeton, Princeton Univ. Press.

Tricas, T. C. and J. E. McCosker. 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proceedings of the California Academy of Science 43: 221-238.

Urian, K. W., R. S. Wells, M. D. Scott, A. B. Irvine, A. J. Read, and A. A. Hohn. 1998. When the shark bites: an analysis of shark bite scars on wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, Florida. The World Marine Mammal Conference, Monaco 20-24 January, 1998, Abstracts: 139.

Wells, R. S. 1991. Bringing up baby. Natural History August: 56-62.

Wells, R. S., A. B. Irvine, and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pages 263-317 *in* Cetacean Behavior: Mechanisms and Functions. L. M. Herman, editor. Wiley, New York.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 *in* Current Mammalogy, Volume 1. H. H. Genoways, editor. Plenum Press, New York.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-425.

Wetherbee, B. M., C. G. Lowe, and G. L. Crow. 1994. A review of shark control in Hawaii with recommendations for future research. Pacific Science 48: 95-115.

Williams, T. M., A. W. Friedl, M. L. Fong, R. M. Yamada, P. Sedivy, and J. E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355: 821-823.

Williamson, G. R. 1963. Common porpoise from the stomach of a Greenland shark. Journal of the Fisheries Research Board, Canada 20: 1085-1086.

Wood, F. G. Jr., D. K. Caldwell, and M. C. Caldwell. 1970. Behavioral interactions between porpoises and sharks. Investigations on. Ceatacea 2: 264-277.

Würsig, B., R. S. Wells, K. S. Norris, and M. Würsig. 1994. A spinner dolphin's day. Pages 65-102 *in* The Hawaiian Spinner Dolphin. K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, editors. University of California Press, Berkeley.

Young, D. D. and V. G. Cockcroft. 1994. Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialization? Journal of Zoology, London 234: 41-53

CHAPTER 3

Habitat Selection by Predators and Prey in Communities with Asymmetrical Intraguild Predation*

---

*A version of this chapter appears as Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92: in press. Reprinted with permission from Oikos.

3.1 ABSTRACT

Competition and predation have broad ecological consequences as they may influence individual behavior and community structure. In some cases, they are linked and predator and prey are also competitors (intraguild predation). I present a game theoretical model of habitat use by predators and prey under conditions of asymmetrical intraguild predation. This model predicts that when the diet of intraguild predators is restricted to intraguild prey and the resource for which predators and prey compete (the basal resource), co-occurrence is only stable when dietary overlap is low and productivity of the basal resource is not high. The addition of alternative resources for predators results in co-occurrence under all conditions. Variation in alternative resource productivity produces a continuum of intraguild prey distributions from matching relative habitat safety, to one that reflects both food and predation risk. When there is a substantial alternative resource for predators, the distribution of predators matches that of alternative resource availability while the distribution of prey is influenced by both habitat riskiness and food availability. The density and distribution of the predator's alternative resource thus influence habitat selection by the intraguild prey. This stresses the importance of indirect interactions in structuring habitat use in communities and the need to view habitat selection in a community context.

3.2 INTRODUCTION

Competition and predation can influence individual behavior, population dynamics, and community structure, and both have received substantial attention from community and behavioral ecologists. The relative importance of competition versus predation in regulating populations and community composition has historically been a subject of much debate, but the effects of these two processes usually are not separable (Kotler and Holt 1989). Predation may influence the co-occurrence of competitor species or even species that do not compete directly, but share a common predator (Holt 1984). In many cases, both competition and predation are important in regulating populations (e.g. McNamara and Houston 1987, Sinclair and Arcese 1995) and allowing co-occurrence of competing species (e.g. Paine 1966, Vance 1974, Leibold 1996). However, these factors are usually investigated in isolation or in simple systems which may not be representative of many natural conditions.

In systems characterized by intraguild predation (IGP), in which predator and prey are also competitors, competition and predation are inseparable. IGP is a common feature of many ecosystems (Polis et al. 1989), and has begun to receive considerable attention among community ecologists as investigators appreciate its potential influence on animal populations, the structure and composition of communities, and the distribution and abundance of animals (see Polis et al. 1989 for a review, Huang and Sih 1991, Holt and Polis 1997). Asymmetrical IGP occurs when a predator and prey compete for a shared (basal) resource (Figure 3.1). Examples of such IGP are found within and among many taxonomic groups including arthropods, fish, rodents, mammalian carnivores, and between sharks and dolphins (Polis et al. 1989, Doncaster 1992, Moran and Hurd 1997, Palomares and Caro 1999, Heithaus in press). In situations of asymmetrical IGP, predators and prey may vary in their competitive ability for shared resources with either predators (e.g. cheetahs, *Acinonyx jubatus*, and lions, *Panthera leo*, Caro 1994, Laurenson 1995) or prey being more efficient competitors (e.g. protists, Morin 1999).

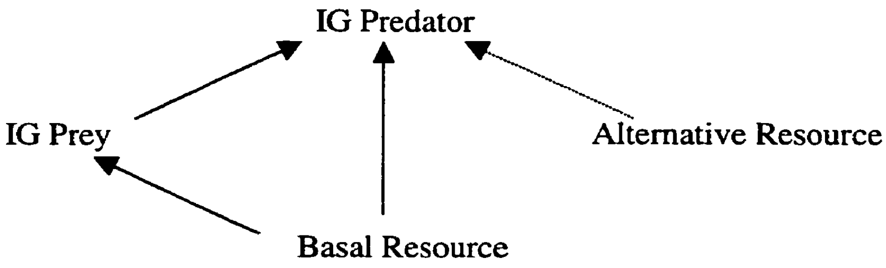


Figure 3.1. Energy flow in a system exhibiting asymmetrical intraguild predation.

Community models of IGP that focus on the numerical responses of populations to various levels of competition and IGP, competitive abilities of species and overall habitat productivity (e.g. Holt and Polis 1997) predict that coexistence of intraguild predators and prey is favored when prey are superior competitors for shared resources, and in habitats with intermediate levels of productivity. These models fail to explain why persistent, strong IGP is observed in some high productivity habitats (Holt and Polis 1997). One drawback of community models is that they ignore individual behavioral decisions regarding habitat use, which may be very important in determining both population dynamics and community structure (Brown et al. 1999). Behavioral decisions may also determine the spatial nature of IGP when individuals can easily move among habitats (e.g. hedgehogs, *Erinaceus europeaus*, and badgers, *Meles meles*, Doncaster 1992, spiders and mantids, Moran and Hurd 1994). Despite the prevalence of IGP in natural communities, and the potential importance of individual behavioral decisions, IGP has received almost no attention from behavioral ecologists (but see Schwinning and Rosenzweig 1990).

The ideal free distribution (IFD, Fretwell and Lucas 1970) has been used extensively to study how competition and predation influence the distribution of animals among habitats that vary in quality, and thus is an appropriate framework for behavioral studies of IGP. The basic IFD describes the equilibrium distribution of individuals among habitats (in the absence of predation and interference competition) at which no individual can improve its fitness by unilaterally switching habitats. Variations of the original IFD model have been used to investigate the influences of competition and predation on individuals' habitat selection both theoretically (e.g. Sutherland and Parker 1985, Parker and Sutherland 1986, McNamara and Houston 1990, Hugie and Dill 1994, Tregenza 1995) and empirically (Grand 1997, Grand and Dill 1997, see Lima and Dill 1990, Tregenza 1995 for reviews). When competitors are unequal, there may be a variety of evolutionarily stable distributions. In the most basic unequal competitors IFD model, there are many potential distributions of different competitor types between habitats, but the ratio of the sums of competitive weights (the relative intake rates of competitor types) among habitats is equal to that of the input rates of resources into the habitats ("input matching"). However, if there is interference or competitive weights are habitat-dependent, the best competitors may all be found in the highest quality habitat, or where competitive differences are the greatest; poor competitors are found only in habitats of low quality or where competitive differences are lower (Sutherland and Parker 1985, Parker and Sutherland 1986, Suthlerland and Parker 1992).

The IFD has also been used to study tradeoffs between food and predation risk. Most models and empirical work assume fixed predation risk in the available habitats or look at differences in the use of predation-free and predation-rich habitats (e.g. Abrahams and Dill 1989, Kotler and Blaustein 1995, Moody et al. 1996, Brown 1998). In these situations, many animals conform to theoretical predictions and their distributions are sensitive to both predation risk and food availability in a habitat. For example, gerbils (*Gerbillus allenbyi* and *G. pyramidum*) faced with barn owl (*Tyto alba*) predation in open (risky) and bush (safe) experimental habitats showed higher giving up densities for patches in open areas and required 4- to 8-times richer patches in the open for open patches to be as valuable as bush habitat (Kotler and Blaustein 1995). Guppies (*Poecilia reticulata*) showed a similar tradeoff, with individuals requiring a much higher energy intake rate to use a patch that contained a predator (Abrahams and Dill 1989). The distribution of unequal competitors under predation risk can be largely influenced by dilution as dilution partially offsets the costs of increased competition (e.g. Grand and Dill 1999).

In many cases, including IGP, predators will be able to modify their distribution in relation to that of their prey so that actual predation risk is not fixed. Hugie and Dill (1994) and Sih (1998) have addressed this problem with IFD models that incorporate a game between predators and prey, as well as among prey by allowing both predators and prey to select habitats differing in intrinsic risk (e.g. cover availability) and food availability. They found that the expected distributions of prey were much different than those found with spatially fixed predator distributions or risk: prey distributed themselves proportional to habitat safety and independent of resource productivity ("safety matching") while predators matched the productivity of their prey's food.

Most communities are complex and each species may be engaged in many predator-prey interactions. The complexity of communities and the presence of alternative prey can influence community composition and stability (e.g. Polis 1991, Polis and Strong 1996). However, the influence of alternative resources on habitat use decisions of predators and prey has not been explored. The presence of alternative resources for top predators is a common feature of many asymmetrical IGP situations (e.g. Polis et al. 1989, Palomares and Caro 1999). For example, in the interaction between lions (intraguild predator) and wild dogs (intraguild prey), lions consume large ungulates that are not in the diet of wild dogs (*Lycaon pictus*, Mills and Gorman 1997). The presence of these alternative resources may decrease rates of IGP (e.g. aphids, Lucas et al. 1998), but the influence of alternative resources on the spatial distributions of species engaged in intraguild predation is unknown.

I use a game theoretic approach to model animal habitat use under conditions of asymmetrical IGP (Figure 3.1). The purpose of this model is to predict how animals should distribute themselves across two habitats based on the level of dietary overlap, relative competitive ability, habitat productivity, inherent habitat riskiness, and the presence and productivity of an alternative resource for IG predators. This model is concerned only with habitat use by IG predators and IG prey and does not consider population responses to intraguild predation.

3.3 THE MODEL

The following terms are used in accordance with Holt and Polis (1997): IG predator, IG prey, and basal resource, where the IG predator is the top predator, the IG prey the middle predator, and the basal resource the food of the middle predator (Figure 3.1). In many communities, IG predators will consume prey other than the IG prey and basal resource. The productivity of that prey is referred to as the alternative resource. The constants and values used in this model are given in Table 3.1.

Both IG predators and IG prey may choose one of two habitats in which to live. N and N' are the total population sizes of the IG prey and IG predator, respectively, and are assumed to be constant. For the purposes of this model, populations of both IG predators and IG prey have no size or age structure. Although many IGP situations are closely linked to size changes and ontogenetic shifts within species (e.g. Polis et al. 1989), I focus on IGP between species to generate simple, general predictions regarding the influence of IGP on habitat use.

The proportions of N' and N in each habitat i are denoted by p'_i and p_i respectively. Assuming that the size of both habitats is equal, the number of IG predators (d') and IG prey (d) in each habitat, i, are

$$d'_i = p'_i N' \tag{1}$$

and

$$d_i = p_i N \tag{2}$$

The death rate of IG prey in habitat i ($\gamma(i)$), based on random encounters between IG predators and IG prey, is described by :

$$\gamma(i) = d_i d'_i R_i \tag{3}$$

Habitat riskiness (R_i, Hugie and Dill 1994) is the product of encounter rate and the probability of prey capture and death in an encounter situation. Habitat features that affect a predator's ability to detect and capture prey, such as habitat complexity (e.g. cover), light level, water turbidity and water depth, will influence habitat riskiness (Gotceitas and Colgan 1989, Hugie and Dill 1994, Miner and Stein 1996).

The probability of death per unit time ($\beta(i)$) for IG prey is the overall death rate divided by the number of prey in the habitat:

$$\beta(i) = \frac{\gamma(i)}{d_i} = R_i d'_i \tag{4}$$

and the expected life span of the prey in habitat i ($l(i)$) is:

$$l(i) = \frac{1}{\beta(i)} \tag{5}$$

based on the assumption that predation by IG predators is the only mortality factor for the IG prey. The rate of prey death divided by the density of predators in habitat i yields the IG predators' probability of prey capture per unit time ($\theta(i)$):

$$\theta(i) = \frac{\gamma(i)}{d'_i} = R_i d_i \tag{6}$$

Table 3.1. Constants used in the model, and their values. Values were chosen to aid in comparisons with other studies (e.g. Hugie and Dill 1994) and to represent a variety of natural situations. Mean values for basal resource productivity and alternative resource productivity were chosen to show the basic response to changes in productivity. Competitive ability values represent IG predators that are half, equally, twice, and four times as efficient as IG prey at consuming basal resources.

Constant	Symbol	Units	Value
Total number of IG prey	N		10,000
Total number of IG predators	N'		1,000
Habitat riskiness	R_i	size/time	0.005 (mean)
Basal resource productivity	P_i	Energy/ time	1,000 (mean)
Use of basal resource by IG predator	U	Proportion	0.05; .5; 1.0
Competitive ability of IG predator	Q		0.5; 1.0; 2.0; 4.0
Alternative resource productivity	A_i	Energy/(size*time)	100; 1,000; 10,000 (mean)
Energy value of IG prey	V	Energy/prey	5
Expected lifespan of IG predators	L'	Time	500
Assimilation efficiency of IG prey	F	Proportion	1
Assimilation efficiency of IG predators	F'	Proportion	1
Metabolic rate of IG prey	M	energy/time	0.0001
Metabolic rate of IG predator	M'	energy/time	0.0001
Offspring cost of IG prey	O	energy	1
Offspring cost of IG predator	O'	energy	1
IG predator collision coefficient	C_i	volume/time	0.05
Dilution coefficient	D	time	0 or 5
IG Predator Interference coefficient	I	time	0 or 5

The prey's net energy intake rate ($e(i)$) is the productivity of the habitat divided by the sum of competitive weights in the habitat. P_i is the rate of basal resource renewal in each habitat, which is constant over time. I assume that all available productivity is consumed by IG predators and IG prey. The basal resource includes all resources consumed by the IG prey. In many cases, the IG predator will not consume all of these resources. Therefore, the term U is added to describe the proportion of the basal resource that is consumed by the IG predator and over which IG predators and IG prey compete. U may vary between 0 (no IGP) and 1 (full use of the basal resource by IG predators). As competition between IG predators and IG prey may be asymmetrical, due to differences in body size, foraging efficiency on a particular resource, or metabolic rate, I include a term, Q, for the competitive weight of IG predators relative to IG prey (for that proportion of P_i over which there is competition). This constant is the relative intake of IG predators compared with that of IG prey. The values of Q used were selected to show how changes in this parameter will affect habitat use decisions. These values ($Q = 0.5, 1, 2, 4$) correspond to IG predators that are half, equally, two, and four times as efficient as IG prey at harvesting basal resources.

The assimilation efficiency of energy from the basal resource by IG prey (F) is assumed to be the same in each habitat. The metabolic rate (M) refers to maintenance costs.

The energy intake rate of IG prey is

$$e(i) = \left[\frac{UP_i}{d_i + Qd_i'} + \frac{(1-U)P_i}{d_i} \right] F - M \tag{7}$$

For the purposes of this model, all individuals are assumed to be capable of reproduction and all net energy is instantaneously allocated to reproduction. The prey's uncorrected fitness in habitat i ($w(i)$) is :

$$w(i) = \frac{l(i)e(i)}{O} \tag{8}$$

where O is the cost of producing a single offspring (e.g. Grand and Dill 1999). This fitness function is similar to Brown's (1992) pF where F is the fitness of a surviving animal and p is the probability of survival.

Because this model assumes no change in population size, for the purposes of simulations (see below) the prey's fitness must be corrected such that the mean fitness for the entire population is 1. To attain this, the uncorrected fitness in a habitat is divided by the mean uncorrected fitness in the population ($\bar{w}$).

$$W(i) = \frac{w(i)}{\bar{w}} \tag{9}$$

where

$$\bar{w} = \sum_i p_i w(i) \tag{10}$$

The overall amount of energy available to IG predators from IG prey must be in units comparable to the productivity of the basal resource. This is accomplished by using an energy value correction (V), which is the relative energy content of an individual prey item compared to a unit of basal resource. IG predator assimilation efficiency (F') is assumed to be the same as IG prey foraging efficiency and is constant across prey types and habitats. M' is the metabolic rate of predators. IG predator net energy intake in habitat i ($e'(i)$) can thus be modeled with the following equation:

$$e'(i) = \left[\theta(i)VF' + \frac{UP_i}{d'_i + (\frac{1}{Q})d_i} F' \right] - M' \tag{11}$$

In many IGP situations, IG predators consume prey items that are neither the IG prey nor the basal resource (alternative resource, Figure 3.1); the rate of alternative resource renewal (A_i) in each habitat is assumed to be constant and this resource is assumed to be fully consumed by IG predators. IG predators do not influence the renewal rate of alternative resources. When an alternative food resource is added for the IG predator its net intake rate becomes:

$$e'(i) = \left[\theta(i)VF' + \frac{UP_i}{d'_i + (\frac{1}{Q})d_i} F' + \frac{A_i}{d'_i} F' \right] - M' \tag{12}$$

The lifespan of IG predators (*L'*) is not dependent on the habitat that they choose, and is constant. Growth (*G'*) and offspring (*O'*) costs are incorporated in a manner identical to that of IG prey. Thus, regardless of the presence of the alternative resource, a predator's uncorrected fitness in habitat *i* (*w'(i)*) is:

$$w'(i) = \frac{L'e'(i)}{O'} \tag{13}$$

The predator's corrected fitness is:

$$W'(i) = \frac{w'(i)}{\overline{w'}} \tag{14}$$

where

$$\overline{w'} = \sum_i p_i' w'(i) \tag{15}$$

The model outlined above assumes that there is no dilution of predation risk with increasing prey density. The number of prey consumed increases linearly with prey density. Dilution (*D*) is incorporated into the predator capture rate and rate of prey death in a manner identical to that of Hugie and Dill (1994), by converting the functional response of the predators to a Holling Type II response (Holling 1959). In this situation, as prey density increases, the per capita death rate of prey decreases.

Another assumption of the basic model is that there is no contest competition among IG predators when consuming IG prey. As predator density increases, the time spent in interactions with other predators may increase, reducing the rate of prey capture. This can be modeled with the addition of terms to describe the frequency of encounter between IG predators (collision coefficient, C_i) and the amount of time spent interacting with another predator given an encounter (*I*) (Hugie and Dill 1994). The addition of both dilution and contest interference yields the following equations for per capita prey death and predator capture rate:

$$\beta(i) = R_i d'_i \left[\frac{1}{1 + R_i D d_i + C_i I d'_i} \right] \tag{16}$$

and

$$\theta(i) = R_i d_i \left[\frac{1}{1 + R_i D d_i + C_i I d'_i} \right] \tag{17}$$

It is possible to analytically solve for ESS conditions under conditions of no intraguild predation ($U = 0$). However, due to the complexity of the model when $U > 0$, graphical solutions are presented. To determine the equilibrium distributions of IG predators and IG prey, I determined the best response curves (Grand and Dill 1999) for both IG predators and IG prey. The best response curve is that distribution of one species that results in equal fitness for individuals of that species in each habitat for a given distribution of the other species. The point of intersection of best response curves gives the equilibrium distribution of both species for a given set of model parameter values. Best response curves can also be used to determine the trajectories of approach to equilibrium distributions from a given starting distribution of IG predators and IG prey (e.g. Grand and Dill 1999). The best response curve for IG prey was generated by determining what value of p_i satisfies the equation $W(1) = W(2)$ (from eqn. 9) for $p_i' = 0$ to 1 (e.g. Grand and Dill 1999). Similarly, the best response curve for IG predators was generated by determining what distribution of IG predators satisfies the equation $W'(1) = W'(2)$ (from eqn. 14) given a variety of distributions of IG prey. All equilibria obtained using best response curves were verified using computer simulation. In all situations, except where noted, the equilibria produced are stable.

Computer simulations were used to verify equilibria. A random proportion of IG predators and IG prey were input into each habitat and were allowed to reproduce relative to the corrected fitness of each habitat (equations 9 and 14) such that the conditions $W(1) = W(2)$ and $W'(1) = W'(2)$ were satisfied. This process was iterated until there was no change in IG predator or IG prey payoffs within both habitats. Incorporating an error rate ($\varepsilon = \pm 0.0001$) added to p and p' that slightly perturbed distributions tested the stability of the equilibria produced by my model. Distributions that continually returned to the same values were considered to be an ESS.

This model can be conceptualized as either an evolutionary game or a behavioral game. In the evolutionary game individuals would not move between habitats, but the densities of predators and prey would change relative to overall fitness in a habitat until an ESS was reached. Alternatively, in the behavioral game, individuals could move between patches to maximize residual reproductive success. Therefore, the temporal scale for systems reaching equilibrium densities may be highly variable and dependent on the movement capabilities of the species involved in the interactions.

3.4 RESULTS

In the absence of competition (pure predator-prey game), prey are distributed inversely proportional to intrinsic habitat risk (safety matching, Hugie and Dill 1994) while the predator distribution matches that of the basal resource discounted by habitat-specific foraging (i.e. riskiness). When dietary overlap is low and the IG predator is a relatively inefficient competitor for the basal resource ($U = 0.5$, $Q = 0.5$), the equilibrium distributions of IG predators and IG prey are relatively unchanged (Figure 3.2). An increase in the relative competitive ability of the IG predator has little influence on the best response curve of the IG prey, but dramatically changes the shape of the IG predator curve (Figure 3.2). However, there is still relatively little change in the stable equilibrium distribution of both IG predators and IG prey (Figure 3.2).

The distribution of basal resource productivity and the relative riskinesses of habitats influence the equilibrium distributions of both IG predators and IG prey. At low levels of IG predator use of basal resources and poor competitive ability ($U = 0.5$, $Q = 0.5$), a change in basal resource distribution does not influence the best response curve of IG predators, but shifts the IG prey curve down as the proportion of basal resource in Habitat 1 (the risky habitat) decreases. If Habitat 1 becomes less risky relative to Habitat 2, the IG predator curve shifts up as does the IG prey curve. The resulting stable distributions result in the IG prey matching the relative safety of each habitat, and IG predators distributed relative to the distribution of basal resource productivity, discounted for habitat-specific foraging efficiency on IG prey (Figure 3.3). IG prey are not excluded from either habitat under any conditions when U and Q are low.

A change in the relative competitive ability of IG predators can dramatically affect the equilibrium distributions when IG predators make full use of basal resources ($U = 1.0$;

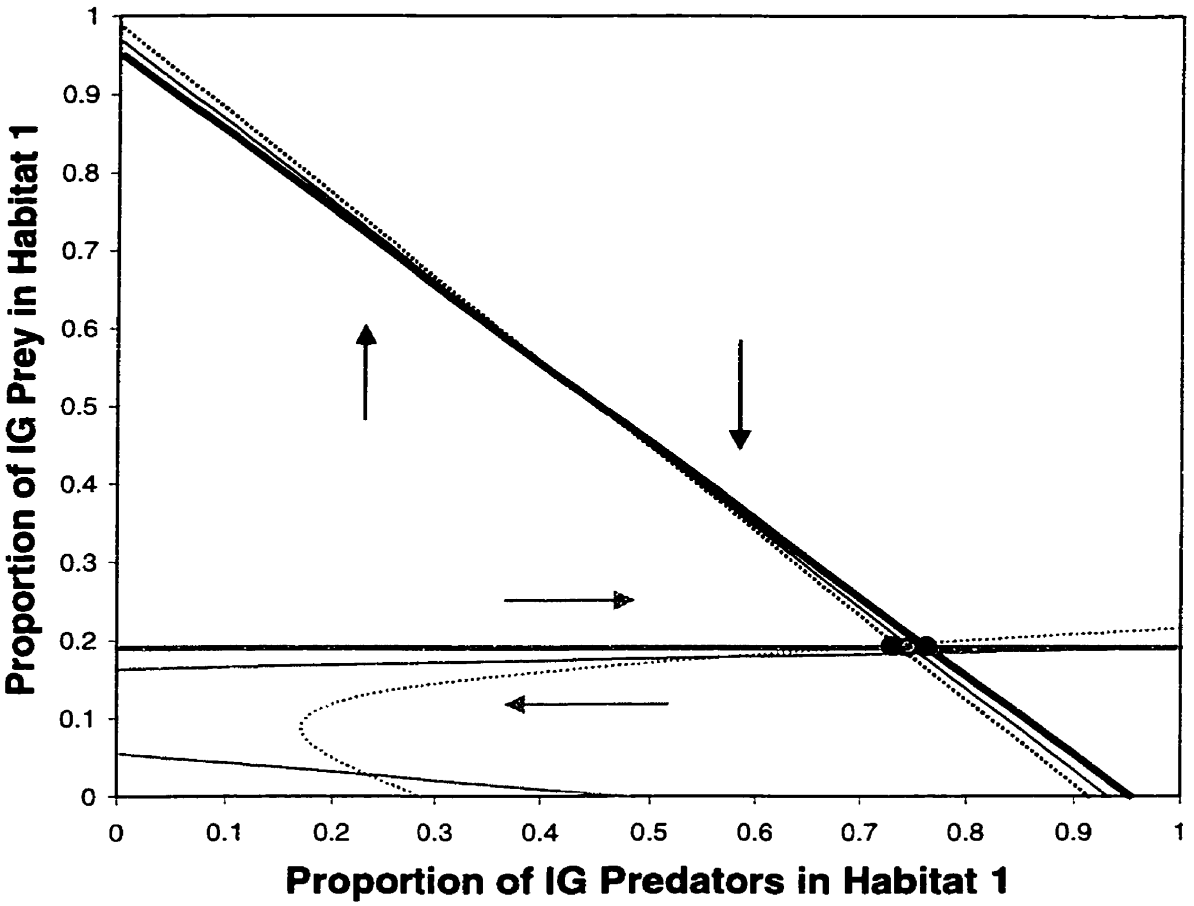


Figure 3.2. Best response curves for IG predators (gray lines) and IG prey (black lines) when dietary overlap is low ($U = 0.5$) and there is no alternative resource. Dots represent equilibria. When IG predators are relatively poor competitors for basal resources (thick lines, $Q = 0.5$), the distribution of IG prey matches that of relative safety and IG predators are distributed proportional to basal resource availability discounted for habitat-specific foraging success. When the relative competitive ability of IG predators increases (thin lines, Q = 1.0, dotted lines, $Q = 2.0$), the IG prey curve shifts slightly up while the IG predator curve shifts right and becomes nonlinear. There is only a small change in equilibrium distributions. Arrows indicate general trajectories for IG predators (gray) and IG prey (black) $P_1 = 700$, $P_2 = 300$, $R_1 = 0.008$, $R_2 = 0.002$.

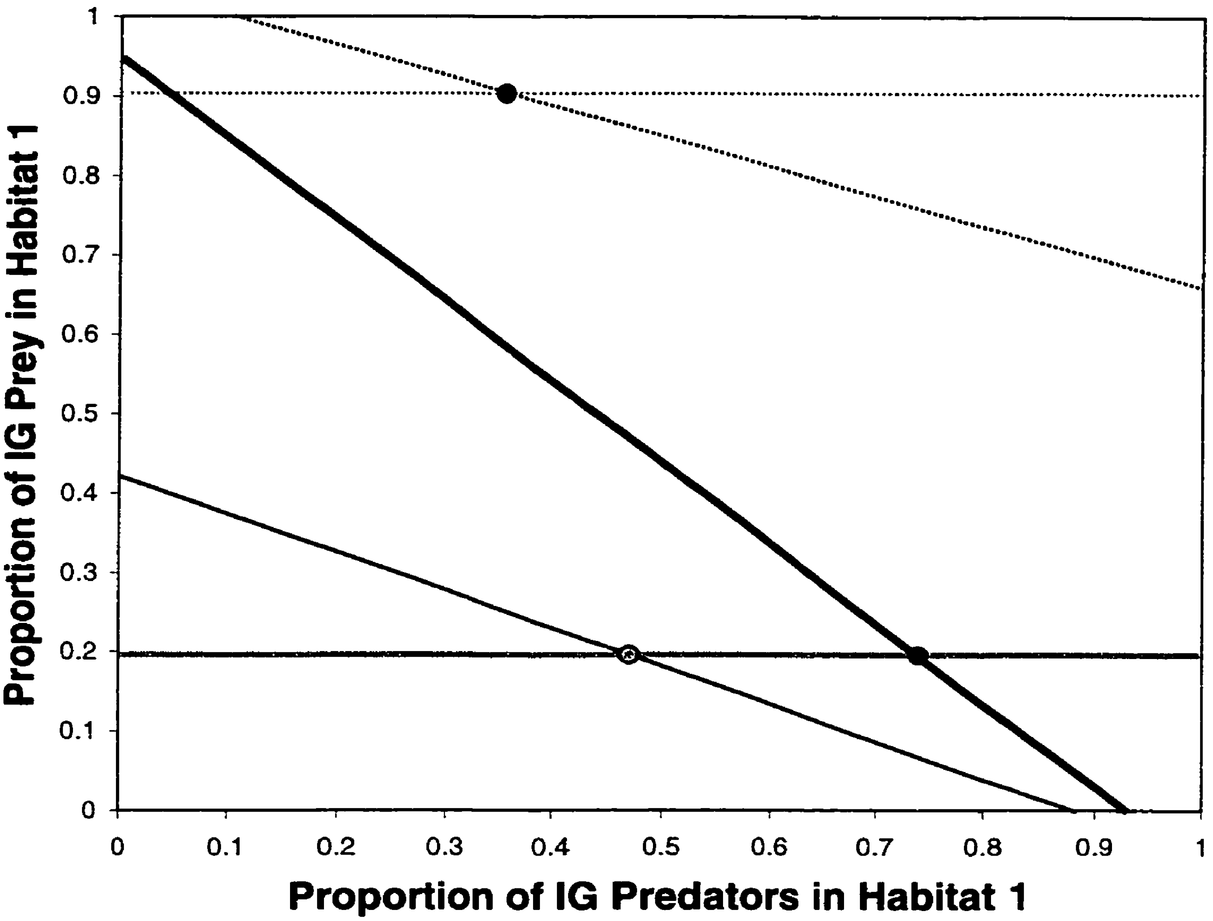


Figure 3.3. Best response curves for IG predators (gray lines) and IG prey (black lines) when competition is low (U =0.5, Q = 0.5) and there are changes in the relative riskiness of habitats or the distribution of basal resource productivity. Thick lines: $P_1 = 700$, $P_2 = 300$, $R_1 = 0.008$, $R_2 = 0.002$. Thin lines: $P_1 = 200$, $P_2 = 800$, $R_1 = 0.008$, $R_2 = 0.002$. Dotted lines: $P_1 = 700$, $P_2 = 300$, $R_1 = 0.001$, $R_2 = 0.009$. An increase in the riskiness of Habitat 1, shifts both best response curves up while a decrease in basal resource productivity shifts the IG prey response curve down but does not affect the IG predator curve.

Figure 3.4). An increase in the relative competitive ability of the IG predator (increase in Q), causes the best response curve of IG predators to shift right while the slope of the IG prey best response curve becomes more negative and the x intercept shifts left. When IG predators are significantly better competitors, IG prey are excluded from the most productive (and high-risk) habitat (Habitat 1) while IG predators match the distribution of basal resource. In general, when IG prey are not excluded from one habitat, their distribution is close to matching the relative safety of the habitats.

Unlike the low competition situation, when IG predators make full use of the basal resource and are relatively efficient predators, the best responses of both IG predators and IG prey fluctuate with changes in relative riskiness and the distribution of basal resources. As the proportion of basal resources in the risky habitat decreases, the best response curve of the IG predator shifts right while the best response curve of the IG prey shifts left. If one habitat has higher basal resource productivity and is a much safer habitat, all IG prey will congregate in this habitat (Figure 3.5).

The overall productivity of the basal resource influences whether IG predators and IG prey co-occur (Figure 3.6). As mean basal resource productivity increases, the best response of IG prey does not change. When IG predators use a smaller portion of basal resource ($U = 0.5$) and are inefficient competitors for basal resource, the IG predator best response curve changes shape and is displaced to the right as the overall productivity of basal resource increases. This can result in situations where there are three potential equilibria. Two equilibria are partially unstable in that perturbations in some directions move the system towards a different equilibrium (Figure 3.6). These equilibria yield co-occurrence and the equilibrium reached will depend on starting conditions. The third, stable, equilibrium results in segregation with IG predators in the productive habitat and IG prey in the less productive habitat.

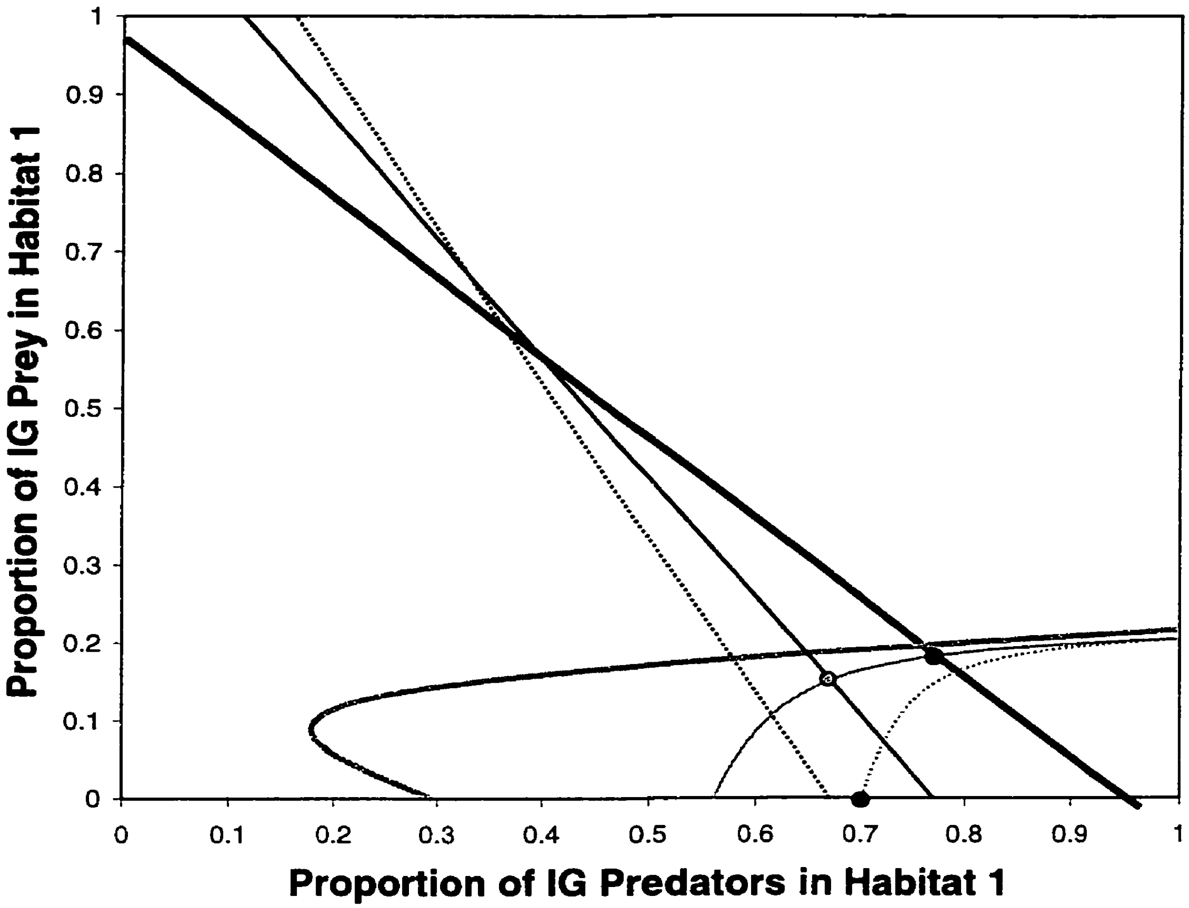


Figure 3.4. Best response curves for IG predators (gray lines) and IG prey (black lines) when dietary overlap (thick line *U* = 0.5, thin and dotted lines *U* = 1.0) and IG predator competitive ability is high (thick and thin lines *Q* = 2, dotted line *Q* = 4.0). Dots represent equilibria. Increases in *U* and *Q* shift the IG predator response curve right and causes the slope of the IG prey curve to decrease. When both *U* and *Q* are high, IG prey are excluded from the productive habitat (Habitat 1). $P_1 = 700$, $P_2 = 300$, $R_1 = 0.008$, $R_2 = 0.002$.

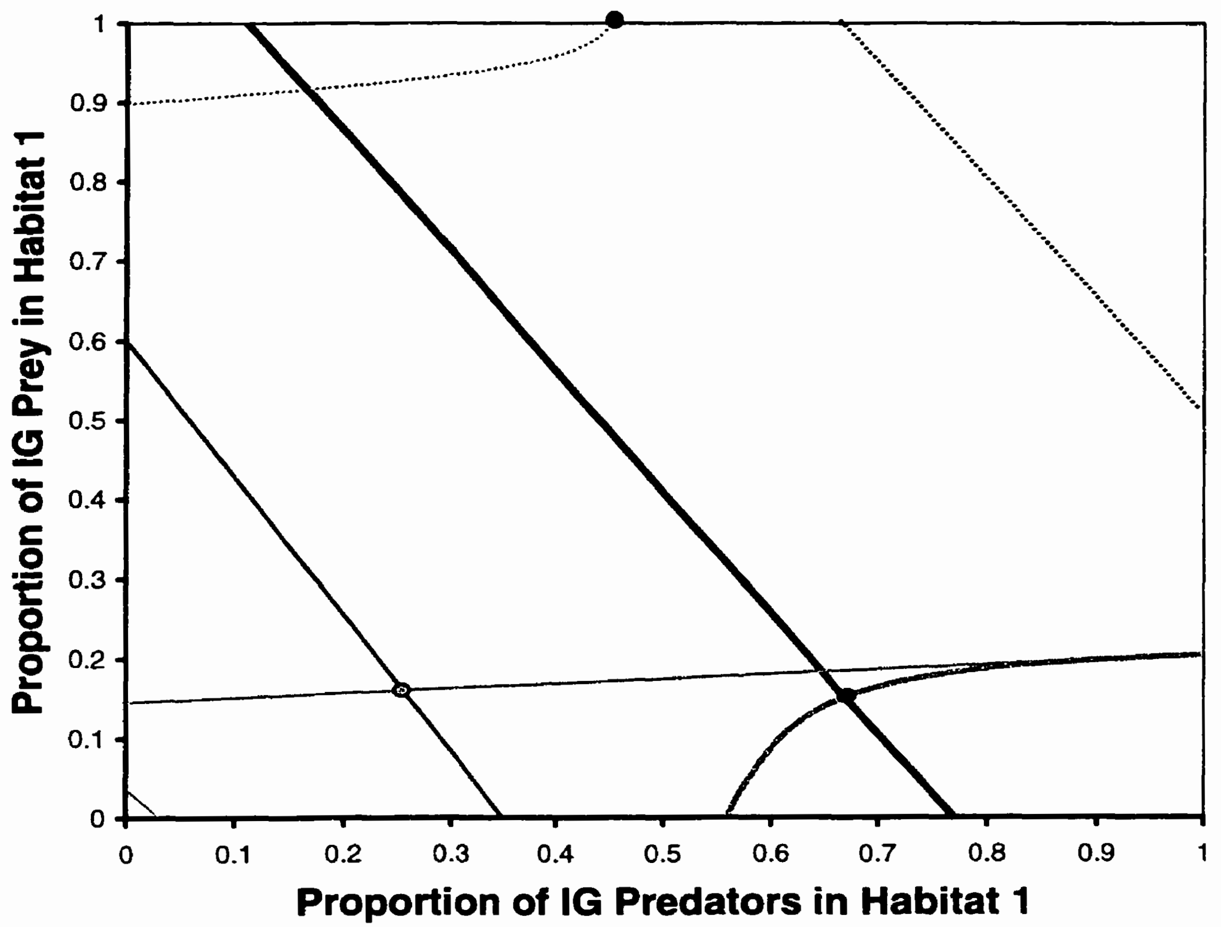


Figure 3.5. Best response curves for IG predators (gray lines) and IG prey (black lines) when competition is high ($U = 1.0$, $Q = 2.0$) and there are changes in the relative riskiness of habitats or the distribution of basal resource productivity. Thick lines: $P_1 = 700$, $P_2 = 300$, $R_1 = 0.008$, $R_2 = 0.002$. Thin lines: $P_1 = 200$, $P_2 = 800$, $R_1 = 0.008$, $R_2 = 0.002$. Dotted lines: $P_1 = 700$, $P_2 = 300$, $R_1 = 0.001$, $R_2 = 0.009$. An increase in the riskiness of Habitat 1 can result in IG prey being absent from a high-risk and low productivity habitat (Habitat 2 for dotted lines). A decrease in basal resource productivity shifts both the IG prey and IG predator response curves down.

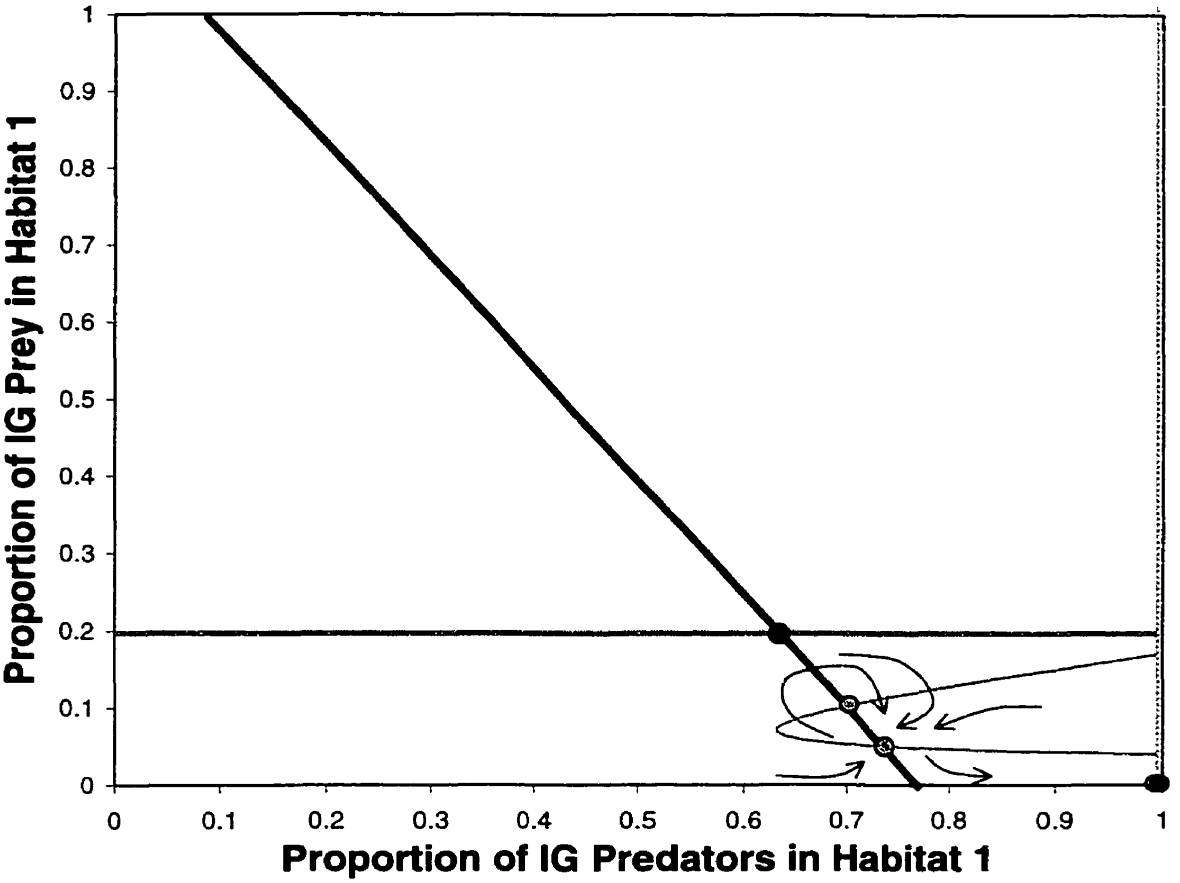


Figure 3.6. Best response curves for IG predators (gray lines) and IG prey (black lines) with change in mean basal resource productivity (thick lines *P(mean)* =1000, thin lines *P(mean)* = 4000, dashed lines *P(mean)* = 10000). Dots represent equilibria. As the productivity of the basal resource increases, the likelihood of co-occurrence decreases. At intermediate levels of productivity, two unstable (co-occurrence) and one stable (segregation) equilibria are possible. At high productivity, there is always segregation. Arrows indicate general trajectories of IG predators and IG prey when *P(mean)* = 4000. $P_1/P_2 = 2.3$, $R_1 = 0.008$, $R_2 = 0.002$

When the basal resource productivity is high, IG predators select the more productive habitat in all situations. The density of predators in this habitat causes IG prey to congregate in the less productive and less risky habitat and the species do not co-occur. If IG predators make full use of the basal resource and are relatively efficient competitors ($Q \geq 1$; e.g. Figure 3.5), an increase in basal resource productivity shifts the best response curve of IG predators to the right but has no effect on the response of IG prey. Thus, as in the low competition situation, enrichment of habitats can result in IG predators excluding IG prey from productive habitats. Increasing basal resource productivity is equivalent to reducing the density of IG predators and IG prey. Thus, spatial segregation of IG predators and IG prey is predicted to occur at low density, and co-occurrence is more likely at high densities.

The addition of an alternative resource for the IG predator changes the predicted equilibrium distributions, but the degree of change depends greatly upon the productivity of the alternative resource relative to that of the basal resource. When alternative resource productivity is quite low relative to basal resource productivity (*A(mean)/P(mean) = 0.1*), the distributions of IG predators and IG prey are almost identical to those when there is no alternative resource (Figure 3.7). An increase in relative productivity of the alternative resource has almost no influence on the IG prey best response curve, but it dramatically shifts that of the IG predator. As the relative productivity of the alternative resource becomes very large, the distribution of IG predators becomes almost exclusively responsive to the distribution of alternative resources between habitats (Figure 3.7). IG predator use of IG prey becomes a case of incidental predation. The fixed IG predator distributions caused by alternative resource productivity allow the distribution of IG prey to respond to both food and predation risk . The magnitude of IG prey response to basal resource availability will be dependent on the distribution of the alternative resource (as this will shift the IG predator response curve) relative to the basal resource (which sets the IG prey curve location). IG prey are aggregated in a single

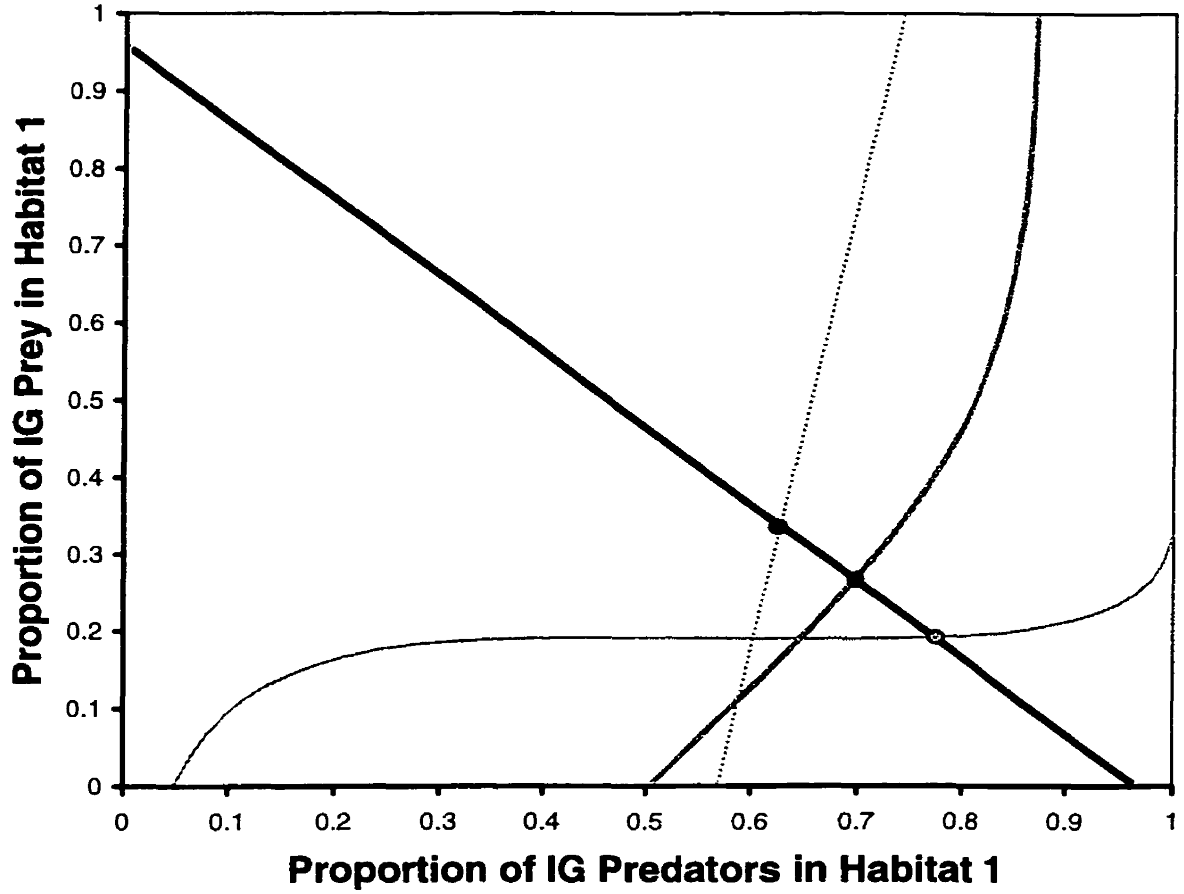


Figure 3.7. Best response curves for IG predators (gray lines) and IG prey (black lines) in the presence of an alternative resource. When alternative resource productivity is relatively low (thin lines, *A(mean)* = 100), the equilibrium distributions of IG predators and IG prey are similar to those when there is no alternative resource (Figure 3.2, thick line). As the productivity of the alternative resource increases (thick lines, *A(mean)* = 1,000; dotted lines, *A(mean)* = 10,000), the distribution of IG predators becomes more heavily influenced by alternative resource distribution and IG prey distributions reflect both habitat risk and relative basal resource productivity. The productivity and distribution of alternative resources do not change the IG prey best response curve. $A_1/A_2 = 1.5$ $P_1 = 200$, $P_2 = 800$, $R_1 = 0.008$

habitat when that habitat is much safer and/or more productive than the alternate habitat. When the majority of alternative resources are found in the habitat with high basal resource productivity, the majority of IG predators are in this habitat and IG prey undermatch the resources in the productive habitat even when that habitat is relatively safe. Conversely, when alternative resources, and thus IG predators, are most abundant in the low basal resource productivity habitat, IG prey greatly overmatch food distribution in all situations except when the low productivity habitat is also much riskier.

The trend described above is similar at all levels of dietary overlap, but occurs at lower ratios of *A(mean)/P(mean)* as dietary overlap decreases (lower values of U). This occurs because IG predators are not getting as much energy from the basal resource, so a relatively small amount of alternative prey will consequently make up a much larger portion of the IG predators' diets. Thus, at low dietary overlap ($U = 0.5$, $Q = 0.5$) there is a rapid transition from IG prey safety-matching to the distribution being determined by both basal resource availability and safety at very low levels of alternative prey productivity. At high levels of alternative resource availability, IG predators and IG prey will co-occur even if basal resource productivity is very high.

The degree of dietary overlap between IG predators and IG prey does not change the basic response of IG predators or IG prey when there is substantial alternative resource productivity, but it does influence their equilibrium distributions. Increasing competition in the presence of a relatively abundant alternative resource has almost no influence on the distribution of IG predators but changes the magnitude of IG prey response to risk and basal resource productivity. Specifically, the proportion of IG prey in habitat 1 decreases with decreasing dietary overlap when habitat 1 is much more productive and relatively safer than habitat 2.

Dilution and contest interference have relatively minor influences on the equilibrium distribution of IG predators and IG prey. When there is low overlap and no alternative resource, dilution slightly depresses the density of IG predators in the high risk and/or high productivity habitat but does not change the distribution of IG prey. Contest interference depresses IG predator density more than dilution. Under these circumstances, IG prey respond primarily to habitat riskiness but also respond to basal resource productivity to a slightly greater extent.

In the presence of an alternative resource, neither dilution nor interference changes the distribution of IG predators. However, both factors influence the magnitude of IG prey response to productivity and habitat riskiness. With dilution and interference, the density of IG prey is slightly elevated in the low risk and/or high productivity habitat. The influences of both dilution and interference are highest when dietary overlap is high.

3.5 DISCUSSION

The equilibrium distributions of predators and prey engaged in intraguild predation can be influenced by a wide variety of factors. Dietary overlap, competitive ability (for basal resources) of IG predators relative to IG prey, the distribution and abundance of basal resource productivity, and the relative riskinesses of habitats influence equilibrium distributions and the probability of co-occurrence of IG predators and IG prey. Of particular interest to behavioral ecologists and community ecologists are the predictions that arise depending on the presence and productivity of alternative resources for the IG predator.

Dietary overlap (U) and relative competitive ability for basal resources (Q) interact in a synergistic fashion. When IG predators do not use a high proportion of the basal resource or are relatively inefficient competitors, a change in the other parameter has a relatively small influence on equilibrium distributions. In general, IG prey safety-match while IG predators are distributed approximately proportional to basal resource productivity (Figure 3.2). If IG predators use a high proportion of the basal resource or are relatively efficient competitors, a change in Q or U can cause dramatic shifts in the best response curves of both IG predators and IG prey, leading to exclusion of IG prey from the productive habitat (Figure 3.5).

Changes in the relative riskiness of habitats and the distribution of basal resource productivity shift equilibrium distributions of IG predators and IG prey, regardless of the IG predator's use of basal resources and relative competitive ability. However, dietary overlap and competitive ability influence the likelihood of IG prey being excluded from a habitat. When dietary overlap is low and IG predators are inefficient competitors, IG prey are never excluded from a habitat (Figure 3.3). However, if dietary overlap is high and IG predators are relatively good competitors, IG prey are excluded from a habitat if it is very risky or if one habitat has relatively low basal resource productivity and relatively high intrinsic risk (Figure 3.5).

Community models of IGP (e.g. Holt and Polis 1997) predict that coexistence of both IG predators and IG prey is not favored when dietary overlap is high and the IG predator's diet is composed exclusively of IG prey and the basal resource. This model provides a behavioral analogue to that of Holt and Polis (1997). Although my model cannot address conditions for coexistence, behavioral decisions by IG predators and IG prey lead to habitat segregation with IG predators exclusively selecting the relatively high-productivity habitat and IG prey exclusively selecting the low-productivity habitat when overall basal resource productivity is high (Figure 3.6). This leads to the testable prediction that co-occurrence is favored in populations found at high population density (or relatively low basal resource productivity) while segregation of IG predators and IG prey should occur in populations found at low population density. When the IG predator's diet includes prey other than the IG prey or the basal resource (alternative prey), however, co-occurence is predicted at high basal resource productivity (or low population density) even when competition is high (high U and Q). In natural systems, IG predators probably consume at least some alternative resources, especially in asymmetrical IGP systems, and the presence of an alternative resource may help explain co-occurrence of IG predators and IG prey over a variety of ecological conditions. Further models incorporating both behavioral decisions and population dynamics will help to elucidate the conditions favoring coexistence and co-occurrence of IG predators and IG prey.

Alternative resources for the IG predator change the equilibrium distributions of both IG predators and, indirectly, IG prey. The presence of alternative prey does not influence the best response curve of the IG prey, but IG predators show a strong response to the distribution of alternative resources. This response of IG predators shifts the equilibrium distribution of both IG predators and IG prey. An increase in the productivity of alternative prey can cause IG prey to switch from safety matching (if dietary overlap is low) or exclusion from productive habitats (if dietary overlap is higher) to a distribution balancing intrinsic risk and basal resource availability.

The importance of the alternative resource in determining the distribution of IG predators (and thus IG prey) means that habitat use of IG prey is strongly influenced, indirectly, by the density and distribution of species that are neither predators nor competitors. Therefore, studies of animal habitat selection may benefit greatly from taking into account the dynamics of entire food webs and communities. Many models based upon the ideal free distribution are not supported by field empirical tests (Tregenza 1995). My model suggests that overlooking other species in a food web and potential indirect interactions may be partially responsible for this lack of empirical support for previous models.

Indirect effects of the alternative resource on IG prey habitat use provide a link between pure predator-prey game models, like that of Hugie and Dill (1994), and studies that deal with spatially fixed predation risk (e.g. Abrahams and Dill 1989, Kotler and Blaustein 1995, Moody et al. 1996, Brown 1998). Increases in the level of alternative resource available to IG predators provides a mechanism that effectively switches predation risk from being mobile to fixed in each habitat. This produces a continuum of IG prey responses from habitat selection based only on intrinsic habitat risk (when alternative resource productivity is low), to a distribution balancing basal resource productivity and intrinsic risk (when there is a substantial alternative resource). This continuum of prey responses is apparent in nature (see *Empirical Support* below), again emphasizing that indirect interactions mediated through a common predator may be important determinants of animal habitat use.

3.5.1 Empirical Evidence

Most empirical studies do not make adequate measurements of habitat risk or resource availability to provide quantitative tests of this model. However, a number of field studies provide qualitative support for the predictions of my model and suggest that alternative resources are important in influencing animal habitat use in the wild. Moran and Hurd (1997) found that adding food to experimental plots (equivalent to changing the distribution of basal resource between two habtiats – experimental and control – while keeping relative habitat riskiness constant) did not change the density of mantids (*Tenodera sinensis*) but caused an increase in the density of their IG predators, wolf spiders (primarily *Lycosa ranida, L. helluo*, and *Trochosa terricola*). Although there was lower dispersal of mantids from food-addition plots, mortality rates were higher because of reduced emigration of predatory spiders and probably increased IGP (Moran and Hurd 1997). Both mantids and wolf spiders are generalist predators of arthropods, but the degree of dietary overlap is unknown (Moran and Hurd 1997). Dietary overlap is probably relatively low and, if predators have an alternative resource, it probably makes up only a small proportion of their diet. The results of this study are qualitatively similar to the predictions of the pure predator-prey game, or an IGP situation with low competition and no (or very low) alternative resource. Spiders (IG predator) increased with increasing basal resource while mantids did not respond numerically to changes in basal resource abundance.

Iberian lynx (*Lynx pardinus*) consume primarily medium-sized European rabbits (*Oryctolagus cuniculus*) but also engage in IGP by consuming the red fox (*Vulpes vulpes*), which feed on medium-sized rabbits, carrion, and invertebrates (Fedriani et al. 1999). The dietary overlap is moderate ($U \sim 0.54$), but relative competitive ability is unknown. As predicted by the model, lynx density is highest in habitats that are high in rabbit density (Mediterranean scrubland) while foraging red foxes are found in pastures, which are lower in rabbit abundance, but are safer.

Most empirical studies of asymmetrical IGP have been conducted in systems where IG predators make use of alternative resources. In England, hedgehogs consume a variety of invertebrates which also make up a large proportion of their IG predators' (badgers) diet. Badgers may also consume alternative invertebrate prey (Doncaster 1992). In a study designed to test whether hedgehogs were excluded from apparently suitable habitats through IGP with badgers, hedgehogs were transplanted from areas with low badger density and high hedgehog density to areas where badgers were very abundant and hedgehogs absent. The difference in badger density between the two areas was thought to be due to differences in the abundance of alternative invertebrate prey (Doncaster 1992). Transplanted hedgehogs had lower survival (largely due to badger predation) and higher dispersal rates than those found in control areas. Almost all the transplanted hedgehogs that survived occupied microhabitats (urban gardens) that were not accessible to badgers. The presence of alternative resources seems to be very important in determining the abundance of both IG predators and IG prey, as predicted by my model. Although my model would not predict the absence of hedgehogs from the high badger habitat initially, it would predict that they would be present in low numbers, which may make them more susceptible to stochastic events.

A final example of asymmetrical IGP that fits the general qualitative predictions of my model comes from southern Africa. In this system, the IG prey, wild dogs interact with two IG predators: lions and, to a lesser extent, spotted hyenas (*Crocuta crocuta*) (Polis et al. 1989, Fuller and Kat 1990, Mills and Gorman 1997). Lions are much more common predator of wild dogs and account for about 39% of wild dog pup deaths and at least 43% of adult deaths (Mills and Gorman 1997). In the Kruger National Park, wild dogs primarily eat impala (*Aepyceros melampus*) and to a lesser extent kudu (*Tragelaphus strepsiceros*) and other ungulates (basal resource). Although lions will eat these species and kleptoparasitize wild dogs, the primary prey species of lions (alternative resource) are wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*) and zebra (*Equus burchelli*) (Mills and Gorman 1997). Hyenas scavenge for almost half of their prey and kleptoparasitize dogs, but will hunt for such prey as buffalo, warthogs (*Phacochoerus aethiopicus*), kudu and impala (Henschel and Skinner 1990). Therefore, lions are common wild dog predators but have low dietary overlap with them while hyenas are uncommon predators but have at least moderate dietary overlap with dogs.

Lions are distributed in relation to the density of their primary prey (alternative resource) which are most common in *Acacia* thickets, *Marula* savanna, and *Combretum* bushveld (Mills and Gorman 1997). These habitats appear to be the most productive in terms of wild dog resources (basal resource), but wild dogs largely avoid them. In fact, there is generally a negative correlation between dog density and basal resource density. Instead, dogs are found in the highest density where lions and, to a lesser extent, hyenas are relatively scarce (Mills and Gorman 1997). This general result fits with model predictions. The relatively high alternative resource availability and low use of shared prey leads to lions being distributed in relation to the alternative resource and dogs making a tradeoff between energy intake and predation risk. In this system, habitat use by wild dogs is indirectly influenced by the distribution of wildebeest, buffalo, and zebra.

3.5.2 Other Models and Assumptions

Unlike the stable distributions predicted in my model, Schwinning and Rosenzweig (1990) found oscillations in the distributions of IG predators, IG prey, and basal resource in their model of a three-tier asymmetrical IGP predator-prey system with predators pursuing prey. The distributions could be stabilized if refuge strength or intraspecific competition among prey was increased. My model and that of Schwinning and Rosenzweig (1990) differ in several respects. First, Schwinning and Rosenzweig (1990) allowed the distribution of the basal resource to fluctuate according to predation rate by the IG predators and IG prey, while I consider basal resource productivity in each habitat to be fixed. Another difference is that there is competition among IG predators for IG prey in my model while there is none in the Schwinning and Rosenzweig (1990) model. The lack of competition among predators causes all predators to do better in the habitat with more prey and this assumption is probably largely responsible for the oscillations observed by Schwinning and Rosenzweig (1990).

There are several assumptions of my model that may be violated in some natural situations and would influence the expected distributions of IG predators and IG prey. First, the model assumes that the foraging rate of the IG prey in a given habitat is not influenced by the presence of IG predators; IG predators only reduce the intake rate of IG prey through consuming resources. In some situations, IG prey reduce their foraging rates in the presence of IG predators because of increased vigilance or other behavioral effects (reviewed in Lima and Dill 1990). In an asymmetrical IGP situation involving two species of dragonfly larvae, the IG prey's food consumption was more than halved when they were kept in the presence of IG predators that had their mouth parts removed (and thus could not feed) (Wissinger and McGrady 1993). IG predator consumption of the basal resource was not influenced by the presence of IG prey that had their mouth parts removed. Similarly, Huang and Sih (1991) found that salamander larvae (*Ambystoma barbouri*, IG prey) reduced their foraging rate on hatchling isopods (*Lirceus frontinalis*, basal resource) in the presence of green sunfish (*Lepomis cyanellus*). Reduction in the foraging rate of IG prey in the presence of IG predators may result in IG prey being eliminated from habitats that are preferred by IG predators because the competitive ability of IG predators for shared resources would be higher than that of IG prey (high Q). The cost of IG prey selecting a habitat with a high proportion of IG predators would thus be even higher than considered in my model, and the slope of IG prey best response curve more negative.

Prey selection by the IG predator could influence expected distributions, but is not included in my model, which assumes that the basal resource and alternative resource are consumed relative to their availability and that IG prey are attacked whenever they are encountered (with success determined by habitat riskiness). In some predator-prey systems, this may not be the case. Predators may switch prey and not attack potential prey when preferred prey are above a threshold density (e.g. Stephens and Krebs 1986); this may reduce the probability that IG prey would be completely eliminated from a habitat when alternative prey or basal resources are abundant. However, if IG prey are energetically superior to alternative prey, they may be preferentially consumed and exclusion of IG prey may be even more likely.

Finally, my model assumes that there are no changes in the relative population sizes of IG predators and IG prey. Obviously, this assumption will be violated in many natural situations, and it is possible that fluctuations in population size may influence the relative fitnesses achieved in each habitat. The influence of population dynamics on habitat selection of IG predators and IG prey is beyond the scope of this work. However, future efforts that combined optimal behavior and predator-prey foraging games with models of population dynamics are likely to provide novel insights into the persistence and dynamics of IGP (e.g. Brown et al. 1999).

This model predicts that indirect effects may be very important in shaping habitat use patterns of IG prey, and demonstrates that behavioral studies of animal habitat use can benefit from taking into account community-level interactions. In the future, more detailed models incorporating factors such as prey selection of the IG predator and changes in IG prey foraging rates as well as empirical tests will further enhance our understanding of how intraguild predation shapes individual behavior, which in turn may influence community patterns. Although some empirical support for this model exists, more detailed field data and rigorous experimental tests will be required to determine the applicability of this approach to the study of intraguild predation. Finally, future models that incorporate behavioral decisions and population dynamics should provide insights into the importance of behavior in determining the spatial organization and structure of communities characterized by intraguild predation.

3.6 ACKNOWLEDGEMENTS

I would like to thank Don Hugie, Larry Dill, and especially Ian Hamilton for discussions of this model and simulation technique. Ian Hamilton, Larry Dill, Ray Heithaus, Tamara Grand, Bernie Roitberg, and Bernie Crespi provided helpful comments on the manuscript. Support was provided by NSERC Canada grant A6869 to Lawrence M. Dill. Simon Fraser University and a National Science Foundation Graduate Fellowship provided personal support during the preparation of this chapter.

3.7 LITERATURE CITED

Abrahams, M.V. and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999-1007.

Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. Annales Zoologi Fennici 29: 301-309.

Brown, J. S. 1998. Game theory and habitat selection. Pages 188-220 *in* Game Theory and Animal Behavior. L. A. Dugatkin and H. K. Reeve, editors. Oxford University Press, Oxford.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80: 385-399.

Caro, T. M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press: Chicago.

Doncaster, C. P. 1992. Testing the role of intraguild predation in regulating hedgehog populations. Proceedings of the Royal Society of London B 249: 113-117.

Fedriani, J. M., F. Palomares, and M. Delibes. 1999. Niche relationships among three sympatric carnivores. Oecologia 121: 138-148.

Fretwell, S. D. and H. J. Lucas Jr. 1970. On territorial behaviour and other factors influencing habitat distribution of birds. Acta Biotheoretica 19: 16-36

Fuller, T. K. and P. W. Kat. 1990. Movements, activity, and prey relationships of African wild dogs (*Lycaon pictus*) near Aitong, southwestern Kenya. African Journal of Ecology 28: 330-350.

Gotceitas, V. and P. Colgan. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80: 158-166.

Grand, T. C. 1999. Foraging site selection by juvenile coho salmon: ideal free distributions of unequal competitors. Animal Behaviour 53: 185-196.

Grand, T. C. and L. M. Dill. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. Behavioral Ecology 8: 437-447.

Grand, T. C. and L. M. Dill. 1999. Predation risk, unequal competitors and the ideal free distribution. - Evolutionary Ecology Research 1: 389-409.

Heithaus, M. R. in press. Predator-prey and competitive interactions between sharks and small toothed whales: A review. Journal of Zoology.

Henschel J. R. and J. D. Skinner. 1990. The diet of the spotted hyaenas Crocuta crocuta in Kruger National Park. African Journal of Ecology 28: 69-82.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomology. 91: 385-398.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the co-occurence of prey species. American Naturailt. 124: 377-406.

Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149: 745-764.

Huang, C. and A. Sih. 1991. Experimental studies on direct and indirect interactions in a three trophic-level stream system. Oecologia 85: 530-536.

Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45 (Supplement A): 151-169.

Kotler, B. P. and L. Blaustein. 1995. Titrating food and safety in a heterogeneous environment: when are risky and safe patches of equal value? Oikos 74: 251-258.

Kotler, B. P. and R. D. Holt. 1989. Predation and competition: the interaction of two types of species interactions. Oikos 54: 256-260.

Laurenson, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385-399 *in* Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. A. R. E. Sinclair and P. Arcese, editors. University of Chicago Press, Chicago.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. American Naturalist 147: 784-812.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lucas, E., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. Ecology 79: 1084-1092.

McNamara, J. M. and A. I. Houston. 1987. Starvation and predation as factors limiting population size. Ecology 68: 1515-1519.

Mills, M. G. L. and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11: 1397-1406.

Miner, J. G. and R. A. Stein. 1996. Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. Transactions of the American Fisheries Society 125: 97-103

Moody, A. L., A. I. Houston, and J. M. McNamara. 1996. Ideal free distributions under predation risk. Behavioral Ecology and Sociobiology 38: 131-143.

Moran, M. D. and L. E. Hurd. 1997. Relieving food limitation reduces survivorship of a generalist predator. Ecology 78: 1266-1270

Moran, M. D. and L. E. Hurd. 1994. Short-term responses to elevated predator densities: noncompetitive intraguild interactions and behavior. Oecologia 98: 269-273.

Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology 80: 752-760

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Palomares, F. and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153: 492-508.

Parker, G. A. and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Animal Behaviour 34: 1222-1242.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138: 123-155.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330.

Polis, G. A. and D. R. Strong. 1996. Food web complexity and community dynamics. - American Naturalist 147: 813-846.

Schwinning, S. and M. L. Rosenzweig. 1990. Periodic oscillations in an ideal-free predator-prey distribution. Oikos 59: 85-91.

Sih, A. 1998. Game theory and predator-prey response races. Pages 221-238 *in* Game Theory and Animal Behavior. L. A. Dugatkin and H. K. Reeve, edirors. Oxford University Press, Oxford.

Sinclair, A. R. E. and P. Arcese. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology 76: 882-891.

Stephens, D. and J. R. Krebs. 1986. Foraging Theory. Princeton University Press: Priceton, NJ.

Sutherland, W. J. and G. A. Parker. 1985. Distribution of unequal competitors. Pages 255-274 *in* Behavioural Ecology - Ecological Consequences of Adaptive Behaviour. R. M. Sibly and R. H. Smith, editors. Blackwell, Oxford.

Sutherland, W. J. and G. A. Parker. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. Animal Behaviour 44: 345-355

Tregenza, T. 1995. Building on the ideal free distribution. Advances in Ecological Research 26: 253-307.

Vance, R. R. 1974. Predation and resource partitioning in one predator- two prey model communities. American Naturalist 112: 797-813.

Wissinger, S. and J. McGrady. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. Ecology 74: 207-218.

CHAPTER 4

Shark Attacks on Bottlenose Dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: Attack Rate, Bite Scar Frequencies, and Attack Seasonality*

---

*A version of this chapter appears as Heithaus, M. R. 2001. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. Marine Mammal Science 17: in press. Reprinted with permission from the Society for Marine Mammalogy.

4.1 ABSTRACT

Shark predation may have been a central factor influencing the evolution of sociality in dolphins as well as a determinant of dolphin habitat use and behavior. To understand the role of predation in driving interpopulation differences in behavior and sociality, it is important to quantify differences in predation risk among populations. This study describes the frequency of shark-inflicted scars and estimates the shark attack rate on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. Shark bite scars were found on 74.2% (95 of 128) of non-calves, and most of these scars were inflicted by tiger sharks (*Galeocerdo cuvier*). Although there were no differences among age/sex classes in the frequency of scarring, significantly more adult males than adult females bore multiple scars. The rate of unsuccessful shark attack was estimated to be between 11%-13% of dolphins attacked each year. Large sharks (>3m) were responsible for a disproportionate number of attacks. However, bites from small carcharhinid sharks on 6.2% of dolphins suggest that some of these small sharks may be dolphin ectoparasites. Both the scar frequencies and attack rate suggest that Shark Bay dolphins face a greater risk of predation than bottlenose dolphins in other locations.

4.2 INTRODUCTION

Shark predation on dolphins has been a subject of much conjecture but relatively little study (see Chapter 2 for a review of shark predation on dolphins). Five species of sharks appear to be relatively frequent predators on dolphins: white (*Carcharodon carcharias*), tiger (*Galeocerdo cuvier*), bull (*Carcharhinus leucas*), sixgill (*Hexanchus griseus*), and sevengill (*Notorynchus cepedianus*) sharks. Five others, dusky (*Carcharhinus obscurus*), oceanic whitetip (*C. longimanus*), mako (*Isurus oxyrinchus*), Pacific sleeper (*Somniosus pacificus*), and Greenland (*S. microcephalus*) sharks, are probably occasional dolphin predators (Heithaus in press a, Chapter 2).

Predation risk may have been an important factor that led to the evolution of group living in dolphins (e.g. Norris 1994). Furthermore, risk of shark predation appears to influence both habitat use and group sizes of dolphins in a variety of locations (e.g. Norris and Dohl 1980a, Wells et al. 1980, 1987, Heithaus in press a, Chapter 2). Despite the possible importance of shark predation in shaping the behavior of dolphins, in many cases, the only evidence of interactions between sharks and dolphins comes from the presence of shark-inflicted wounds and scars. The frequency of such wounds has been used as an indirect measure of the threat that sharks pose to dolphins (e.g. Wood et al. 1970, Heithaus in press a). However, this method is fraught with difficulties since scars and wounds are the result of failed predation attempts and the actual rate of shark attack is higher than that measured by wound frequencies. Also, there are likely to be biases caused by differences in the probability of an attack being successful, due to such factors as the sizes of the dolphin and the attacking shark (Heithaus in press a). Despite these drawbacks, scarring frequency can still be useful in comparisons among dolphin populations with similar adult body size and likely to face predation threats from similar shark species (Heithaus in press a, Chapter 2).

The frequency of shark-inflicted wounds and scars has been reported from several locations. In South Africa, between 10.3% and 19.3% of bottlenose dolphins have scars or wounds from sharks (Cockcroft et al. 1989) while 28% of humpback dolphins (*Sousa plumbea*) in the same area show evidence of shark attacks (Cockcroft 1991). In Sarasota, Florida 31% of bottlenose dolphins bear shark bite scars (Urian et al. 1998) compared to 36.6% for bottlenose dolphins in Moreton Bay, Australia (Corkeron et al.

1987a). In other areas, the frequency of shark scars is much lower. For example, scars are seldom seen on dolphins in the open ocean (Wood et al. 1970) and no shark bites have been observed on bottlenose dolphins in the Adriatic Sea (Bearzi et al. 1997).

The aims of this study were to document the frequency of shark-inflicted scars and wounds and to estimate shark attack rates on dolphins in Shark Bay, Western Australia for comparison with other areas. In addition, this study investigated age/sex differences in scarring frequencies and the seasonality of shark attacks.

4.3 METHODS

4.3.1 Study Site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia. The study site was located in the Eastern Gulf, near the Monkey Mia Dolphin Resort (see Chapter 5 for a detailed description of the study site). This area has been the site of dolphin research since 1982 (e.g. Smolker et al. 1992, Connor et al. 1992, 1999); over 600 dolphins have been individually identified and sexes and approximate ages of many individuals are known (Smolker et al. 1992).

Tiger sharks are the dominant species of large shark in the Eastern Gulf of Shark Bay. They accounted for over 94% ($n = 252$ of 267 sharks captured) of large shark catches during research fishing for large sharks in the dolphin study area (Heithaus in press b). Tiger shark abundance is seasonally variable with high shark densities from September through May before dropping dramatically in June-August (Heithaus in press b, Chapter 5). During times of low tiger shark abundance, two other shark species that could be a threat to dolphins may enter the Eastern Gulf of Shark Bay - white and mako sharks (Connor and Heithaus 1996, Heithaus in press b). However, these species occur in very low abundance with no white sharks and one mako shark were caught in over 6,300 hours of drumline fishing (Heithaus in press b). The only other potential dolphin predator caught in the study area was the dusky shark ($n = 2$), but these individuals were too small to be a predation threat to dolphins (Heithaus in press a, in press b). Finally, Shark Bay supports populations of many species of small carcharhinid sharks that are unlikely to be a predation threat to dolphins (Last and Stevens 1994, Heithaus in press b).

4.3.2 Shark Wounds

Between May 1998 and July 1999, during surveys conducted from a 4.5 m runabout, dolphins were checked for the presence of shark-inflicted wounds while they were bow riding, swimming underwater, or surfacing within 2 m and usually within 1 m of the observer (Figure 4.1). Observations were made in Beaufort wind conditions 0 or 1, with most observations made in Beaufort 0 conditions. Due to the proximity of dolphins, the observation conditions, and because most dolphins were surveyed multiple times, it is likely that bites were rarely missed in dolphin body zones that were surveyed.

The dolphin's body was divided into 12 zones: head, body, and tail/peduncle for dorsal, ventral, left, and right surfaces. In the field, all bites were drawn onto a figure of a dolphin to aid in the recording of data. In addition, photographs were taken whenever possible for further analysis (Figure 4.1). Of 290 observations, 266 (92%) were made by the author. Furthermore, only two individuals were not surveyed at least once by the author. Therefore, the results are not influenced by variation among observers.

Wounds were only considered to have been caused by sharks if they were crescent-shaped or consisted of deep and widely-spaced tooth rakes that could not have been caused by another dolphin. The approximate date of attack for fresh wounds was estimated in several manners. For dolphins encountered frequently (many individuals were encountered multiple times each month), date of attack could be estimated within a few weeks based on the date when a wound was first observed. For other wounds, time of attack was estimated by comparing the physical appearance of the wound to other wounds of known age and published rates of shark bite wound healing (e.g. Corkeron et al. 1987b). The relative freshness of a bite (e.g. scar >1 year, or wound <1 year) was estimated for all bites. In general, the proportion of fresh wounds is likely to be an underestimate since shark-inflicted wounds on bottlenose dolphins may heal completely in approximately six months (Corkeron et al. 1987b).

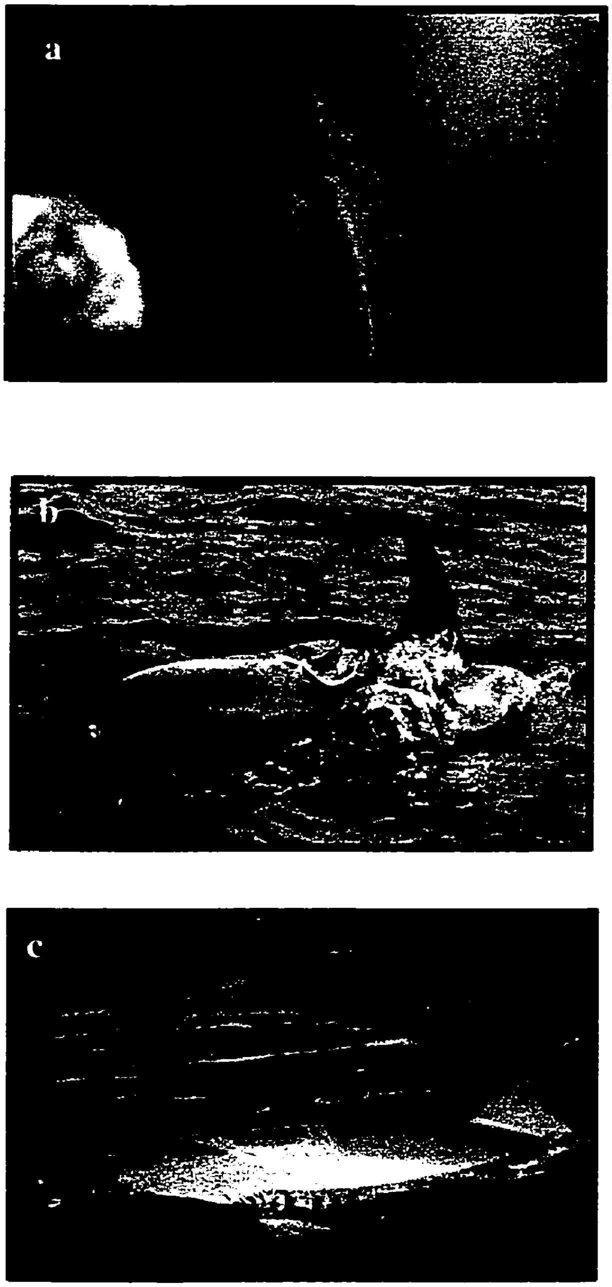


Figure 4.1. Shark bite scars on dolphins. a) Observations were made from close range in calm conditions. Notice that scarring from both upper and lower jaws of the shark is present. b) Fresh bite on an adult female dolphin. It was impossible to determine the species or size of attacking shark based on the incomplete nature of the bite. c) Shark bite on the dorsal surface of a juvenile dolphin.

Although it is often impossible to determine the species of shark responsible for inflicting a wound, some bites can be assigned to a particular shark species or family based on bite characteristics (e.g. Corkeron et al. 1987a, Long and Jones 1996). The potential dolphin predators in Shark Bay all have characteristic bites, especially tiger sharks. Carcharhinid sharks have jaws that are crescent-shaped with numerous, pointed teeth, and bites on cetaceans are generally clean-cut (Long and Jones 1996). Mako sharks have crescent-shaped jaws with numerous functional rows of extremely narrow teeth (Long and Jones 1996, M. Heithaus personal observation). White shark bites are wide and parabolic, with relatively wide teeth that are larger in the upper jaw. These bites may be ragged in appearance (Long and Jones 1996). In contrast to these sharks, tiger sharks have a diagnostically broad head and widely spaced, large teeth that are of equal size on both jaws (Long and Jones 1996, M. Heithaus personal observation). Tiger sharks also tend to leave slashing bites that are not clean-cut (M. Heithaus personal observation). The size of many shark bites was so large that only a white shark or a tiger shark could have caused them. In these cases, the species responsible for the bite could be determined if tooth puncture marks were present for both upper and lower jaws. If tooth punctures were of the same size in upper and lower jaws, the bite was considered to have been inflicted by a tiger shark.

Bite widths were estimated for 69 bites in the field and shark total length was estimated within a 20-30 cm range based on jaw width – total length (TL) relationships (Jaw (cm) = 0.12TL – 7.99, $n = 93$ sharks, $P < 0.0001$)[1]. Since the entire bite width is necessary for accurate estimates of shark length, all estimates are likely minimum size estimates. However, because of the broad shape of the tiger shark's jaw, it is often possible to determine if bites are only from the anterior portion of the jaw. No size estimates were made for bites of this nature. Estimates were only made for bites that were observed at close range for an extended period (e.g. when the dolphin was bow riding), and only relatively fresh bites, which were not subject to stretching or deformation by animal growth, were included in analyses. The midpoint of the estimated size range was used for analyses of shark size classes responsible for attacks. The width of 21 bites was estimated multiple times with each observation made at least two weeks

---

[1] S. Dudley, unpublished data. Natal Sharks Board, Umhlanga Rocks, South Africa

apart. The average error between estimates of shark size for the same bite was 0.09 m (SD = 0.07 m, range 0 - 0.20 m), suggesting that shark size estimates were consistent. Thus, even if biases exist in absolute size estimates, relative shark sizes among bites is consistent.

4.3.3 Analysis

Data were analyzed to determine 1) the observed scarring frequency on dolphins in Shark Bay, 2) the estimated actual scarring frequency, 3) age/sex class differences in scarring frequency, 4) the wound distribution on dolphins' bodies, and 5) the annual unsuccessful shark attack rate. A dolphin was only included in analyses 1, 2, or 3 if at least 9 zones were observed, and for analysis 3 only if the sex was also previously known. Furthermore, no unidentified dolphins were included in analyses to avoid biases associated with counting the same individual in an analysis multiple times. All dolphins and observed zones were used to estimate scarring frequency of various body zones, and statistical tests for non-random bite distribution on dolphins' bodies were corrected for the number of times each body region was surveyed. Finally, all dolphins were used for analyses of the annual attack rate. In this analysis, I assume that all fresh wounds were seen on all dolphins surveyed during a field season (including those not surveyed for wounds). Thus, estimates of unsuccessful attack rate are conservative.

Observed scarring rates (analysis 1) assumed that all scars were seen on dolphins with at least nine body zones surveyed. Obviously, this will underestimate the actual scarring frequency. Thus, a randomization procedure was used to estimate the true scarring frequency of dolphins in Shark Bay (analysis 2). In this procedure, all unsurveyed zones on each dolphin were randomly assigned as either having a bite or not having a bite based on the frequency of scars in that zone generated by analysis 4 (Table 4.1). This process was iterated 500 times to determine the expected distribution of bites among unsurveyed zones. The mean number of unscarred individuals that were assigned a bite during randomizations and the mean number of individuals that had a single bite that were assigned a second bite were added to the observed number of individuals with one or multiple bites, respectively. This allowed me to estimate the actual proportion of dolphins with at least one bite and the proportion of dolphins with multiple bites.

Table 4.1. Frequency of scarring in the twelve zones of dolphins' bodies. DH = dorsal head, DB = dorsal body, DP = dorsal peduncle/tail, RH = right head, RB = right body, RP = right peduncle/tail, LH = left head, LB = left body, LP = left peduncle/tail, VH = ventral head, VB = ventral body, VP = ventral tail/peduncle.

	DH	DB	DP	RH	RB	RP	LH	LB	LP	VH	VB	VP
N	138	138	137	136	135	134	136	136	134	36	35	32
Scars	9	29	8	1	30	10	3	34	6	0	3	0
Frequency	0.065	0.210	0.058	0.007	0.222	0.075	0.022	0.25	0.045	0.000	0.086	0.000

4.4 RESULTS

Nine or more body zones were surveyed on 138 known dolphins including 128 non-calves (122 of known sex). The average number of zones surveyed was 9.6 (Table 4.1). Overall, 74.2% (*n* = 95) of non-calves had scars or wounds from shark bites. Of these, 40 (42.1% of attacked dolphins, 29.6% of all dolphins) had more than one bite. Overall, 174 shark bites were recorded on non-calves (*n* = 128), with an average of 1.36 ± 0.26 (SE) bites/individual or 1.83 ± 0.26 (SE) bites/attacked individual. One individual had a minimum of 9 bites, and six individuals exhibited at least 5 bite scars.

Estimated scarring rates based on the randomization procedure were slightly higher than observed rates. If all body zones for all dolphins had been surveyed, the expected scarring frequency of non-calves would be 77.0% ± 0.1% (SE). Multiple scars would be expected on 33.6% ± 0.1% (SE) of dolphins (43.6% ± 0.1% (SE) of dolphins with scars). A total of 1.43 ± 0.24 (SE) bites/individual or 1.85 ± 0.26 (SE) bites/attacked individual would be expected if all dolphins were completely surveyed.

Scarring frequency was highest for adult males with 39 of 46 (84.8%) dolphins having at least one bite. However, there were no significant differences in the scarring frequencies among adult males, adult females (29 of 40, 72.5%), juvenile males (15 of 21, 71.4%), or juvenile females (9 of 14, 64.3%; $\chi^2 = 2.9$, df = 3, $P = 0.41$). There also was not a significant difference in scarring frequency of mothers with calves (23 of 30, 76.7%) and adult females without calves (6 of 10, 60%, $\chi^2 = 1.0$, df = 1, $P = 0.31$). The lowest scarring frequency was found in calves (4 of 10, 40%). The proportion of adult males (21 of 46, 42.6%) with multiple shark bites was significantly higher than that of adult females (10 of 40, 25.0%, $\chi^2 = 4.4$, df = 2, $P = 0.035$), but there were no other significant differences in multiple scarring frequencies among age/sex classes.

In 1998, 17 fresh bites (<1 year old) were recorded, whereas 20 fresh wounds were documented in 1999. Based on the assumption that every fresh wound was recorded (including those on dolphins with < 9 zones surveyed), the annual unsuccessful attack rates are 11.0% (*n* = 17 of 154 dolphins sighted) for 1997-1998 and 13.4% (*n* = 20 of 149 dolphins sighted) for 1998-1999. Because it is unlikely that all fresh wounds were observed, these estimates are conservative. Scars are not permanent and at least four scars recorded in 1998 had disappeared by 1999.

The distribution of shark bite scars along the dolphin's body length was not random ($\chi^2 = 87.8$, df = 2, $P < 0.0001$, Table 4.1). Corrected for the number of observations on each body portion, many more scars than expected were located on the body trunk area while many fewer bites than expected were found in tail/peduncle and head zones. There was not a significant difference in the distribution of scars among the dorsal surface, flanks, and ventral surface ($\chi^2 = 100.1$, df = 2, $P = 0.06$), but there was a tendency for more bites than expected dorsally and fewer than expected ventrally. There was not a significant difference in the scarring frequency on left and right surfaces ($\chi^2 = 0.74$, df = 1, $P = 0.90$).

Most bites that could be attributed to a particular species of shark were consistent with the bite pattern of tiger sharks. These wounds include broad tooth lacerations that are widely spaced, show the relatively broad head of the tiger shark and a characteristic slashing bite. No bites inflicted by sharks over 2 m TL could definitively be attributed to a species other than a tiger shark. All identifiable small wounds, from sharks less than 2 m TL, were clean bites that were highly crescent shaped with narrow gaps between teeth. Thus, they are not consistent with a tiger shark bite, but are consistent with a bite from a whaler shark (*Carcharhinus* sp.).

Estimates were made of the size of an attacking shark for 69 bites (Figure 4.2). The average shark length was estimated to be 3.2 m (SD = 0.4). There was a significant difference between the average sizes of sharks that inflicted scars on juveniles ($\bar{x} = 3.0$, $n = 23$ bites) and adults ($\bar{x} = 3.3$m, $n = 46$ bites) ($t = 3.4$, df = 67, $P < 0.01$).

The size distribution of sharks (> 2.0 m TL) making unsuccessful attacks was significantly different from the size distribution of tiger sharks caught by drumline in the study area ($\chi^2 = 28.7$, df = 7, $P < 0.001$; shark size distribution data from Heithaus in press b, Chapter 5). In general, a much smaller proportion of scars on dolphins were inflicted by small sharks than would be expected from their abundance alone while large size classes of tiger sharks were responsible for more scars than expected (Figure 4.3). However, the largest tiger shark size class (> 4.0 m) did not leave more scars than expected based on their abundance.

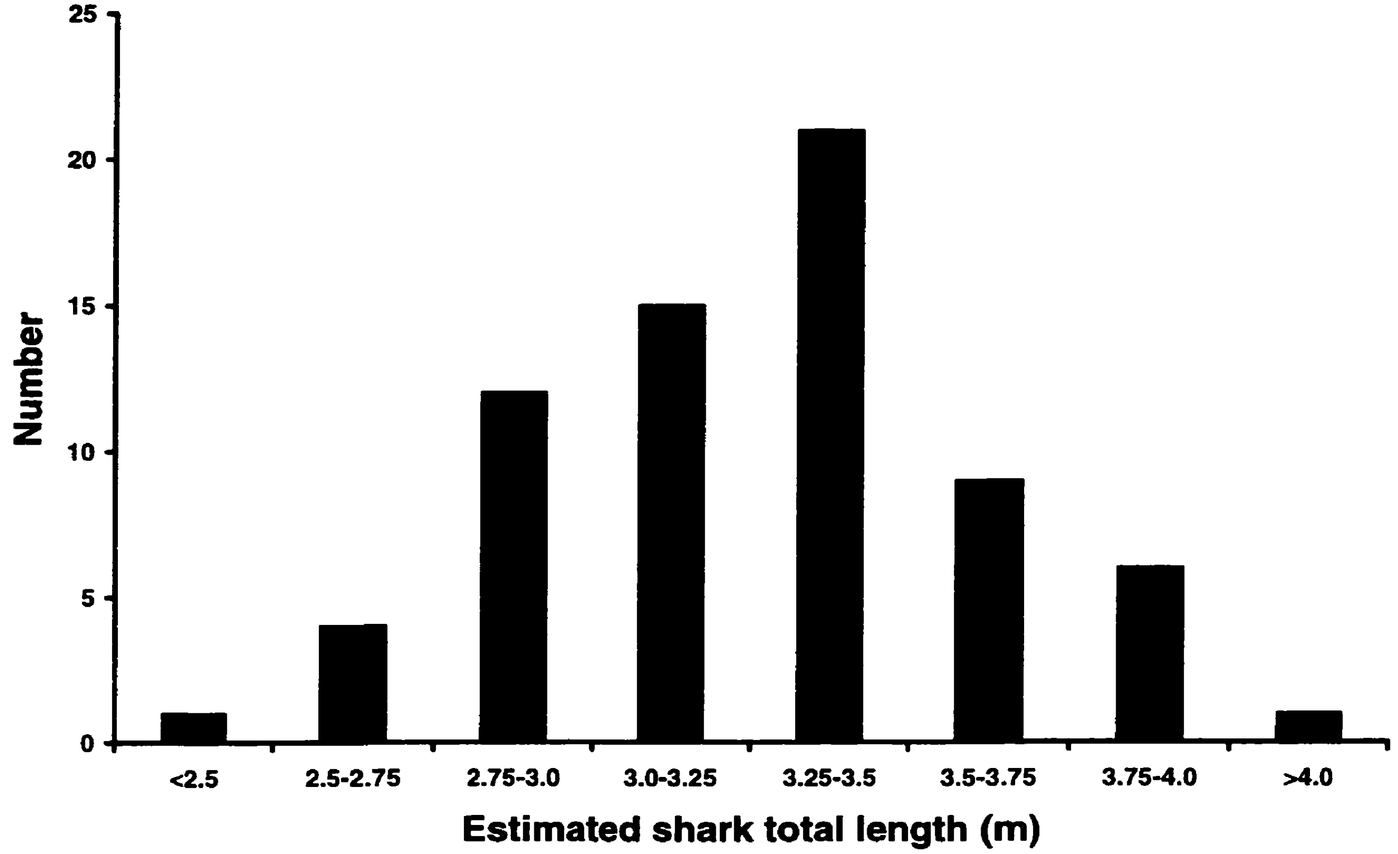


Figure 4.2. Size distribution of sharks attacking bottlenose dolphins. Shark size estimates are based on field estimates of shark bite width and jaw width-total length relationships for tiger sharks (Jaw (cm) = 0.12TL (cm) – 7.99 cm, S. Dudley unpublished data).

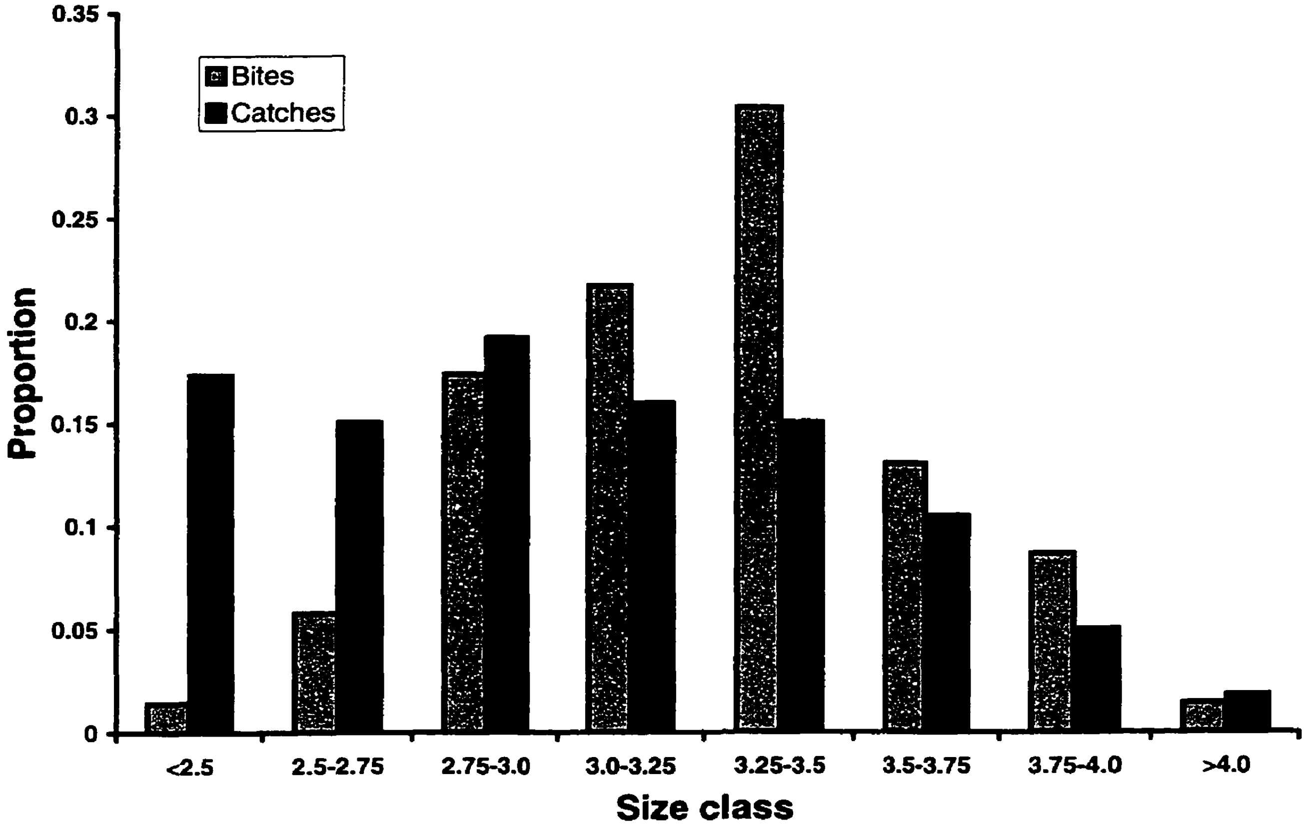


Figure 4.3. Size classes of sharks attacking bottlenose dolphins compared to the size distribution of tiger sharks caught by drumline in Shark Bay. Small tiger sharks attack dolphins relatively less often than do large sharks. Shark size distribution data from Heithaus (in press b).

Bites from very small sharks (< 1.5 m; not included in the above analyses) were recorded on 8 individuals (6.2%). This type of wound was probably frequently missed during surveys and heals relatively quickly, making this an underestimate of the frequency of dolphins attacked by small sharks.

The approximate time of year of fresh wound accumulation could be determined for 33 bites. Significantly more attacks than expected, based on sample effort, occurred during months of high water temperature (September – May), when tiger shark abundance is high ($n = 32$ fresh wounds), than during colder (June – August), low tiger shark density, months ($n = 1$ fresh wound; $\chi^2 = 8.5$, df = 1, $P < 0.01$; water temperature and shark abundance data from Heithaus in press b, Chapter 5).

4.5 DISCUSSION

The frequency of shark scarring on bottlenose dolphins in Shark Bay is higher than in other locations. Shark scars are common on bottlenose dolphins in both Moreton Bay and Sarasota (36.6% and 31%, respectively, Corkeron et al. 1987a, Urian et al. 1998) compared to South Africa (10-19%, Cockcroft et al. 1989) and the Adriatic Sea (0%, Bearzi et al. 1997). However, the observed scarring frequency on dolphins in Shark Bay (74.2%) was more than twice that of Sarasota and Morteon Bay and the estimated scarring rate is approximately 77%. It is unlikely that the relative differences in scar frequency are due to sampling biases. Scar frequencies were measured through observations of captured animals in Sarasota and South Africa, a technique which will detect all scars. Also, this study used methods similar to those applied in Moreton Bay and the Adriatic Sea, so the magnitude of difference in scarring rates is unlikely to be caused by sample bias.

While the observed differences in scarring rate are most likely not sampling artefacts, scarring data include biases, as only survivors of attacks bear scars. If there are large discrepancies among locations in the probability of death during an attack, it is impossible to use scar data as the basis for understanding geographic differences in predation risk (e.g. Cockcroft et al. 1989, Heithaus in press a). However, dolphins in Shark Bay are probably not substantially less likely to be killed in an attack than dolphins elsewhere. Bottlenose dolphins in Shark Bay are smaller than are those at the other study sites (Ross and Cockcroft 1990, Connor et al. 2000) and encounter similar sharks. Tiger sharks are one of the primary dolphin predators in all of these areas except the Adriatic (Corekeron et al. 1987a, Cockcroft et al. 1989, Wells 1991, Randall 1992, Heithaus in press b). However, white sharks, which are rare in Shark Bay (Heithaus in press b) are another major predation threat to dolphins in South Africa (Cockcroft et al. 1989), and also occur in Moreton Bay (Corkeron et al. 1987a). If white sharks are more efficient predators on bottlenose dolphins in these locations, death rates may be higher in Moreton Bay and South Africa than in Shark Bay. However, if shark attack rates were equal for dolphin populations of Sarasota, Moreton Bay, South Africa, and Shark Bay then death rates would have to be 2.7, 2.5, and 3.1-3.5 times greater in these areas, respectively, than in Shark Bay to obtain the observed differences in scarring rates. Given the smaller body size of dolphins in Shark Bay, these discrepancies in death rate seem unlikely. Therefore, risk of attack by sharks appears to be higher for dolphins in Shark Bay than in other locations where shark – dolphin interactions have been studied.

The annual attack rate on dolphins in Shark Bay also supports the hypothesis that predation risk is high. The unsuccessful attack rate, in Shark Bay, of at least 11-13% of dolphins in the study area attacked each year is substantially greater than the 0.8% annual attack rate estimated for Sarasota (Urian et al. 1998). With this high attack rate in Shark Bay, more than one attack per dolphin is expected over the course of a 20-30 year life span. Given that some scars disappear over time, this attack rate seems reasonable based on the observation of 1.4 scars/dolphin.

The attack rate measured by wounds on dolphins should underestimate the actual rate of shark predation attempts on dolphins since wounds are only evidence of failed predation attempts. In South Africa, where the scar frequency is between 10% and 19%, Cockcroft et al. (1989) estimated that up to 2.2% of the bottlenose dolphin population is killed by sharks each year. Due to dolphin body size differences and the high large shark densities in both locations, it is possible that more dolphins are killed by sharks each year in Shark Bay than in South Africa even if a slightly greater proportion of attacks are successful in South Africa.

Few age/sex differences in scarring rate were observed. However, more adult males bore multiple scars than did adult females. Heithaus (in press a, Chapter 2) suggested that different age/sex classes of dolphins may differ in their responsiveness to predation risk. This hypothesis is supported by the findings of the present study as well as Urian et al.'s (1998) finding that male dolphins in Sarasota had a higher scarring rate than female dolphins and males tended to accumulate scars over their lives while females did not. Behavioral differences between male and female dolphins, in the presence of sharks, have been documented in Moreton Bay where female dolphins appear to avoid close proximity to sharks while males are less evasive (Corkeron et al. 1987a).

Tiger sharks were the most common large shark caught in the study area during shark research fishing, especially in warm months (Heithaus in press b, Chapter 5). Furthermore, during warm months other potential dolphin predators were not captured. The finding that dolphins were attacked almost exclusively during warm months and that tiger sharks were responsible for bites from large sharks when the attacker could be identified supports the conclusion that tiger sharks are the largest predation threat to dolphins in Shark Bay. Despite this, dolphins are not a major food item of tiger sharks, and are rarely found in their stomachs (Simpfendorfer et al. in press, Heithaus in press b). This raises several questions. 1) Are attacks truly predatory in nature or do they actually represent aggressive competition? 2) Why do tiger sharks attack dolphins if they are rarely successful? 3) If tiger sharks are rarely successful predators, is dolphin behavior likely to be influenced by the risk of tiger shark attack? First, large tiger sharks and dolphins in Shark Bay show low dietary overlap (Simpfendorfer et al. in press, Heithaus in press b, Chapter 5) so attacks are unlikely to be related to competition. Second, dolphins represent a high quality prey item. Thus, there is a large benefit to a shark if an attack is successful, and even if an attack is unsuccessful, the shark is likely to realize some energetic gain by removing blubber. Finally, predatory attacks do not have to be successful frequently to have a large influence on prey behavior (e.g. Lima 1998). Therefore, dolphin behavior (e.g. habitat use, group size selection) may be influenced by the risk of attack from tiger sharks even if the mortality rate from such attacks is low.

A comparison of the distribution of shark sizes attacking dolphins with that of sharks caught on drumlines shows that larger tiger sharks are more likely to attack dolphins than are smaller tiger sharks. In general, tiger sharks under 2.75 m rarely attack dolphins and tiger sharks under 3.0 m are unlikely to pose a major predation risk to non-calf dolphins in Shark Bay. The finding that very large (> 4.0 m) tiger sharks left scars on dolphins relatively less often than other large size classes may be due to higher successful attack rates by the largest sharks or their relatively low abundance in the study area. The differences observed in average bite size on juvenile and adult dolphins suggests either that smaller sharks are capable of attacking smaller dolphins and/or larger sharks attacking juveniles are more likely to succeed in their predation attempt (leaving fewer scarred survivors).

The distribution of bites found on dolphins was not random. In general, there were fewer scars found on the ventral body surface than either the dorsal or lateral surfaces and scars were concentrated on the body trunk area. This is surprising considering that most shark attacks on cetaceans appear to be directed posteriorally and ventrally. For example, Long and Jones (1996) found that most white shark attacks on living odontocetes occurred in the tail/peduncle and ventral zones. The observed scarring pattern in Shark Bay is probably due to a combination of factors including the possibility that dolphins, when attempting to evade a shark attack, are likely to turn their back toward a shark to reduce the probability of exposing their more vulnerable ventrum. Also, sharks that manage to attack a dolphin's ventrum, head, or tail are likely to be more successful in a predation attempt than one attacking dorsal or trunk areas. Thus, fewer scars would be found in ventral and posterior zones despite more attacks being directed towards these zones.

The observation of bites from sharks under 1.5 m TL and the presence of bites from small sharks out of the pectoral fins of several dolphins raises the possibility that some small carcharhinid sharks are dolphin parasites. These attacks are certainly not predation attempts as small sharks would not be able to kill even a young dolphin. Dolphin blubber, however, is a high-quality food item and sharks may occasionally attack dolphins to gain small, high-quality meals. Such behavior would be considered parasitic since predation requires that a prey item is killed (Ricklefs 1990). "Ectoparasitic" behavior is found in deep sea sharks including the cookie-cutter shark (*Isistius brasiliensis*) (Jones 1971, Norris and Dohl 1980b), and Portuguese dogfish (*Centroscymmus coelolphis*) (Clarke and Merrett 1972, Mauchline and Gordon 1983) which gouge mouthfuls of flesh from deep-diving cetaceans. Apparent ectoparastic behavior has been observed on at least one occasion when a small shark (<1.3 m) made repeated rushes at an adult male dolphin which continually evaded the attacks. The possibility that small caracharhinid sharks are cetacean ectoparasites warrants further investigation.

This study has shown that predation risk from sharks appears to be higher in Shark Bay than in other locations. Detailed studies of social behavior underway in various locations should allow comparative studies of dolphin social behavior and ecology in areas of low (e.g. Adriatic Sea), moderate (e.g. Sarasota, Moreton Bay) and high (e.g. Shark Bay) shark predation risk. Such comparative studies would be of great value as they would help to elucidate the role of predation risk in shaping patterns of sociality, distribution, and behavior.

4.6 ACKNOWLEDGEMENTS

I would like to thank Lynne Barre, Justin Mclash, Jenny Burghardt, Larry Dill, Seana Buchanan, Colby Genrich, Patrick Greene, Doro Heimier, and Hugh Finn for help during field research. Sheldon Dudley, Geremy Cliff, and Vic Peddemors helped me obtain jaw width – total length relationships and members of the Shark Bay Dolphin Research Group helped provide age/sex class data. Ian Hamilton, Larry Dill, Bernie Crespi, Bernie Roitberg, Ray Heithaus, and two reviewers provided helpful comments on a previous version of this manuscript. Grants and support were provided by NSERC Canada grant A6869 to L.M. Dill, National Science Foundation, the American Museum of Natural History, Monkey Mia Dolphin Resort, Mercury Marine, Shakespeare Electronics, Kodak Australia, Singapore Airlines, and public donations. A portion of this research was made possible by a Shane Award from the Society for Marine Mammalogy. This research was carried out while I was a visiting research associate at the Department of Anatomy and Human Biology (University of Western Australia) and under the authority of Department of Conservation and Land Management permits DI000044 and NE001649 and Simon Fraser University Animal Care permit.

4.7 LITERATURE CITED

Bearzi, G., G. Notabartolo-di-Sciara and E. Politi 1997. Social ecology of bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). Marine Mammal Science 13:650-668.

Clarke, M. R. and N. Merrett. 1972. The significance of squid, whale and other remains from the stomachs of bottom-dwelling deep-sea fish. Journal of the Marine Biological Association, U.K. 52:599-603.

Cockcroft, V. G. 1991. Incidence of shark bites on Indian Ocean hump-backed dolphins (*Sousa plumbea*) off Natal, South Africa. Report to the International Whaling Commisson, Special Issue 12:277-282.

Cockcroft, V. G., G. Cliff and G. J. B. Ross. 1989. Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. South African Journal of Zoology 24:305-310.

Connor, R. C., R. A. Smolker and A. F. Richards. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). Proceedings of the National Academy of Sciences, USA 89:987-990.

Connor, R. C. and M. R. Heithaus. 1996. Great white shark approach elicits flight response in bottlenose dolphins. Marine Mammal Science 12: 602-606.

Connor, R. C., M. R. Heithaus and L. M. Barre. 1999. Superalliance of bottlenose dolphins. Nature 397:571-572.

Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. Pages 91-126 *in* Cetacean Societies: Field Studies of Dolphins and Whales. J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead, editors. University of Chicago Press, Chicago.

Corkeron, P. J., R. J. Morris and M. M. Bryden. 1987a. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. Aquatic Mammals 13:109-113.

Corkeron, P. J., R. J. Morris and M. M. Bryden. 1987b. A note on healing of large wounds in bottlenose dolphins. Aquatic. Mammals 13:96-98.

Heithaus, M. R. in press a. Predator-prey and competitive interactions between sharks and cetaceans: a review. Journal of Zoology, London: in press.

Heithaus, M. R. in press b. The biology of tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes: in press

Jones, E. C. 1971. *Isistius brasiliensis*, a squaliod shark, the probable cause of crater wounds on fishes and cetaceans. Fishery Bulletin US 69:791-798.

Last, P. R. and J. D. Stevens. 1994. Sharks and Rays of Australia. CSIRO: Australia.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25-34.

Long, D. J. and R. E. Jones. 1996. White shark predation and scavenging on cetaceans in the eastern north Pacific Ocean. Pages 293-307 *in* Great White Sharks: The Biology of Carcharodon carcharias. A. P. Klimley and D. G. Ainley, editors. Academic Press, New York.

Mauchline, J. and J. D. M. Gordon. 1983. Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology 75:269-278.

Norris, K. S. 1994. Predators, parasites, and multispecies aggregations. Pages 287-300 *in* The Hawaiian Spinner Dolphin. K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, editors. University of California Press, Berkeley.

Norris, K. S. and T. P. Dohl. 1980a. The structure and function of cetacean schools. Pages 211-261 *in* Cetacean Behavior: Mechanisms and Functions. L. M. Herman, editor. Wiley, New York.

Norris, K. S. and T. P. Dohl. 1980b. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin US 77:821-849.

Randall, J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Australian Journal of Marine and Freshwater Research 43:21-31.

Ricklefs, R. F. 1990. Ecology. W. H. Freeman & Co., New York.

Ross, G. J. B. and V. G. Cockcroft. 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). Pages 101-128 *in* The Bottlenose Dolphin. S. Leatherwood and R. R. Reeves, editors. Acedemic Press, New York.

Simpfendorfer, C. A., A. B. Goodreid and R. B. McAuley. in press. Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes: in press.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W, Pepper. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38-69.

Urian, K. W., R. S. Wells, M. D. Scott, A. B. Irvine, A. J. Read and A. A. Hohn. 1998. When the shark bites: an analysis of shark bite scars on wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, Florida. The World Marine Mammal Science Conference, Abstracts (Monaco, 20-24 January): 139.

Wells, R. S., A. B. Irvine, and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pages 263-317 *in* Cetacean Behavior: Mechanisms and Functions. L. M. Herman, editor. Wiley, New York.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 *in* Current Mammalogy, Volume 1. H. H. Genoways, editor. Plenum Press, New York.

Wells, R. S. 1991. Bringing up baby. Natural History. August:56-62.

Wood, F. G. Jr., D. K. Caldwell and M. C. Caldwell. 1970. Behavioral interactions between porpoises and sharks. Investigations on Cetacea 2:264-277.

CHAPTER 5

The Biology of Tiger Sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: Sex Ratio, Size Distribution, Diet, and Seasonal Changes in Catch Rates[*]

*A version of this manuscript appears as Heithaus, M. R. 2001. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes: in press. Reprinted with kind permission from Kluwer Academic Publishers.

5.1 ABSTRACT

Tiger sharks, *Galeocerdo cuvier*, are apex predators in a variety of nearshore ecosystems throughout the world. This study investigates the biology of tiger sharks in the shallow seagrass ecosystem of Shark Bay, Western Australia. Tiger sharks ($n = 252$) were the most commonly caught species (94%) compared to other large sharks. Tiger sharks ranged from 148-407cm TL. The overall sex ratio was biased towards females (1.8:1), but the sex ratio of mature animals (>300 cm TL) did not differ from 1:1. Contrary to previous accounts, tiger sharks were caught more often in all habitats during daylight hours than nocturnally. Tiger shark catch rates were highly correlated with water temperature and were highest when water temperatures were above 19°C. The seasonal abundance of tiger sharks is correlated to both water temperature and the occurrence of their main prey: sea snakes and dugongs, *Dugong dugon*. Stomach contents analysis indicated that sea turtles and smaller elasmobranchs were also common prey. The importance of major seagrass grazers (dugongs and green sea turtles, *Chelonia mydas*) in the diet of tiger sharks suggests the possibility that these sharks are keystone predators in this ecosystem.

5.2 INTRODUCTION

Tiger sharks, *Galeocerdo cuvier*, are an apex predator in many tropical and warm-temperate ecosystems around the world (Randall 1992). Growing to sizes of 5.5 m, they are capable of consuming large-bodied prey, and have a highly varied diet that includes teleosts, elasmobranchs, birds, sea snakes, turtles, marine mammals, crustaceans, molluscs, and anthropogenic food sources (Randall 1992, Simpfendorfer 1992, Lowe et al. 1996, Simpfendorfer et al. in press). Tiger sharks exhibit ontogenetic shifts in diet (Simpfendorfer 1992, Lowe et al. 1996) where small sharks tend to consume primarily fishes and sea snakes but, as they grow, sharks diversify their diet by including larger prey items (e.g. sea turtles and marine mammals). As one of the few predators on large marine animals, tiger sharks may influence prey species behavior and population sizes (Simpfendorfer et al. in press, Chapter 9).

Previous studies have demonstrated that there is geographic variation in the diets of tiger sharks, suggesting they are capable of taking advantage of locally abundant resources. In Hawaii, tiger sharks have a broad diet; teleost fishes make up a large portion of the diet of all size classes of sharks, and marine mammals and sea turtles are relatively uncommon, even in large sharks (Lowe et al. 1996). Sea birds are the most common prey item for tiger sharks in the Northwestern Hawaiian Islands (DeCrosta et al. 1984). In contrast, sea snakes are one of the most important prey items of tiger sharks in Queensland, Australia (Simpfendorfer 1992) and New Caledonia (Rancurel and Intes 1982). Finally, in Western Australian waters, turtles and marine mammals are two of the most common prey items found in tiger sharks, but even within Western Australia there is substantial geographic variation in diets (Simpfendorfer et al. in press).

Tiger sharks are believed to migrate into higher latitudes during warm periods (Bigelow and Schroeder 1948, Stevens 1984, Randall 1992), but evidence for this is largely anecdotal. It is unclear whether these migrations are in response to thermal conditions and physiological constraints or are the result of changes in prey abundance or distribution. In general, the influence of prey availability on tiger shark movements has been overlooked although they can move relatively large distances (e.g. Kohler et al. 1998, Holland et al. 1999) and appear to take advantage of seasonally abundant food resources. For example, tiger sharks are only present in large numbers at the Houtman

Abrolhos Islands, Western Australia, during the Western rock lobster fishing season when discarded bait is an abundant food source (Simpfendorfer et al. in press).

This chapter investigates the biology of tiger sharks in the seagrass ecosystem of Shark Bay, Western Australia. It describes the influence of fishing techniques on tiger shark catches, as well as tiger shark sex ratio, size distribution, diet, seasonal abundance and site fidelity. Finally, this study is the first to investigate the influences of water temperature and prey availability on tiger shark catch rates.

5.3 METHODS

5.3.1 Study site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia (Figure 5.1a). The bay is relatively shallow throughout with extensive shallow seagrass banks (<4.0 m depth), numerous narrow, swift-current channels (6.0-12 m), and broad expanses of relatively deeper waters (6.0-15 m). Shark Bay contains the most extensive seagrass meadows reported in the world (Walker 1989) and supports a large population of tiger sharks that have not been subjected to commercial fishing pressure since 1994 (C. Simpfendorfer personal communication). Even before the 1994 commercial shark fishing ban, fishing pressure was from only a single operator whose efforts were focused in the Western Gulf (C. Simpfendorfer personal communication). The study site was located in the Eastern Gulf, offshore of the Monkey Mia Dolphin Resort (approx. 25° 45'S, 113° 44' E; Figure 5.1b). The habitats represented in the study area include seagrass shoals, channels, and open deep waters (Figure 5.1c).

Water temperature was measured at a consistent location (Figure 5.1 c), 1 m below the surface, each day at 0700. There was seasonal variation in water temperature within the study area (Figure 5.2). Water temperatures during warm months (September-May) were generally above 20° C but dropped as low as 14° C in winter months (June-August). Temperatures tended to drop rapidly in mid to late May, then increased gradually in late August. During cold months, water temperatures in the Western Gulf, and especially near Dirk Hartog Island, are considerably warmer due to a warm-water current (Cresswell 1991). "Warm" and "cold" seasons were defined based on both water temperature differences and changes in the community present in the study site (see below). For the purposes of this paper data from 1997 and 1998 were pooled due to similar conditions. The data from the cold months of 1999 are analyzed separately from those of 1997/1998 because of differences in the community present during these months. There are no differences in water temperature among habitats due to the generally shallow nature of the bay and to the water being well mixed by strong tidal currents and wind (M. R. Heithaus, unpublished data).

5.3.2 Study methods

Tiger sharks, as well as other large sharks, were captured using drumlines equipped with a single hook (Mustad Shark Hook size 12/0, 13/0, or 14/0) fished at a depth of 0.7-2.0 m. Up to ten lines, baited with approximately 2 kg of Australian salmon, *Arripis truttaceus*, were set at dawn or dusk in at least two zones (one shallow, one deep; Figure 5.1). Lines were spaced approximately 0.7 km apart and were checked every 2-4 hours. Bait presence/absence was noted on lines that did not catch sharks. Hook soak time was measured as the time from deployment until line removal. If bait was not present at a check, or a shark was caught, the bait was considered to be lost half way between the previous check (when bait was present) and the time when loss or a shark was detected.

During warm months, bait loss occurred more rapidly and at a much higher frequency in shallow habitats than in deep habitats, making it impossible to accurately measure differences in catch rates among habitats. Other factors, including potential differences in the effectiveness of odor corridors from baits and differing catch radii among habitats would make comparisons among habitats based on catch rates difficult to interpret. Therefore, habitat use by tiger sharks will not be addressed in this Chapter (see Chapter 7).

Figure 5.1. *a*) Shark Bay, Western Australia (indicated by arrow). *b)* The study area (*) was located in the Eastern Gulf of Shark Bay. *c*) Study zones are represented by black polygons. Shark fishing was not conducted in the zone west of Monkey Mia and first zone to the north of Monkey Mia. The lightest color represents shallow water (< 2m at MSLW) and successively darker colors represent waters 2-5 m, 5-7 m, 7-9 m, and >9 m. Land is black. * indicates the location of water temperature measurements. @ indicates the position of the monitoring station and the black circle represents the approximate detection range. Letters denote the habitat of zones. Several zones in deeper water contain more than one habitat. S = shoal, O = open deep water, C = channel.

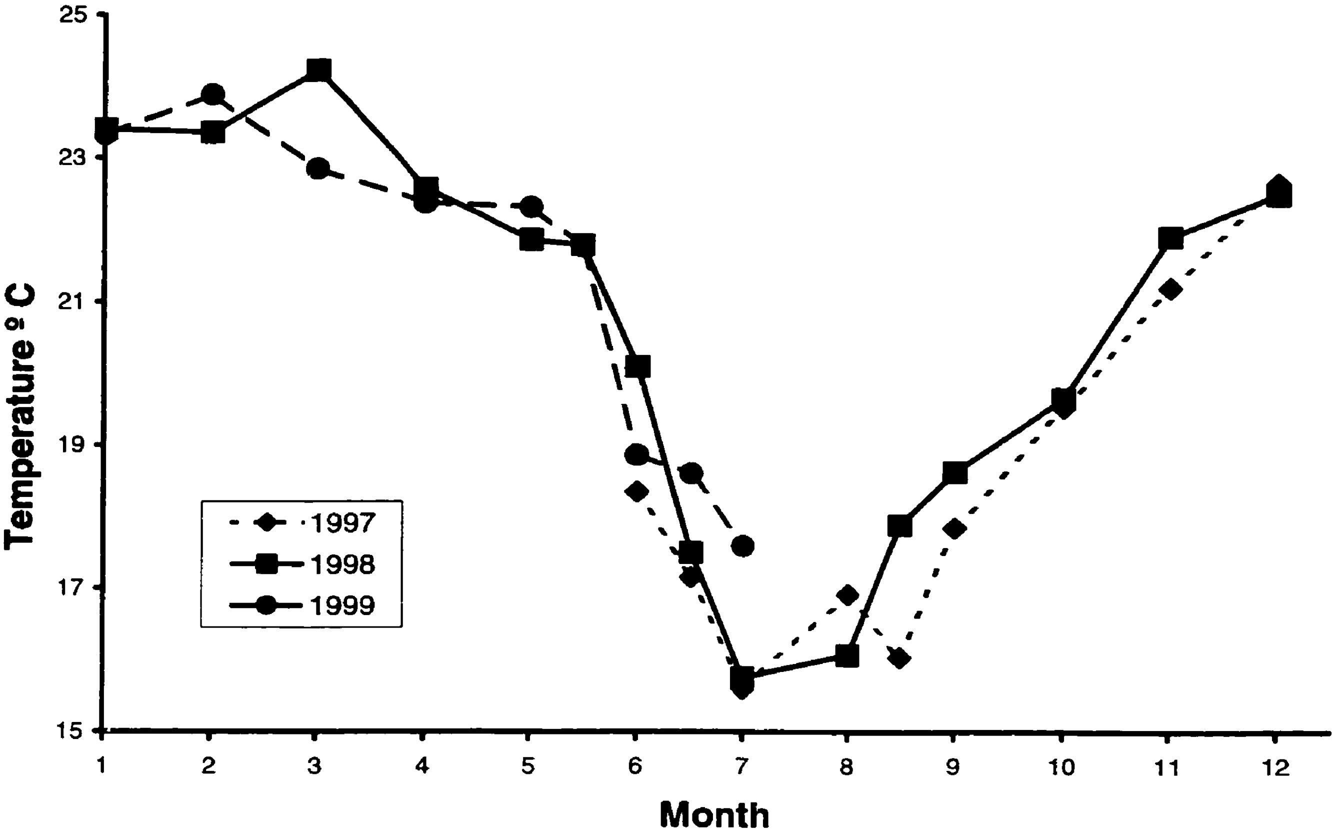


Figure 5.2. Water temperature in the Eastern Gulf of Shark Bay, offshore of Monkey Mia. Water temperatures during transitional months are given as two week means.

Once a shark was caught, it was brought alongside a 4.5 m vessel while the drumline anchor was retrieved. To minimize stress to the shark, it was allowed to swim beside the vessel while idling forward slowly. Each shark was then measured (fork length and total length), sexed, tagged (rototag in either dorsal or pectoral fin), and released. Stomach contents were collected from dead tiger sharks and when tiger sharks regurgitated next to the boat and contents could be recovered. In most cases, it was not possible to collect all regurgitated material. However, the stomach contents were considered to be completely recorded when a tiger shark fully everted its stomach next to the boat and all contents could be recovered. Only prey items that were not fully digested (e.g. fleshy material still present) were included in analyses.

Site fidelity of tiger sharks was measured with recaptures of tagged sharks and acoustic monitoring. Between March and July 1999, five male and three female tiger sharks ($\bar{x}$ = 358 cm TL, s = 20.8) were fitted with internally implanted acoustic transmitters (V32, VEMCO, Shad Bay, NS) following the methods of Holland et al. (1999). A VR20 (VEMCO) fixed-site monitoring station, with a detection range of approximately 1.5 km (M. R. Heithaus, unpublished data) was deployed inside the study area (Figure 5.1*c*) for a total of 192 days (100 warm, 92 cold). Data were downloaded every 20 - 40 days. Based on the timing of transmitter deployments and monitoring station activity, there were 692 shark days of sampling during cold months compared to 623 during warm months. Statistical analysis of detection data treated each individual as a single data point to avoid pseudoreplication.

Seasonal changes in the relative abundance of potential prey (dugongs, sea turtles, sea snakes, and sea birds) was surveyed using belt transects. Ten transects were established in various habitats (Figure 5.1) and were surveyed, from a 4.5 m boat, a total of 870 times between March 1997 and July 1999 (Table 5.1.) All turtles and sea birds at the surface within 30 m of the vessel, dugongs within 100 m, and sea snakes (1998 and 1999 only) within 5 m were recorded. Transects were only conducted in Beaufort sea state 3 or less to reduce sighting biases associated with weather conditions.

Table 5.1. Number of transects surveyed.

Season	Transects
Warm 1997	101
Cold 1997	134
Warm 1998	115
Cold 1998	170
Warm 1999	194
Cold 1999	156
Total	870

5.4 RESULTS

5.4.1 Fishing methods

As a result of low catch rates during June-August, analyses of fishing methods (i.e. hook size and bait portion) are restricted to sets in warmer months, when tiger shark catch rates were high. The portion of salmon used as bait (e.g. head, middle, or tail section) significantly influenced the probability of shark capture. Heads (0.39 sharks hook^{-1}) were significantly better for capturing sharks than were middle portions (0.22 sharks hook^{-1}) or tails (0.22 sharks hook^{-1}) ($\chi^2 = 18.2$, df = 2, $P < 0.001$). Bait retention time is probably responsible for this difference in catch rate. The average time before bait loss, on hooks that did not catch sharks, was much longer for heads ($\bar{x} = 379$ min, s = 192 min) than either middle ($\bar{x} = 290$ min, s = 196 min) or tail ($\bar{x} = 304$ min, s = 215 min, t = 4.2, df = 506, $P < 0.001$) sections. Bait retention times also varied seasonally. Average time until bait loss on hooks that did not capture sharks was much higher in winter ($\bar{x} = 578$ min, s = 269 min) than in summer ($\bar{x} = 313$ min, s = 200 min; t = 16.3 , df = 835, $P < 0.0001$). Fishes observed removing or feeding on baits included tiger sharks, other small sharks (*Carcharhinus* spp.), guitarfish (Rhynchobatidae), schools of small teleosts, and silver toadfish (*Lagocephalus scleratus*).

Hook size significantly influenced catch rates. Corrected for bait portions used for each hook size, 12/0 hooks caught significantly fewer tiger sharks than expected while 13/0 hooks performed better than expected ($\chi^2 = 7.5$, df = 2, $P < 0.05$).

Tiger sharks were caught significantly more often during diurnal sets (2941 fishing hours, 181 sharks, 0.06 sharks/hour) than nocturnal sets (769 hours, 22 sharks, 0.03 sharks/hour; $\chi^2 = 12.1$, df = 2, $P < 0.001$). This trend was evident within both shallow and deep habitats.

5.4.2 Relative abundance, size distribution, growth, maturity, and sex ratio

A total of 252 tiger sharks were caught, and accounted for 94.4 % of shark catches (n = 267). Other species of sharks were caught outside the months of peak abundance for tiger sharks (Nov-Mar), and included mako sharks, *Isurus oxyrinchus*, (n=

2), silky sharks, *Carcharhinus faliciformis* (n = 2), small dusky sharks, *Carcharhinus obscurus* (n = 2), gray reef sharks, *Carcharhinus amblyrhynchos* (n = 1), nervous sharks, *Carcharhinus cautus* (n = 2), and sandbar sharks, *Carcharhinus plumbeus* (n = 6).

Tiger sharks ranged in size between 148 and 407 cm TL (Figure 5.3). Average female total length ($\bar{x}$ = 292 cm, s = 53 cm, median = 291 cm) was smaller than that of males ($\bar{x}$ = 309 cm, s = 49 cm, median = 320 cm) (t = 2.2, df = 186, $P < 0.05$). The average size of sharks was greater in warmer months ($r^2 = 0.82$, F = 22.8, df = 6, $P < 0.01$) as small sharks (< 250 cm) were caught infrequently in the warmest months (Figure 5.4). The largest sharks in the sample (> 400 cm) were caught only during months when temperatures generally were decreasing (April and May).

Size at maturity could not be determined for females. Based on clasper calcification, males matured at approximately 300 cm TL. The smallest mature male was 298 cm while the largest immature male was 300 cm. Only seven male sharks between 290 and 305 cm were caught making a determination of precise length at maturity difficult.

Growth rates were estimated for all sharks that were recaptured (see below). Actual growth between captures and yearly growth rate estimates are given in Table 5.2. Although there are potential errors in the measurements, most sharks appear to grow at a rate of 20-26 cm per year. However, the only individual recaptured twice (2412) showed different growth rates during the two periods between recaptures (Table 5.2).

The overall sex ratio observed was biased towards females (1.8:1; $\chi^2 = 16.8$, df = 1, $P < 0.001$), but this was mainly due to an extremely skewed sex ratio of animals under 300 cm TL (2.3:1, $\chi^2 = 22.3$, df = 1, $P < 0.0001$). The sex ratio of sharks over 300 cm TL was not significantly different from 1:1 ($\chi^2 = 1.0$, df = 1, NS). There was no significant monthly variation in overall sex ratio or sex ratio of large sharks ($\chi^2 = 6.0$, df = 17, NS; and $\chi^2 = 9.0$, df = 17, p = NS, respectively).

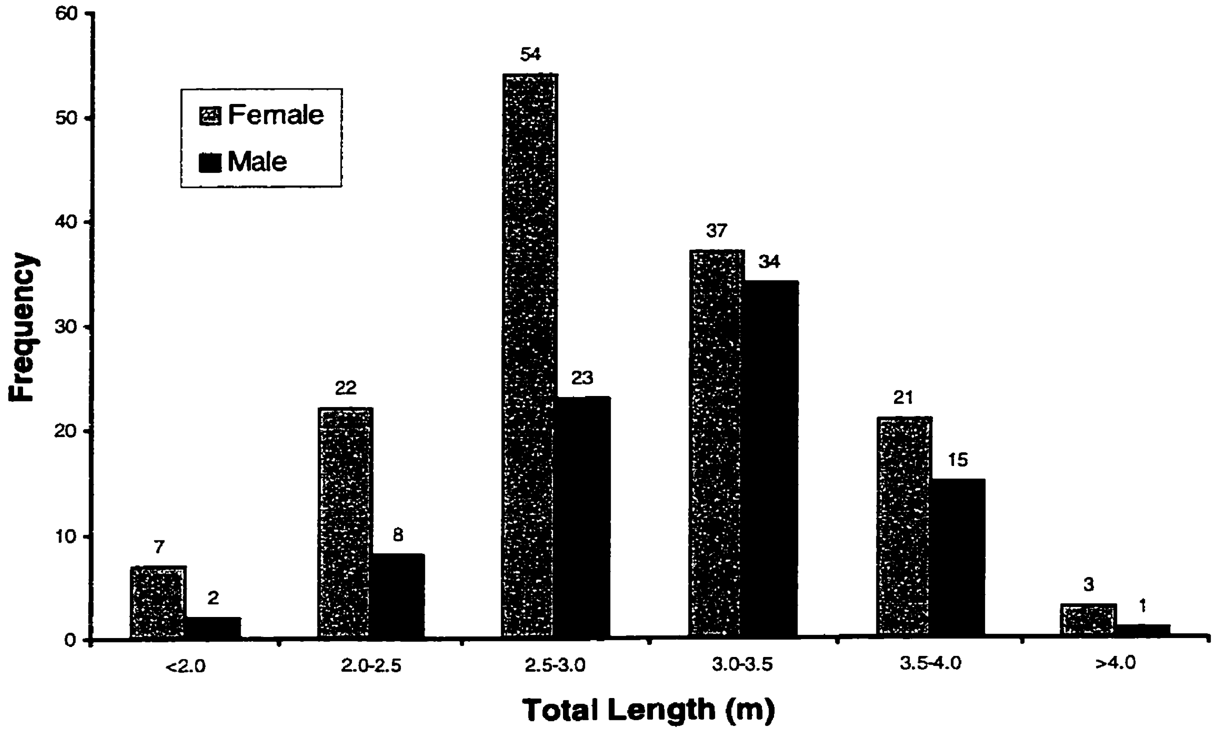


Figure 5.3. Size distribution of tiger sharks caught by drumline. Light bars are females and dark bars represent males. Note the skewed sex ratio of sharks under 3 m TL. Numbers above the bars represent sample size.

5.4.3 Seasonal abundance

There were significant seasonal changes in catch rates within the study area. Tiger shark catch rate was extremely high in warm months but low from June through early August (1997/1998: $\chi^2 = 163.6$, df = 10, $P < 0.0001$, 1999: $\chi^2 = 60.1$, df = 5, $P < 0.0001$; Figure 5.5, 5.6). However, tiger sharks were caught more often in June/July 1999 than the same period in 1997/1998 when catch rates were extremely low ($\chi^2 = 22.0$, df = 2, $P < 0.0001$). In contrast, there was no significant difference in catch rates among years during warm months ($\chi^2 = 2.9$, df = 2, NS).

There was a significant correlation between tiger shark catch rate and water temperature (Figure 5.5; $r = 0.86$, $F = 13.3$, df = 15, $P < 0.001$). Tiger shark catch rate dropped rapidly at a sea surface temperature of approximately 21-22° C in late May, and by early June 1998 (20° C), tiger sharks were almost never caught (Figure 5.6). Tiger shark catches picked up rapidly in late August, when the temperature had risen to between 16° C (1997) and 17° C (1998). Patterns of tiger shark catch rate were somewhat different in 1999. Water temperatures began to decrease in late May, as did catch rates. Despite a greater decrease in water temperature in early June, tiger sharks were still caught, although in reduced numbers. In July, the average temperature was slightly below 18° C and tiger sharks could still be caught.

5.4.4 Site fidelity and Recaptures

Sixteen tagged tiger sharks were recaptured (6.3%) within the study area after 0 – 491 days at liberty (Table 5.2). Additionally, 6 tiger sharks were recaptured that had obviously shed tags, yielding a minimum recapture rate of 8.7%. One 340 cm TL male tiger shark was recaptured ten days after release by a shark fishing vessel on an offshore coral bank (135 m depth) in the Indian Ocean (27° 13.72' S, 113° 6.74' E) over 150 km southwest of Monkey Mia (minimum swimming distance approximately 280-320 km). Another, female, tiger shark (215 cm TL) was captured by a prawn trawler in the Western Gulf of Shark Bay (25° 43' S, 113° 17' E) 148 days after release.

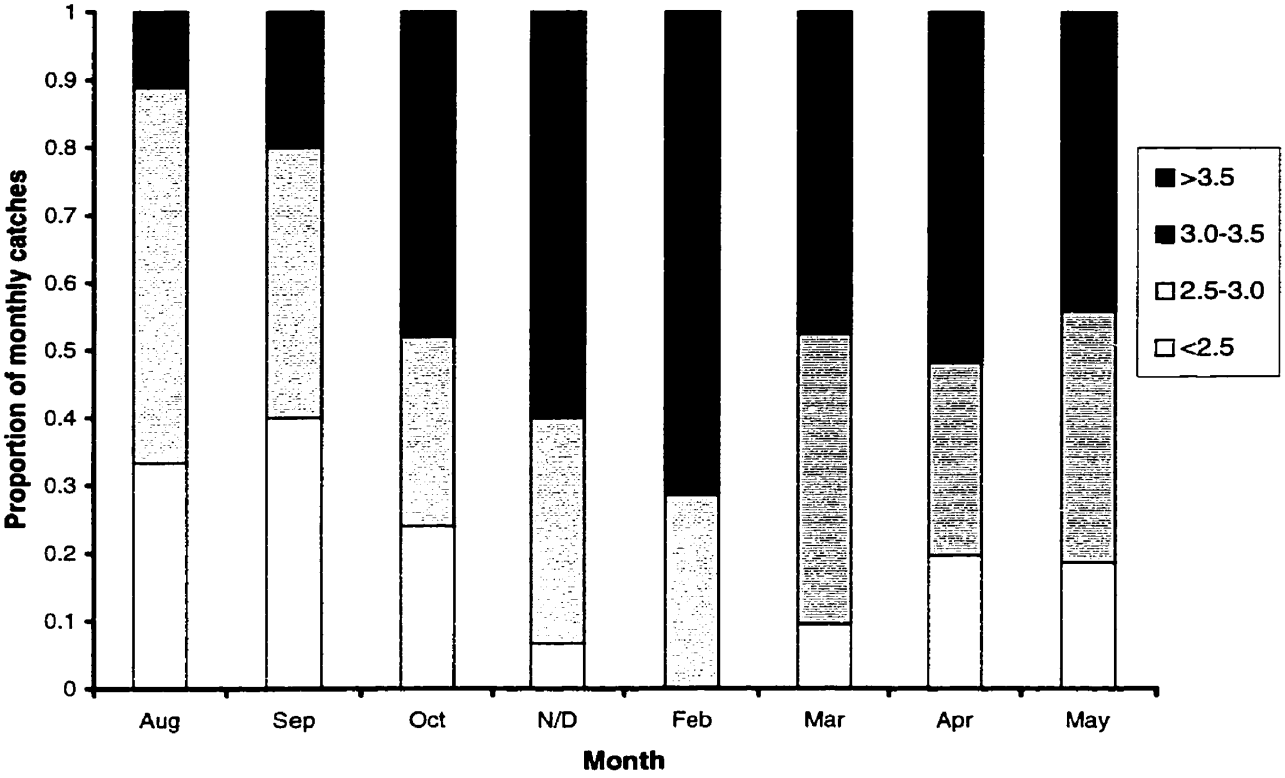


Figure 5.4. Seasonal changes in the relative abundance of shark size classes. The proportion of small sharks caught decreases dramatically in the warmest months. November and December data are combined due to a low sample size in December.

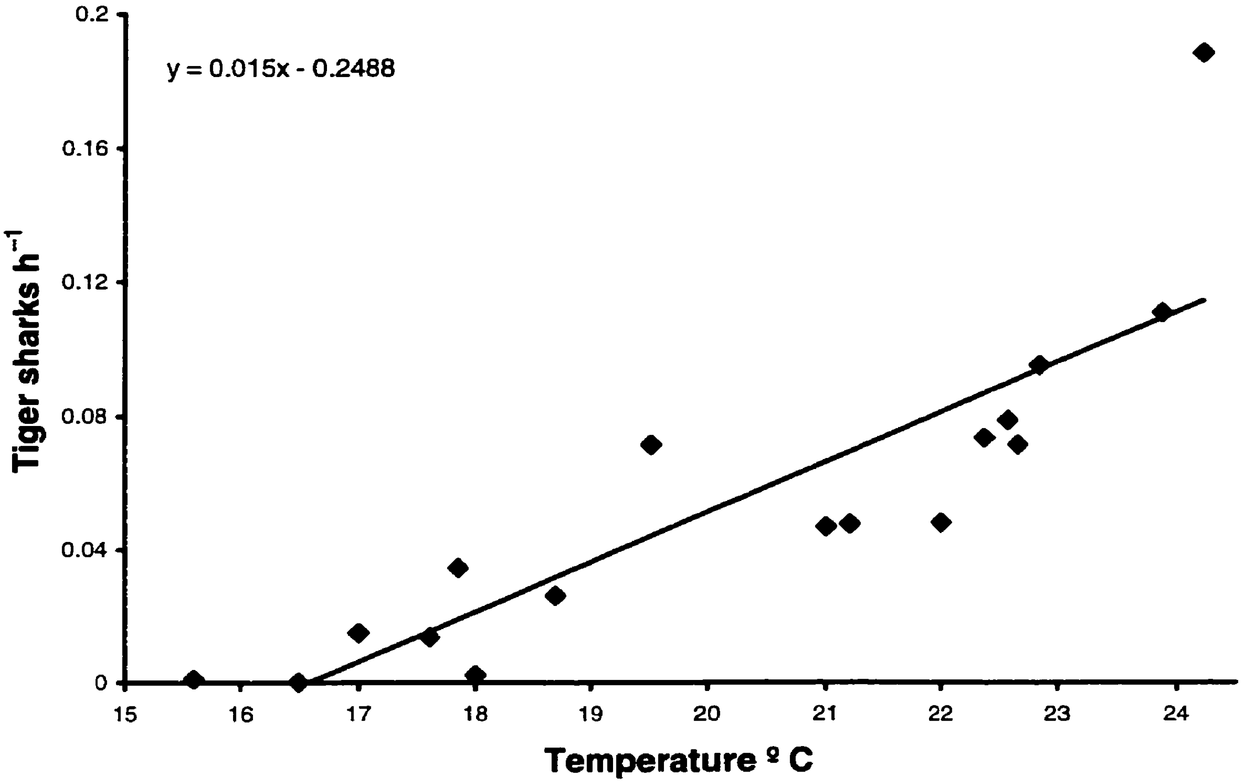


Figure 5.5. Correlation between water temperature and catch rate. Tiger shark catch rate is significantly influenced by water temperature ($r = 0.86$, $F = 13.3$, $df = 15$, $P < 0.001$).

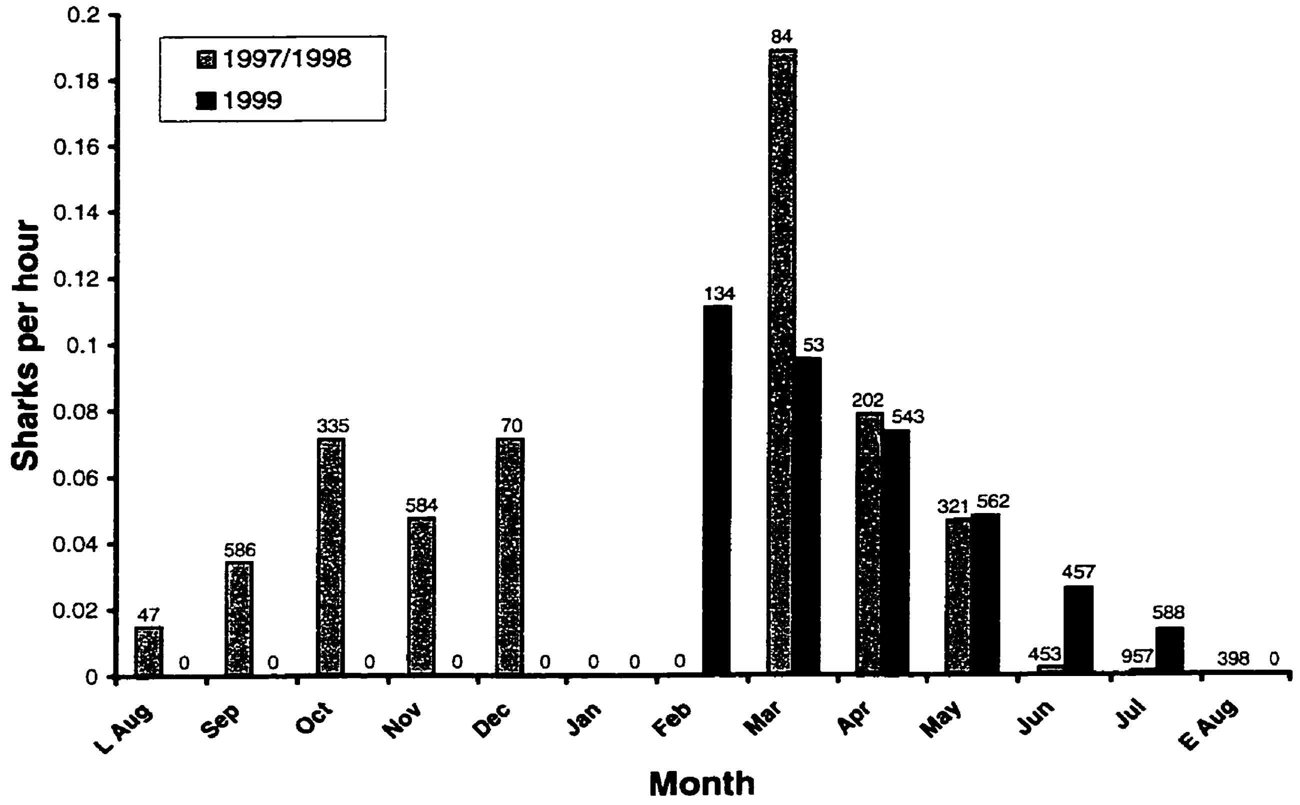


Figure 5.6. Seasonal changes in shark catch rates. Tiger shark abundance is very high in the warmest months of the year and lower during colder months. There is interannual variation in catch rates during cold months. Note the increase in catch rate in late August. Light bars are from 1997 and 1998. Dark bars are from 1999. Fishing hours are given above bars.

Three male and two female tiger sharks (62.5%) fitted with internal transmitters were detected by the monitoring station after 12 to 207 days at liberty. Three sharks were detected once, one three times, and one seven times. The season of detections was not random (χ^2 = 13.5, df = 4, P < 0.01) with all sharks detected during warm months. Both sharks that were detected on multiple occasions were detected at least once after an intervening cold period, as was one of the single detections.

5.4.5 Diet

Stomach content data were obtained for 15 sharks between 213 – 389 cm TL (Table 5.3). Complete stomach contents were obtained from four necropsies and four sharks that everted their stomachs. Dugongs were found in 7 sharks (47%), and in all sharks for which complete contents were obtained with the exception of a 213 cm individual. However, 6 (86%) contained less than 1 kg of dugong flesh. No dugong bones were recovered. Sea snakes, primarily *Hydrophis elegans*, were the most commonly represented prey item, occurring in 9 sharks (60%), but snakes were only found in 5 sharks with complete contents (62%). Sea turtles were another commonly represented prey item, found in 4 sharks (27%). Unlike dugongs and sea snakes, turtles were only found in sharks over 299 cm, and several sharks had eaten more than one turtle. Turtle bone or shell was found in all four sharks that had consumed turtles. Teleosts (garfish (Hemirhamphidae), toadfish (Diodontidae), and unidentified fishes) were only found in the smallest shark in the sample. Elasmobranchs (black stingray, *Dasyatis thetidis*, n = 2 and guitarfish, Rhinobatidae, n = 1) were the only other prey group represented by more than one item. One tiger shark stomach contained bird remains that could not be identified to the species level.

5.4.6 Prey availability

The number of turtles did not vary seasonally inside the study area in 1997 (χ^2 = 0.4, df = 1, NS) or 1998 (χ^2 = 2.2, df = 1, NS), but in 1999, turtle density in cold months was approximately half that observed during warm months (χ^2 = 31.0, df = 1, P <0.001; Table 5.4). Dugongs were much more abundant in the study area during warm months in

Table 5.2. Recaptures of tiger sharks in the Eastern Gulf of Shark Bay. In the case of multiple recaptures, capture date indicates the most recent capture of a shark before recapture. TL1 = total length (cm) at capture date, TL2 = total length at recapture date. Distances are rounded to the nearest 0.5 km. There was one additional recapture of a 353 cm male in May 1998, but the tag number could not be read. E = estimated length

Tag	Sex	Capture	Recapture	Days	TL1 (cm)	TL2 (cm)	Growth (cm)	Growth/yr (cm)	Distance (km)
2282	F	17 Mar 98	25 Mar 98	8	290	290	0	-	3.0
2296	F	13 Oct 97	19 Nov 97	37	374	-	-	-	4.5
2412	M	20 Oct 97	25 Mar 98	146	342	350	8	20	4.5
2412	M	25 Mar 98	13 Mar 99	353	350	361	11	12	3.0
3346	M	22 Oct 97	3 May 98	184	356	368	12	24	7.0
3347	M	19 Oct 97	23 Feb 99	491	280	315	35	26	1.5
3356	M	19 Oct 97	17 Mar 98	139	338	E340-350	-	-	3.5
3447	F	24 May 99	24 May 99	0.1	302	302	0	-	1.0
3490	F	15 Jun 99	26 Jun 99	11	268	269	1	-	0.5
3702	M	25 Mar 98	30 Mar 98	5	282	282	0	-	2.5
3712	F	8 Apr 98	25 Feb 99	323	299	322	23	26	3.0
3719	M	22 Apr 98	8 May 99	380	259	286	27	26	1.5
3735	F	6 May 98	19 Jun 98	44	393	394	1	-	0.0
3744	F	24 Aug 98	4 Apr 99	219	294	310	16	27	3.5
4161	M	23 Nov 97	25 Mar 98	123	351	360	9	26	3.5

Table 5.3. Stomach contents of tiger sharks from the Eastern Gulf of Shark Bay. Stomach contents were obtained through either necropsies or collection of regurgitated material. Stomach contents were considered to be complete if a shark fully everted its stomach and all items could be collected. Numbers in each prey column represent the minimum number of individual prey items in each shark. C = All macroscopic stomach contents collected (Y or N), D = dugong, S = sea snake, T = sea turtle, F = teleost, B = bird, E = elasmobranch.

TL	Sex	Obtained	C	D	S	T	F	B	E	Other
213	F	Necr.	Y				4			Squid
253	F	Evert	Y	1	1					
254	F	Evert	Y	1	1					
262	M	Evert	N		1					
265	F	Evert	N		1					
273	M	Evert	N		1					
280	M	Evert	N						1	
299	F	Evert	Y	1	1	2				
303	F	Necr.	Y	1	1					
308	F	Necr.	Y	1		1		1		
314	F	Evert	N		1					
320	M	Evert	Y	1	1	1				
340	F	Evert	N							Burley
367	F	Evert	N						1	
389	F	Necr.	Y	1		2			1	

all years (1997: $\chi^2 = 58.2$, df = 1, $P < 0.0001$; 1998: $\chi^2 = 93.0$, df = 1, $P < 0.001$; 1999: $\chi^2 = 41.4$, df = 1, $P < 0.0001$; Table 5.4) and were largely absent between late May and mid August of 1997 and 1998. Dugong abundance began to increase in late August of both years. In 1999, dugongs were present throughout the cold months and dugong density was greater than that of the cold months of 1997 and 1998 ($\chi^2 = 27.5$, df = 2, $P < 0.001$).

In 1998, sea snake (primarily *Hydrophis elegans*) abundance was high during warm months but very low during cold months ($\chi^2 = 24.5$, df = 1, $P < 0.001$; Table 5.4) when only one sea snake was observed (in late August). In 1999, sea snake abundance was higher in the warm months than in the cold months ($\chi^2 = 25.9$, df = 1, $P < 0.001$), but snakes were observed in the study area throughout June and July in densities greater than in cold months of 1998 ($\chi^2 = 12.4$, df = 1, $P < 0.001$).

Pied cormorants (*Phalacrocorax varius*) are the dominant sea birds in the study area, accounting for more than 99% of all sea bird sightings. Cormorants are found in the study area year round, but are approximately 30% more abundant during cold months (1997: $\chi^2 = 5.68$, df = 1, $P < 0.05$; 1998: $\chi^2 = 18.5$, df = 1, $P < 0.001$; 1999: $\chi^2 = 19.4$, df = 1, $P < 0.001$).

Table 5.4. Density (sightings km^{-2}) of tiger shark prey species.

Year	Season	Dugongs	Sea snakes	Turtles	Birds
1997	Warm	0.22	-	0.25	1.9
	Cold	0.01	-	0.23	2.7
1998	Warm	0.17	0.43	0.26	1.5
	Cold	0.005	0.01	0.27	2.4
1999	Warm	0.21	0.65	0.33	1.6
	Cold	0.06	0.15	0.16	2.1

5.5 DISCUSSION

Both hook size and type of bait had a significant influence on tiger shark catch rates. This has important implications for comparative studies of sharks as studies which employ different fishing methods may not be comparable. Also, when conducting studies across seasons or years, it is important to correct for differences in fishing methods. Shark catch rates were also significantly influenced by the time of day fishing occurred with significantly higher catches of tiger sharks during the day. The tiger shark has generally been considered nocturnal, moving inshore to feed in shallow waters at night, but these conclusions are drawn largely from anecdotal observations by fishermen (e.g. Randall 1992). Studies of tiger sharks in Hawaii suggested that small sharks feed primarily during the night, while large sharks feed at all times (Lowe et al. 1996). The present study suggests that, in Shark Bay, tiger sharks are not primarily nocturnal. Further studies will be required to determine tiger shark diel behavior.

The prevalence of large sharks caught during this study suggests that the Eastern Gulf of Shark Bay is a commonly used habitat for mature sharks of both sexes. The reason for the variation in sex ratio between small (<300 cm) and large (>300 cm) sharks is unclear. The heavy skew towards females in small size classes and an even sex ratio of larger sharks suggests that there is either differential mortality of females, compared to males, just before maturity or, more likely, there is spatial segregation of male shark size classes. Size segregation in tiger sharks has been suggested previously (Lowe et al. 1996), but this study suggests that the segregation could be sex-biased. Tiger sharks are known to cannibalize other tiger sharks (Compagno 1984), and size segregation could be due to small sharks avoiding larger sharks to minimize predation risk. However, if cannibalism were the cause for size-segregation, all juvenile sharks should avoid adults, not just males.

Site fidelity of tiger sharks is largely unknown. Several tiger sharks tagged off the coast of Florida were recaptured within 20 miles of their tagging site 1-1.5 years later (Randall 1992). In Hawaii, up to 25 % of tiger sharks tagged were found to return to the location where they had been captured previously (Holland et al. 1999). In Shark Bay, the recapture rate is lower (6-9%), but underestimates the proportion of sharks that show site fidelity as 62.5% of sharks with internal transmitters returned to the study area. The discrepancy in return rates may be due to the greater sampling efficiency of acoustic monitoring which continuously monitors for the presence of individuals in the area while fishing is conducted over a shorter time scale and requires animals to encounter baits, attack baits, and be hooked. Tiger sharks appear to show site fidelity over short and long time periods. Some individuals remain in the study area for extended periods during warm months, as four individuals were recaptured within two weeks of initial capture and 70% of detections occurred during a single warm period. Both acoustic detections and recaptures suggest that tiger sharks also return to the study area after a prolonged absence with individuals either recaptured or acoustically detected after an intervening period of cold water.

Simpfendorfer et al. (in press) found that teleosts and sea snakes were the most common prey items of tiger sharks in Shark Bay, followed by sea turtles and dugongs. This study indicates a higher frequency of occurrence of dugongs in the diet of tiger sharks. Although differences in occurrence of small prey were detected, this may be due to sampling differences (i.e. necropsy vs. predominantly regurgitation). However, the difference in the occurrence of large prey cannot be explained by sample bias, and observed differences may be largely due to differences between sample areas within Shark Bay. Simpfendorfer et al. (in press) sampled primarily in the Western Bay and in the oceanic waters bordering the Bay. These areas are characterized by both rock and coral habitats while the Eastern Bay is dominated by seagrass habitats. These habitat differences probably lead to large differences in prey avaliability (e.g. dugongs and sea turtles associated with their food source, seagrass) which could explain the differences in diet within Shark Bay.

Despite the small sample size, the relative importance of dugongs in the diet of sharks is noteworthy. Most (86%) sharks contained less than a kilogram of dugong and it is unclear whether they are active predators on dugongs or if they largely scavenge carcasses. However, the availability of dugongs carcasses is likely too low to account for the high frequency of dugong occurrence in the diets of tiger sharks in both the Eastern and Western Gulf (Simpfendorfer et al. in press), suggesting that, while tiger sharks will scavenge dugongs, they are probably also active predators.

Tiger shark predation may be important in regulating the dugong and turtle populations in Western Australia (Simpfendorfer et al. in press), including Shark Bay. Green turtles and dugongs are seagrass grazers (e.g. Lanyon et al. 1989) and have the potential to influence the standing stock of seagrass (Preen 1995, de Iongh et al. 1995) which provides the foundation for much of the Shark Bay ecosystem (Walker 1989). Therefore, if tiger sharks influence dugong and turtle populations, it is possible that tiger sharks are a keystone predator (Paine 1966) through trophic interactions. The possibility that tiger sharks are a keystone predator in seagrass ecosystems should be a subject of future research.

Tiger shark catch rates were much higher during warm months than during cold months. This result cannot be explained by differences in bait retention time in warm and cold months as baits stayed on hooks significantly longer during winter. Analysis of the relative importance of water temperature and prey availability in determining tiger shark abundance is difficult, as seasonal trends are similar; however, neither water temperature nor overall prey availability alone adequately explains seasonal changes in tiger shark catches. A thermal constraint does not appear to be the sole determinant of tiger shark catch rates. First, several tiger sharks were captured when the water temperature (15° C) was close to the minimum recorded. Also, tiger sharks were still being caught during July 1999 when water temperatures were 2° C colder than those of June 1998 when sharks were not caught.

Overall prey availability also does not seem to explain changes in tiger shark catch rates. During the times that tiger sharks are not caught, there are still food resources present. Turtle density generally does not change seasonally and seabird abundance increases once tiger shark catch rates have decreased. Furthermore, the cold season with the highest shark catch rates (1999) was the only year in which turtle abundance declined in the cold months. However, aerial surveys by Preen et al. (1997) found that turtle density was higher in waters greater than 18° C in Shark Bay. It is possible that, although turtle density does not change in the study area there is an increase in numbers in the Western Gulf in winter, resulting in greater food resources for tiger sharks than the Eastern Gulf.

The importance of dugongs and sea snakes in the diet of tiger sharks in Shark Bay may provide insight into the seasonal changes in shark catch rates. Changes in tiger shark catch rates closely coincide with both the departure and arrival of dugongs and sea snakes in the study area, and it is possible that tiger shark movements are in response to movements of these important, high quality prey resources. Dugongs (for large sharks) and sea snakes are probably the most energetically profitable prey items for tiger sharks in the study area. Due to differences in swimming speed and maneuverability, sea snakes probably require relatively little energy expenditure during prey capture compared to fast-swimming teleosts. Also, dugongs provide a fat-rich food source superior to turtles which require tiger sharks to ingest a large amount of indigestible material (e.g. bone and shell). During winter months, dugongs move to deeper waters north of the study area and congregate along the warmer waters of Dirk Hartog Island where there is also an abundance of turtles, teleosts, and sea snakes (Preen et al. 1997, MRH personal observation). The possibility that tiger sharks are moving in response to changes in dugong distribution is supported by a significant correlation between large dugong groups and large sharks along Dirk Hartog Island in aerial surveys of Shark Bay in winter (Anderson 1982). Further support comes from data collected in June/July 1999 when sea snakes and dugongs were still present (albeit in lower densities), and tiger sharks were caught as well.

Another possibility is that shark movements are driven by changes in prey availability in an area far removed from Shark Bay, and sharks are leaving to take advantage of a seasonally abundant resource elsewhere. Given the long distance movement of at least one Shark Bay tiger shark, this is a possibility. Future studies involving shark fishing near dugong concentrations at Dirk Hartog Island in winter, satellite tracking of tiger sharks and studies of dugong movements should shed light on the extent of shark seasonal movements and provide insight into the factors underlying them.

One critical assumption of this study is that catch rates effectively measure the abundance of tiger sharks in the study area and thus that reductions in catch rates indicate movements out of the study area. It is possible that low catch rates reflect lower feeding rates of tiger sharks rather than actual changes in abundance. Several observations independent of catches argue against this possibility. First, tiger sharks have been captured during periods of low water temperature indicating that feeding is not entirely suspended at low temperatures. Second, free-swimming tiger sharks (tagged and untagged) were only sighted during warm months. Finally, no detections were made of acoustically tagged sharks during cold months despite a larger sample. Based on these lines of evidence, there is strong support for the hypothesis that catch rates in Shark Bay are a true reflection of tiger shark abundance. Therefore, this study suggests that seasonal fluctuations in the abundance of tiger sharks in a subtropical seagrass ecosystem are not exclusively explained by variation in water temperature, and appear to be linked to movements of high quality prey species. Also, individual sharks show site fidelity to the study area over both short and long time periods, and a large portion of sharks may use this seagrass habitat repeatedly.

5.6 ACKNOWLEDGMENTS

I thank Colin Simpfendorfer and Rory McAuley for their help in initiating this project by providing bait, fishing gear and advice. Chris Lowe, Larry Dill, and the crew of the Fisheries Western Australia R/V Flinders also provided advice. Lynne Barre, Jenny Burghardt, Justin McLash, Colby Genrich, Seana Buchannan, Patrick Greene, Scott Burghardt, Ian Hamilton, Hugh Finn and Larry Dill provided field assistance. Grants and support were provided by National Geographic Expeditions Council, National Geographic Special Projects, NSERC Canada grant A6869 to L.M. Dill, National Science Foundation, PADI Foundation, the Columbus Zoo, Australian Geographic, Monkey Mia Wildlife Sailing, Monkey Mia Dolphin Resort, Mercury Marine, Shark Bay Fish Factory, Tradewids Supermarket, Shakespeare Electronics, Humminbird, the Burghardt family, Green Cape Wildlife Films, Kodak Australia, Singapore Airlines, Eurocom Computers, and public donations. Brad Barton, David Charles, Ron Swann, and Alex Fraser provided logistical support throughout the project. Special thanks to Harven Raven for providing temperature data. Thanks also go to Richard Holst and Jo Heyman for their generosity and hospitality. This research was carried out while I was a visiting research associate at the Department of Anatomy and Human Biology (UWA) and under the authority of Fisheries WA permit 69/97, Department of Conservation and Land Management permits SF002347 and NE001808, and Simon Fraser University Animal Care permit. Larry Dill, Ray Heithaus, Ian Hamilton, Colin Simpfendorfer, Bernie Crespi, Bernie. Roitberg, and Alejandro Frid provided comments on this manuscript.

5.7 LITERATURE CITED

Anderson, P. K. 1982. Studies of dugongs at Shark Bay, Western Australia. I. Analysis of population size, composition, dispersion, and habitat use on the basis of aerial survey. Australian Wildlife Reseach 9: 69-84.

Bigelow, H. B. and W. C. Schroeder. 1948. Fishes of the western North Atlantic. I. Sharks. Memoir Sears Foundation Marine Research 1: 59-576.

Compagno, L. J. V. 1984. FAO species catalogue. Volume 4. Sharks of the world. Part 2 – Carcharhiniformes. FAO Fisheries Synopsis 125: 1-655.

Cresswell, G. R. 1991. The Leeuwin Current – observations and recent models. Journal of the Royal Society of Western Australia 74: 1-14.

DeCrosta, M. A., L. R. Taylor Jr. & J. D. Parrish. 1984. Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. Pages 75-95 *in* Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol 2, University of Hawaii Sea Grant Miscelaneous Report 84-01.

de Iongh, H. H., B. J. Wenno and E. Meelis. 1995. Seagrass distribution and seasonal biomass change in relation to dugong grazing in the Moluccas, East Indonesia. Aquatic Botnay 50: 1-19.

Holland, K. N., B. W. Wetherbee, C. G. Lowe and C. G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134: 665-673.

Kohler, N. E., J. G. Casey and P. A. Turner. 1998. NMFS Cooperative tagging program, 1962-93: an atlas of shark tag and recapture data. Marine Fisheries Revivew 60: 1-87.

Lanyon, J. M., C. J. Limpus and H. Marsh. 1989. Dugongs and turtles: grazers in the seagrass system. Pages 610-634 *in* Biology of Seagrasses. A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, editors. Elsevier, New York.

Lowe, C. G., B. M. Wetherbee, G. L. Crow and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes 47: 203-211.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Preen, A. 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Marine Ecology Progress Series 124: 201-213.

Preen, A. R., H. Marsh, I. R. Lawler, R. I. T. Prince and R. Shepherd. 1997. Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef, and Exmouth Gulf, Western Australia. Wildlife Research 24: 185-208.

Rancurel, P. and A. Intes. 1982. Le requin tigre, *Galeocerdo cuvieri* Lacépède, des eaux Néocalédoniennes examen des contenus stomacaux. Tethys 10: 195-199.

Randall, J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Australian Journal of Marine and Freshwater Research. 43: 21-31

Simpfendorfer, C. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. Australian Journal of Marine and Freshwater Research 43: 33-43.

Simpfendorfer, C. A., A. B. Goodreid and R. B. McAuley. In press. Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes.

Stevens, J. D. 1984. Biological observations on sharks caught by sportfishermen off New South Wales. Australian Journal of Marine and Freshwater Research 42: 151-199.

Walker, D. I. 1989. Regional studies – seagrass in Shark Bay, the foundation of an ecosystem. Pages 182-210 *in* Biology of Seagrasses. A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, editors. Elsevier, New York.

CHAPTER 6

The Use of Crittercam to Study Habitat Use and Behavior of Large Sharks*

* A version of this chapter appears as Heithaus, M. R., G. J. Marshall, B. M. Buhleier, and L. M. Dill. 2001. Employing Crittercam to study habitat use and behavior of large sharks. Marine Ecology Progress Series: in press. Reprinted with permission from Inter Research.

6.1 ABSTRACT

Investigations of shark habitat use and foraging ecology have been hampered by inaccuracies inherent in many current methods. Although catch rates and acoustic telemetry may be appropriate for studying habitat use at a broad geographic scale, they are often not adequate for fine-scale determination of habitat use. Also, these techniques cannot provide data on how sharks behave in different habitats or on feeding behavior or social interactions. In this Chapter, I present a method that allows analysis of shark habitat use using an attached underwater video camera with an integrated time-depth recorder ("Crittercam") which provides accurate, and continuous habitat use data on a fine geographic scale, as wells as a record of shark behavior. Deployments on tiger sharks that were tracked simultaneously (n = 22) show that habitat use estimates of individual sharks may differ between Crittercam and acoustic tracking data. However, average habitat use measured by acoustic tracking may be accurate if sample sizes are large.

6.2 INTRODUCTION

Investigations of animal habitat use and behavior are important to understanding the ecology of animals and are vital to making informed conservation decisions. In many terrestrial systems and some aquatic systems, it is possible to determine habitat use patterns with considerable accuracy. However, it is much more difficult to quantify habitat use and behavior of large marine animals that may range widely and are not easy to observe directly, such as sharks.

Acoustic telemetry has been used to investigate shark habitat use while most behavioral observations are restricted to captive studies or anecdotal accounts. Acoustic telemetry can be used successfully to determine broad-scale habitat use and to study sharks that remain in a restricted area for a prolonged period (e.g. nursery areas) allowing many individuals to be tracked several times. For example, acoustic tracking of large tiger sharks (*Galeocerdo cuvier*) around the Hawaiian Islands showed that these animals are not strictly coastal and may use relatively shallow offshore banks (Holland et al. 1999). Also, Morrissey and Gruber (1993) showed that young lemon sharks (*Negaprion brevirostris*) selected warm, shallow waters over rocky substrates in North Sound, Bimini, Bahamas.

While acoustic tracking was appropriate for the above-mentioned studies, the technique may not be as useful for investigating habitat use by highly mobile large sharks on a fine scale, particularly where habitats are patchy and there are distinct habitat boundaries (e.g. tiger sharks in Shark Bay, Chapter 5). Acoustic tracking is not adequate in such circumstances because position fixes on the animal have a degree of uncertainty, and it is usually impossible to know the exact location of a tagged shark or the habitat it is occupying if it is near a boundary. And, even when shark habitat use can be accurately determined, it is impossible to know the behavior of sharks in various habitats with acoustic tracking.

Studies of shark foraging ecology and feeding behavior are extremely difficult as predation events are rarely witnessed, and most information comes from either anecdotal observations or stomach contents analysis. Studies of stomach contents are useful, but they are limited in the hypotheses they can be used to test. For example, when prey types vary in digestion rate, the relative importance of a particular prey type may be under- or over-represented. Also, these studies often cannot identify the habitat in which a shark fed, making definition of critical habitats difficult.

Crittercam is an animal-borne video, audio, and data collection system that can provide data that are impossible to collect with conventional techniques. Crittercam has been used successfully in studies of habitat use, foraging ecology, and behavior of pinnipeds (e.g. Parrish et al. 2000), and has the potential to provide unique insights into the behavior and ecology of large sharks.

6.3 METHODS

6.3.1 Crittercam

The Crittercam consists of an integrated video camera (either Hi-8 or digital) and time-depth recorder (TDR) encased in a small hydrodynamic housing (Hi-8: 10.1 cm diameter, 31.7 cm in length; digital: 8.8 cm diameter, 25.4 cm in length) (Marshall 1998; Figure 6.1). The unit contains a computer allowing the camera to be programmed to record continuously or at intermittent intervals for a total recording time of 6 (Hi-8 units) or 2.5 hours (digital units). Temperature and water depth information may be recorded continuously throughout a deployment, up to 7 days, at a user-defined interval (usually every 2-7 seconds). Crittercams can also be programmed to release from the animal at a pre-specified time using a burnwire system. In addition, all units incorporate a backup magnesium link that dissolves in seawater. Backup link dissolution times can range from several hours to several days, depending on the thickness of the link used. Crittercams are positively buoyant and float to the surface upon release and are recovered using the signal from a built-in VHF transmitter (MOD-050, 150.0 – 151.0 MHz; Telonics, Mesa, AZ) and TR-4 VHF receiver (Telonics). During deployments, animals instrumented with Crittercams may be acoustically tracked using a Sonotronics (Tucson, AZ) ultrasonic transmitter (75.0-76.0 kHz) attached to the Crittercam. The maximum detection range for ultrasonic transmitters generally is between 500 – 1000 m, and the VHF signal can be detected at over 20 km.

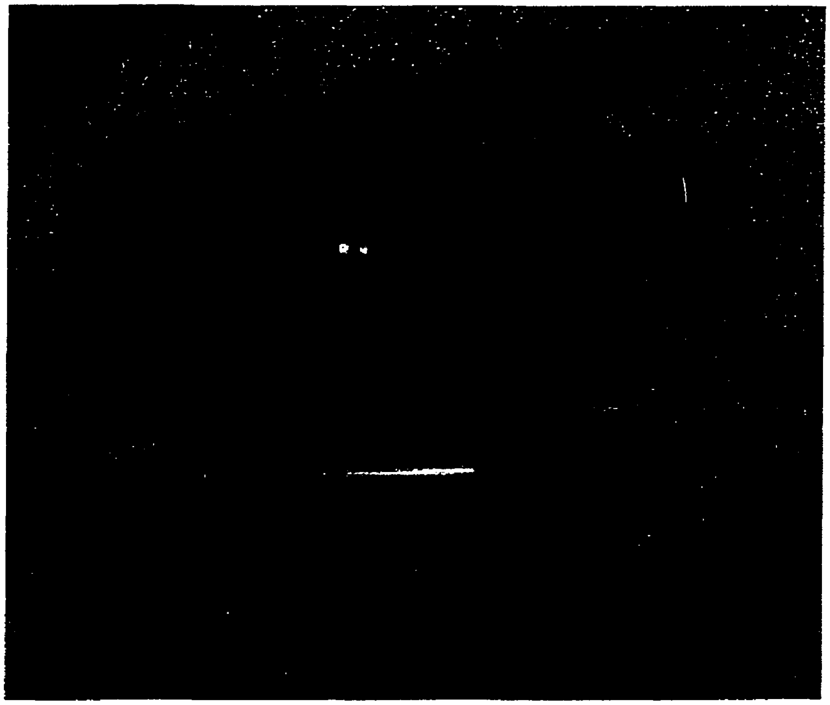


Figure 6.1. Hi-8 (top) and digital video (bottom) Crittercam units. A dorsal fin clamp used to attach Crittercams is attached to the Hi-8 unit. Clamps are lined with coarse sandpaper to grip the shark's fin, but do not cause tissue damage or leave any noticeable marks on the dorsal fin.

Crittercam is usually attached to the dorsal fin of a captured shark (Figures 6.1, 6.2). The clamp is designed to be held together just posterior to the trailing edge of the dorsal fin and no invasive techniques are required beyond capture. Video recorded using the dorsal fin attachment provides a view of a substantial amount of habitat (Figure 6.3) and turns rapidly with the shark. The camera is approximately at the sharks' midline, and above the center of mass which minimizes drag and camera swing. No obvious shark responses to the dorsal fin clamp have been noted.

If sharks cannot be captured, a Crittercam may be attached to the shark with a Floy tag (generally 5 cm anterior and lateral to the dorsal fin) and a tether. The use of a short tether results in a diminished field of view of the surrounding habitat as a significant portion of the frame is taken up by the shark's body. If a long tether is used, the Crittercam is configured to "fly" slightly above the shark, resulting in a large field of view of the habitat around the shark. However, when the shark turns rapidly, the camera is slow to react and is likely to miss recording prey items taken.

6.3.2 Study Methods

During a study of tiger shark habitat use, I deployed Crittercams on 40 sharks in Shark Bay, Western Australia between 1997-1999. These data allow me to test the influence of Crittercams on shark behavior and to determine the accuracy of acoustic tracking in measuring habitat use. The study area in Shark Bay is generally shallow throughout (6-15 m deep), but is intersected by many shallow shoals ($\bar{x} = 2.3$ km^2) that are largely covered by seagrasses (see Figure 5.1). There are relatively distinct boundaries between habitats, making Shark Bay an appropriate location to test the accuracy of acoustic tracking data. Crittercams were attached using Floy tags with short tethers (n=6) or dorsal fin mounts (n = 34) on sharks caught by drumline (Chapter 5, Heithaus in press). A subset of these instrumented sharks (n = 28) were tracked acoustically, from a 4.5 m research vessel using a Sonotronics DH-4 directional hydrophone and USR-5W receiver. During acoustic tracks, the boat generally maintained a distance of 100 – 200 m from the shark. The position of the tracking boat was frequently changed relative to that of the shark to aid in estimates of shark position and to avoid the possibility that the shark was being "chased" by the tracking boat.

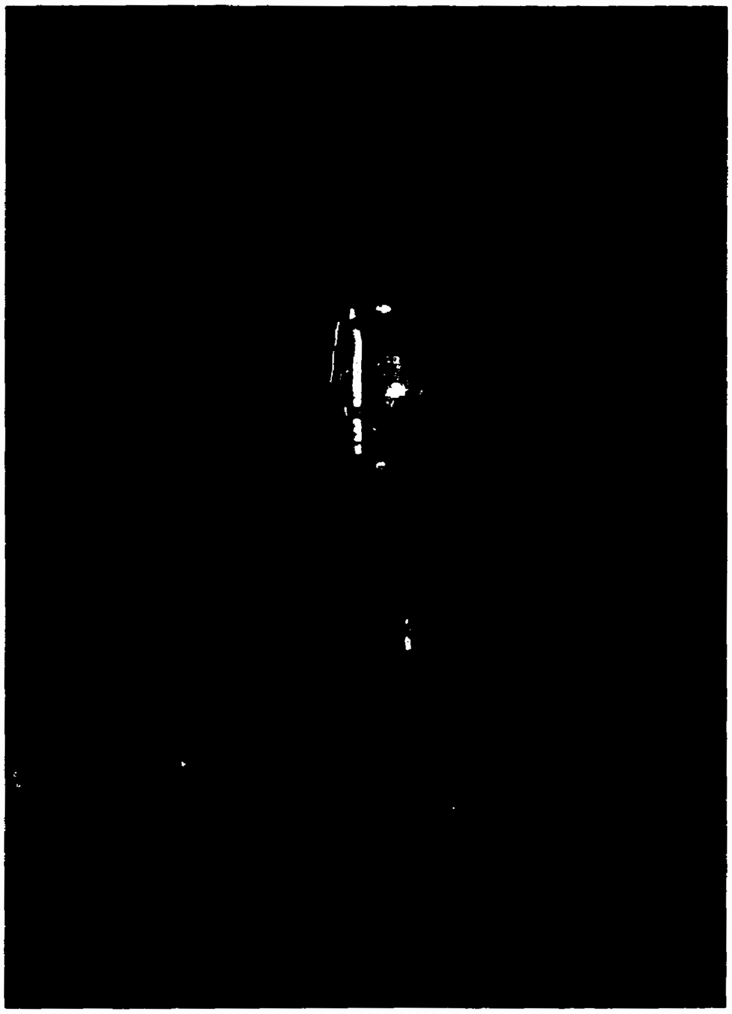


Figure 6.2. Crittercam deployed on 3.2 m tiger shark.

Figure 6.3. View of a video frame during a Crittercam deployed with a dorsal fin clamp on a 3.4 m tiger shark. Notice the surrounding seagrass habitat and the loggerhead sea turtle (*Caretta caretta*) in the middle left.

Throughout the track, the boat position (GPS coordinate), estimated distance and direction to the shark, and the habitat the shark was occupying, were recorded every five minutes. The habitat that a shark was occupying was estimated using the boat position, estimated distance and direction to the shark, and habitat maps. If the shark was likely in a habitat other than that of the boat, the boat was moved to the estimated position of the shark to determine its habitat once the shark had moved a sufficient distance away. Video data were collected continuously on deployments ranging from 15 to 360 min. In addition to Crittercam deployments, 8 other tiger sharks were fitted with VEMCO (Shad Bay, NS) internal acoustic transmitters (V32, 28.5-32.8 kHz) following the methods of Holland et al. (1999) and tracked, according to the above methods, using a VEMCO V11 directional hydrophone and VR60 receiver.

Habitat use was determined from acoustic tracking data by the proportion of five-minute position fixes in each habitat while habitat use was determined from Crittercam using the proportion of time spent in each habitat. It is important to note that it is not necessary to know the precise location of a shark to determine habitat use from Crittercam. Instead, the habitat an individual is occupying is determined from direct video observations and depth data from the TDR. If determining exact positions of animals was important to a research question, however, Crittercam video data could be used to correct position estimates made from acoustic tracking during a deployment. To make comparisons of habitat use data comparable, data from acoustic tracking and Crittercam were only analyzed for the period where both methods were used concurrently.

6.4 RESULTS AND DISCUSSION

No sharks showed obvious behavioral responses to the Crittercam. Also, the speed of travel by tiger sharks fitted with Crittercam ($n = 40$, $\bar{x} = 1.9$ km/hr, $SD = 0.73$ km/hr) was not significantly different from that of sharks fitted only with acoustic transmitters ($n = 8$, $\bar{x} = 2.0$ km/hr, $SD = 0.70$ km/hr ; $t = 0.27$, $p = 0.79$). Further evidence that tiger sharks are not disturbed by Crittercam comes from the observation of foraging behavior within 30 - 70 minutes of release in 5 animals. One shark captured an unidentified prey item off the substrate, and another performed a burst swim to capture a prey item (unidentified). Two sharks made course deviations to inspect potential prey, but did not attempt to capture them. Finally, one individual carrying a Crittercam was recaptured on a drumline 70 minutes after release.

There was no significant difference in the average proportion of time that sharks spent over shallow seagrass habitats measured by Crittercam ($\bar{x} = 0.34$, SD = 0.22) and estimated from acoustic tracking ($\bar{x} = 0.32$, SD = 0.21) (paired t-test for 22 individuals that spent at least 10% of their time over shoals, $t = 1.8$, $p = 0.09$; Table 6.1). However, for particular individuals, there were substantial differences between techniques in the measured time spent over shoals. In some cases, Crittercam revealed that a tiger shark spent almost twice as much time in a shallow habitat than was estimated by acoustic tracking (Table 6.1). Such discrepancies are likely due to errors in estimates of shark position inherent in acoustic tracking techniques. These data suggest that acoustic tracking can provide an accurate measure of average habitat use when many individuals are tracked, but may not be appropriate for understanding the behavior and habitat use of individual sharks. Also, acoustic tracking data may not be appropriate in locations where habitats are more variable and patchy than in Shark Bay (e.g., near reef areas), and the use of Crittercam would be beneficial in such locations. Crittercam may also benefit studies of shark habitat use by allowing sample sizes to be increased substantially, since sharks fitted with Crittercam do not have to be tracked manually. Furthermore, the use of Crittercam deployments without acoustic tracking removes potential effects of tracking boats on shark behavior.

Another benefit of Crittercam is the ability to observe directly the behavior of a free-swimming shark over a significant time period, allowing important questions of shark foraging to be addressed. Video collected from tiger sharks allowed us to observe both apparent and definite shark foraging behavior in 12 sharks as well as the behavior of both sharks and potential prey during encounters (see Chapter 7). Feeding behavior has also been observed in one Crittercam deployment on white sharks (Marshall 1998).

Table 6.1. Comparison of the proportion of time tiger sharks spent over shallow shoals based on acoustic tracking data (5-minute position fixes) and concurrent Crittercam video data.

Shark	Tracking	Crittercam	Ratio
1	0.11	0.23	2.09
2	0.77	0.92	1.19
3	0.28	0.33	1.18
5	0.1	0.13	1.30
8	0.13	0.1	0.77
13	0.1	0.15	1.50
15	0.15	0.1	0.67
18	0.17	0.21	1.24
19	0.1	0.21	2.10
21	0.2	0.19	0.95
22	0.1	0.2	2.00
23	0.67	0.73	1.09
28	0.28	0.28	1.00
30	0.4	0.46	1.15
31	0.4	0.36	0.90
32	0.31	0.25	0.81
33	0.39	0.32	0.82
35	0.47	0.49	1.04
36	0.33	0.33	1.00
37	0.8	0.78	0.98
38	0.4	0.39	0.98
39	0.31	0.32	1.03
Mean	**0.32**	**0.34**	

Intraspecific interactions were not observed during tiger shark deployments, but this may partially be due to relatively poor water visibility in Shark Bay (usually < 4 m). In a white shark video, another white shark gave way to the instrumented animal in response to apparent aggressive displays (Marshall 1998). Studies of sharks that are found in high densities (e.g., Caribbean reef sharks, *Carcharhinus perezi*) or travel in groups (e.g., sevengill sharks, *Notorynchus cepedianus*, Ebert 1991) may benefit from the application of Crittercam technology, as previously unobservable interactions may be recorded, and systematic behavioral studies undertaken.

Besides tiger sharks in this study, Crittercam deployments have been made on white (*Carcharodon carcharias*; n = 9), salmon (*Lamna ditropis*; n = 5), nurse (*Ginglymostoma cirratum*, n = 2), bull (*Carcharhinus leucas*; n = 1), and lemon (n = 1) sharks (Marshall 1998, G. Marshall unpublished data). Deployments have been made on sharks between approximately 200 cm TL (salmon shark) and 405 cm TL (tiger shark); all have been Hi-8 units. Deployments on smaller sharks (approximately 180-200 cm TL) are now possible with digital units.

Crittercam can provide unique insights into the behavior and ecology of large sharks. It allows investigators to gather accurate data on shark habitat use, swimming depth, and water temperature while providing images of predatory and social behavior. Future studies that incorporate Crittercam technology, especially in areas of good water visibility, will greatly enhance our current understanding of large sharks, and should aid in drafting conservation strategies for these apex predators by helping to define critical foraging habitats and prey species.

6.5 ACKNOWLEDGMENTS

I would like to thank the National Geographic Special Projects team, especially Greg Marshall, Birgit Buhleier, Derrik Cheung, Medhi Bakhtiari, and Lynne Barre for providing Crittercam systems and logistical support. Greg Marshall, Birgit Buhleier, and Larry Dill provided advice and assistance. Further financial support for fieldwork in Australia was provided by the PADI Foundation, the National Geographic Expedition's Council, and NSERC Canada (grant A6869 to L.M. Dill). This work was conducted under the authority of Fisheries WA permit 69/97, Department of Conservation and Land Management permits SF002347 and NE001808, and Simon Fraser University Animal Care permit. Thanks to Larry Dill, Lynne Barre and Ian Hamilton for comments on this chapter.

6.6 LITERATURE CITED

Ebert, D. A. 1991. Observations of the predatory behaviour of the sevengill shark *Notorynchus cepidianus*. South African Journal of Marine Science 11: 455-465.

Heithaus, M. R. in press. The biology of tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes.

Holland, K. N., B. W. Wetherbee, C. G. Lowe and C. G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134: 665-673.

Marshall, G. J. 1998. Crittercam: an animal-borne imaging and data logging system. MTS Journal 32: 11-17.

Morrissey, J. F. and S. H. Gruber. 1993. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environmental Biology of Fishes 38: 311-319.

Parrish, F. A., M. P. Craig, T. J. Ragen, G. J. Marshall, and B. M. Buhleier. 2000. Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. Marine Mammal Science 16: 392-412.

CHAPTER 7

Habitat Use and Foraging Behavior of Tiger Sharks (*Galeocerdo cuvier*) in a Seagrass Ecosystem

7.1 ABSTRACT

Understanding the foraging behavior and spatial distribution of top predators is crucial to gaining a complete understanding of communities. However, studies of top predators are often logistically difficult and it is important to develop appropriate methods for identifying factors influencing their spatial distribution. Sharks are top predators in many marine communities, yet no studies have quantified the habitat use of large predatory sharks or determined the factors that might influence shark spatial distributions. I used acoustic telemetry and animal-borne video cameras ("Crittercam") to test the hypothesis that tiger shark (*Galeocerdo cuvier*) habitat use is determined by the availability of their prey. I also used Crittercam to conduct the first investigation of foraging behavior of tiger sharks. To test for habitat preferences of sharks, the observed proportion of time in each habitat for each individual was compared to the predicted values for that individual based on correlated random walk and track randomization methods that were developed to be applicable to tracking data in many situations. Although there was individual variation in habitat use, tiger sharks preferred shallow seagrass habitats, where their prey is most abundant. Despite multiple encounters with potential prey, sharks rarely engaged in prolonged high-speed chases, and did not attack prey that were vigilant. I propose that the tiger sharks' foraging tactic is one of stealth and sharks rely upon close approaches to prey in order to be successful. This study shows that using appropriate analysis techniques and a variety of field methods it is possible to elucidate the factors influencing habitat use and gain insights into the foraging behavior of elusive top predators.

7.2 INTRODUCTION

Understanding patterns of habitat use and foraging behavior of top predators is important to gaining insight into the dynamics of communities. Patterns of habitat use determine the likelihood of both direct and indirect interspecific interactions, which can influence community structure and stability (e.g. Brown et al. 1999). Therefore, understanding the factors that influence spatial distributions of top predators is critical to predicting the consequences of environmental perturbations and human disturbance on these species and the communities they inhabit. Despite the importance of such studies, it is often difficult to gather data on top predators as they are frequently elusive, have large home ranges, and exist at low population densities. Thus, new methods with meaningful statistical tests could greatly enhance our understanding of top predators in diverse habitats.

Sharks are an example of top predators for which there is little information regarding habitat use and foraging behavior. Yet large sharks may be keystone predators, influencing the structure of ecosystems through predator-prey interactions (e.g. Heithaus in press a, Simpfendorfer et al. in press). This study was undertaken to develop methods applicable for gaining insights into their habitat use and to apply new technologies to begin to understand their foraging behavior.

Tiger sharks (*Galeocerdo cuvier*) are a large coastal species (Randall 1992) capable of taking large prey (e.g. Simpfendorfer 1992, Lowe et al. 1996, Heithaus in press a, Simpfendorfer et al. in press). In the seagrass ecosystem of Shark Bay, Western Australia, tiger sharks may be at the apex of a trophic cascade as they are the major predator on dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*), the bay's principle grazers (Heithaus in press a, Simpfendorfer et al. in press). Tiger sharks are also important in determining the habitat use and behavior of their prey species, including those that they rarely consume. For example, although bottlenose dolphins (*Tursiops aduncus*) in Shark Bay are rarely killed by tiger sharks (Heithaus in press b, Simpfendorfer et al. in press), dolphin habitat use is greatly influenced by tiger shark predation risk (Chapter 9). Because of their ability to influence the behavior, and perhaps populations, of their prey, gaining an understanding of tiger shark habitat use, and the factors influencing their spatial distribution, is required to understand the Shark Bay seagrass ecosystem, and others like it.

Previous studies of many large predators have relied on tracking data to determine movement patterns and habitat use (e.g. Mills and Gorman 1997, Goldman and Anderson 1999, Holland et al. 1999), but have generally obtained only small sample sizes. While such studies are useful in determining broad scale movements they often cannot provide reliable data on small-scale patterns of habitat use, which are critical for understanding the dynamics of spatially heterogeneous ecosystems. This is partially due to errors in determining the exact position of the animal, which can result in large discrepancies between measured and actual habitat use (Heithaus et al. in press). Large sample sizes tend to ameliorate these errors when researchers are interested in average habitat use patterns of a sample (Heithaus et al. in press). However, even when habitat use is measured accurately, it is difficult to determine the expected values for habitat use of each individual if they had no habitat preference, and the use of appropriate statistical techniques is critical (Porter and Church 1987, Arthur et al. 1996, Heithaus and Hamilton in review).

Animal habitat use can be influenced by a wide variety of factors including food availability, competition, predation risk, and reproductive and social considerations. For some top predators, food availability seems to be a determinant of habitat use (e.g. lions, *Panthera leo*, Mills and Gorman 1997; polar bears, *Ursus maritimus*, Stirling et al. 1993), but this is not universal. For example, wild dog (*Lycaon pictus*) densities are not high in areas of high food density and appear to be influenced by the distribution of lions, which are both potential competitors and predators (Mills and Gorman 1997). Large tiger sharks in Shark Bay are unlikely to face either predation risk or interspecific competition for their primary prey. Thus, I hypothesized that tiger shark habitat use should be determined by prey availability.

The foraging behavior of many top terrestrial predators has received considerable attention, but such studies of top marine predators are rare. Knowledge about shark foraging comes largely from inferences based on stomach contents analysis (e.g. Simpfendorfer 1992, Lowe et al. 1996), anecdotal accounts (e.g. Ebert 1991), observations under baited conditions (e.g. Strong 1996), or observations immediately following an attack (e.g. Klimley 1994). These methods, while providing useful information on shark foraging, all have associated biases. These include differences in digestion rates of prey items, unnatural behavior due to baiting, and biases towards predation events that are near the surface and of extended duration. A recent technological innovation, a small animal-borne video camera ("Crittercam"), allows systematic studies of the foraging behavior of sharks and other large marine predators to be undertaken with minimal disturbance to the animal and allows recording of both predator and prey behavior throughout an encounter (Marshall 1998, Heithaus et al. in press, Chapter 6).

The goals of this study were to 1) develop methods for measuring habitat preferences of top predators using tracking data, 2) quantify tiger shark movements and habitat use, 3) determine whether tiger shark habitat use is random or matches food availability, and 4) investigate tiger shark foraging behavior.

7.3 METHODS

7.3.1 Study Site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia (Figure 7.1). The bay is relatively shallow throughout (6 – 15 m) with extensive shallow seagrass banks (< 4.0 m depth). Shark Bay contains the most extensive seagrass shoals reported in the world (Walker 1989) and supports large populations of tiger sharks and their prey (Heithaus in press a). The study site was located in the Eastern Gulf (approx. 25° 45'S, 113° 44' E; Figure 7.1a). For the purposes of this paper, habitats have been classified as either shallow ($\leq$4.0 m) or deep ($\geq$ 4.5 m) (Figure 7.1b).

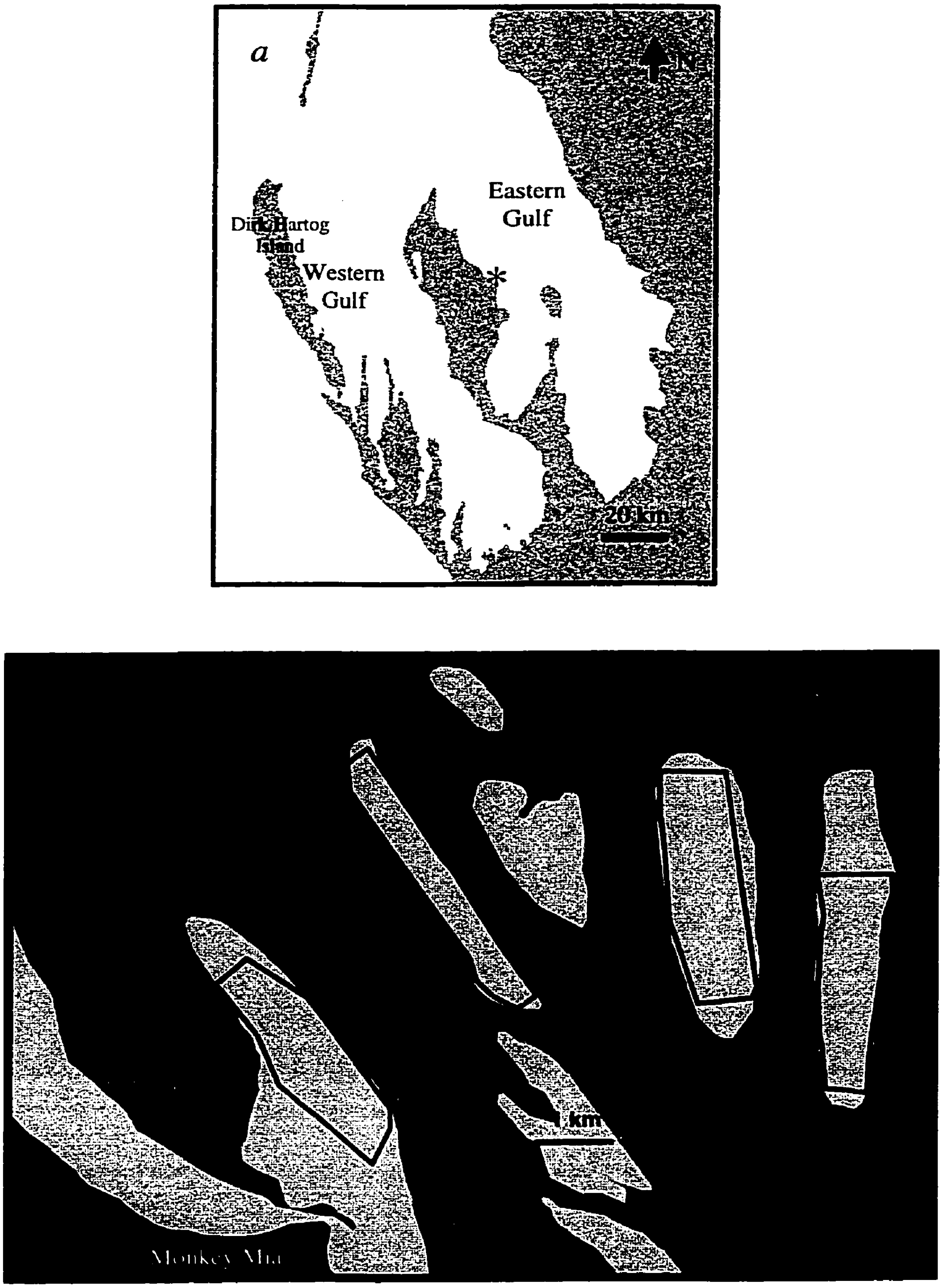


Figure 7.1. *a*) Shark Bay, Western Australia. Monkey Mia is indicated with an asterisk. Land is gray. *b*) Location of study zones offshore of Monkey Mia. Light shading indicates shallow habitats and the gray shading represents deep habitat. Land is black. Polygons represent sample zones with transects located in the middle of the zones. Prey availability was assessed in all zones. Shark fishing did not occur in the two zones closest to Monkey Mia.

7.3.2 Study Methods

7.3.2.1 Prey Availability

Habitat differences in the availability of potential prey (dugongs, sea turtles, sea snakes, and sea birds) were determined using belt transects. From March 1997 to May 1999, ten transects located in various habitats (Figure 7.1b) were surveyed a total of 410 times (200 deep, 210 shallow), from a 4.5 m boat. Transects were conducted during months that tiger sharks are present in the study area (Chapter 5). All turtles and sea birds at the surface within 30 m of the vessel, dugongs within 100 m, and sea snakes (1998 and 1999 only) within 5 m were recorded. Transects were only conducted in Beaufort sea state 3 or less (with most occurring in Beaufort 0 or 1) to reduce sighting biases associated with weather conditions.

7.3.2.2 Tiger Shark Captures

Sharks were captured using drumlines equipped with a single hook (Mustad Shark Hook size 12/0, 13/0, or 14/0) baited with Australian salmon (*Arripis truttaceus*) and fished at a depth of 0.7 - 2.0 m. Lines were spaced approximately 0.7 km apart and were checked every 2-4 hours. Once a shark was caught, it was measured, sexed, and tagged (see Chapter 5 for detailed shark handling methods). Comparisons of catch rates among habitats cannot provide an accurate measure of shark habitat use due to differential bait loss and possible differences in catch radii among habitats (Heithaus in press a, Chapter 5). Therefore, two other methods were employed to measure shark habitat use.

7.3.2.3 Acoustic Tracking

Although tracking data have several drawbacks, these can be overcome with methods for correcting position fixes (see below), large sample sizes, and appropriate analysis techniques. Only large sharks that were swimming powerfully on lines were chosen for acoustic tracking (Appendix 1). Sharks were then brought alongside the boat and inverted until they entered a state of tonic immobility, which reduces stress to the shark (Holland et al. 1999). Internal transmitters (V32, 28.5 – 36.0 kHz, VEMCO, Shad Bay, Nova Scotia) coated in a 7:3 mixture of bee's and paraffin wax were inserted into the peritoneal cavity of eight sharks through an approximately 10 cm incision. The incision was then closed with braided nylon string and triangle-head surgical needles for large animals. Transmitters were implanted within 5 minutes of a shark entering tonic immobility and all sutures (n = 6) were completed an average of 15 minutes after restraint. Two of the transmitters (Appendix 1: IN7, IN8) were equipped with depth sensors to allow comparisons with depth data obtained by Crittercam (see below).

Upon release, sharks were tracked from a 4.5 m research vessel using a directional hydrophone (V11, VEMCO) and an acoustic receiver (VR-60, VEMCO). Every 5 minutes I recorded the boat GPS location, direction to the shark, estimated distance to the shark (based on distance-signal strength trials conducted before implantation), and the shark's habitat. In general, I kept 200 – 300 m from the shark, and the position of the boat relative to the shark was changed frequently. If the estimated habitat of the shark was possibly different from that of the boat, the boat was moved to the shark's estimated position after it had moved a sufficient distance away.

7.3.2.4 Crittercam

Crittercam is an animal-borne video camera that integrates environmental data collection (temperature and depth) and acoustic tracking capabilities (Marshall 1998). A major advantage of Crittercam is that habitat use of a shark is continuously monitored by video instead of being estimated by acoustic telemetry (Figure 7.2). Tiger sharks do not show any obvious behavioral reactions to Crittercam and their movements are similar to those tracked with standard acoustic tracking techniques (Heithaus et al. in press).

As with acoustic tracking, only large sharks that were swimming powerfully on lines were selected for Crittercam deployments. Crittercams were positioned on the dorsal fin with a soft clamp or using a Floy tag with a short tether (see Chapter 6 for a description of attachment methods), and the shark released. Cameras were left attached to sharks for up to 11 hours, with most deployments being less than 6 hours (Appendix 2). During a deployment, sharks were acoustically tracked with a Sonotronics (Tucson, AZ) directional hydrophone (DH-4) and receiver (USR-5W) using the above methods. Position estimates and the habitat a shark was using at each fix were corrected using Critttercam video and depth data (Heithaus et al. in press). Some tracks were terminated

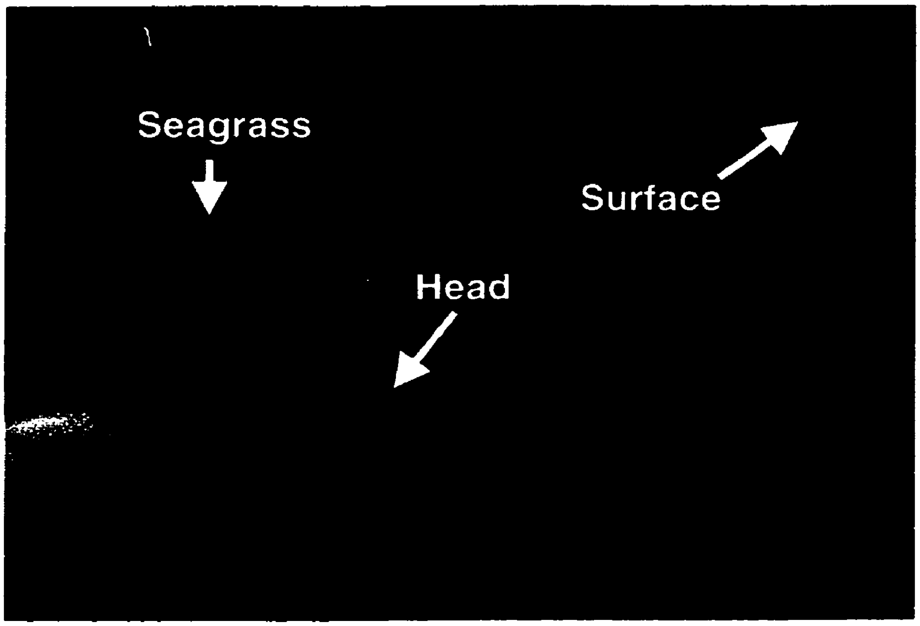


Figure 7.2. Video frame from Crittercam attached to C38. Note that the shark is swimming over a shallow seagrass habitat.

before Crittercam release. Upon release, cameras were located and retrieved using a VHF receiver. During Crittercam deployments, water temperature and shark swimming depth were recorded every 2-7 seconds. For analyses of swimming depth, each individual shark contributed a single mean value to overall mean values.

7.3.2.5 Measuring Expected Habitat Use, Shark Speed, and Displacement

It is difficult to estimate the proportion of time a tracked animal should spend in each habitat if moving randomly, especially if the animal has a poorly defined home range over the tracking period (e.g. Arthur et al. 1996, Heithaus and Hamilton in review). This problem arises primarily because 1) the location (or habitat) in which a track is started can influence the proportion of time an animal will spend in each habitat even if it has no habitat preference, and 2) the spatial distribution of habitat patches can influence expected habitat use (Porter and Church 1987, Heithaus and Hamilton in review). To overcome these problems, I devised two Monte Carlo procedures that used observed tracks to generate estimates of expected habitat use if there is no habitat preference. For the first method, a correlated random walk (CRW, Figure 7.3), each track was subdivided into component "moves" that were defined as the direction and distance moved between any two 5-min position fixes. I used the observed move distances (in random order), but the 45° direction bin (e.g. N-NE, S-SW, etc) of each move was selected randomly based on the probability that a move was made in a particular direction based on empirical data from all sharks (Figure 7.4). The exact angle traveled within a 45° bin (e.g. 41°, 183°) was selected randomly (i.e., each angle within the bin was equally likely to be selected). Because sharks may not conform to a CRW (see Results), I also devised a randomization method (RZ) that retained the angle and distance traveled for each move. The order of moves was then randomized to create a new, random track (Figure 7.5).

For both RZ and CRW methods, I generated 1000 random tracks for each individual, each using the starting point of the original track. The random tracks were mapped into a GIS (MapInfo, MapInfo Corp.) map of the study site and a habitat designation (deep or shallow) was assigned to each fix location (defined as the endpoint of a move). The number of fixes in each habitat was determined for each random track,

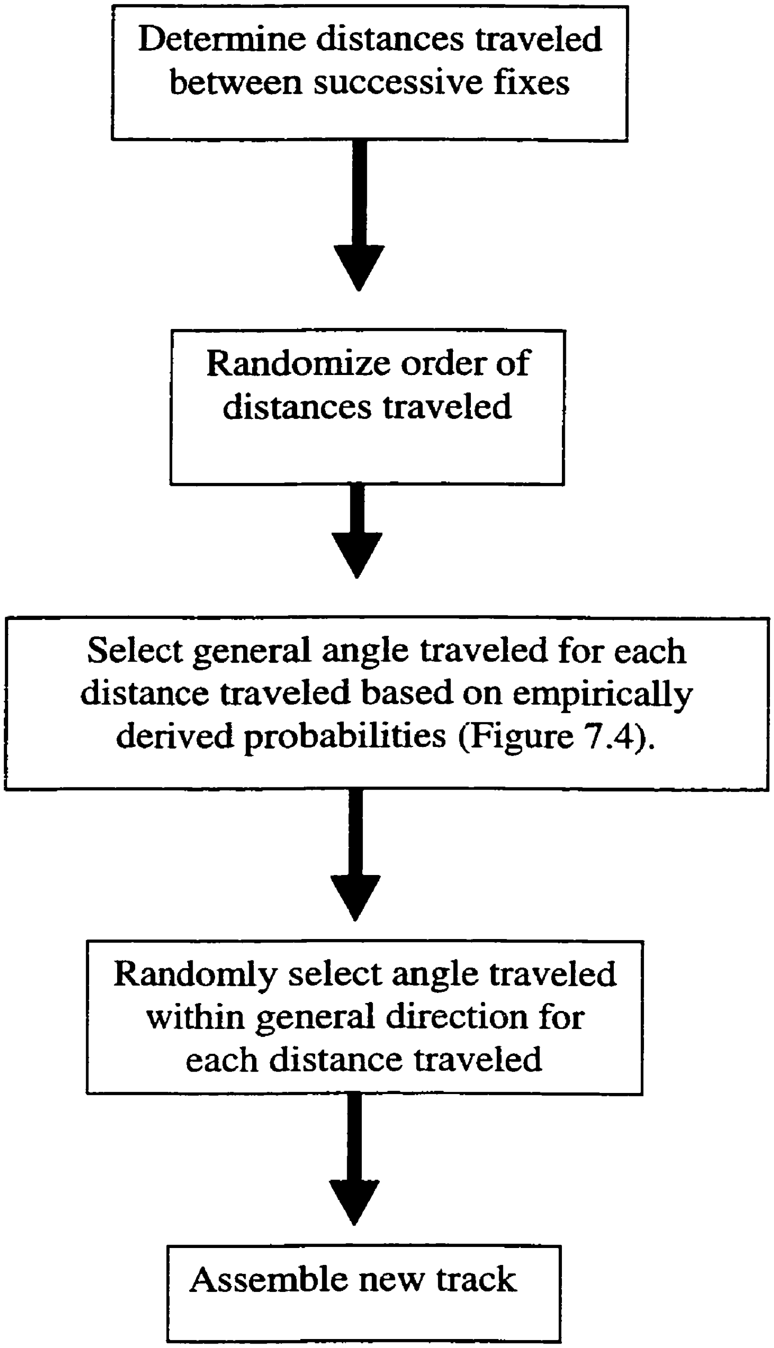


Figure 7.3. Flow diagram of the method used to generate expected habitat use measures with no habitat preference for the correlated random walk (CRW) method.

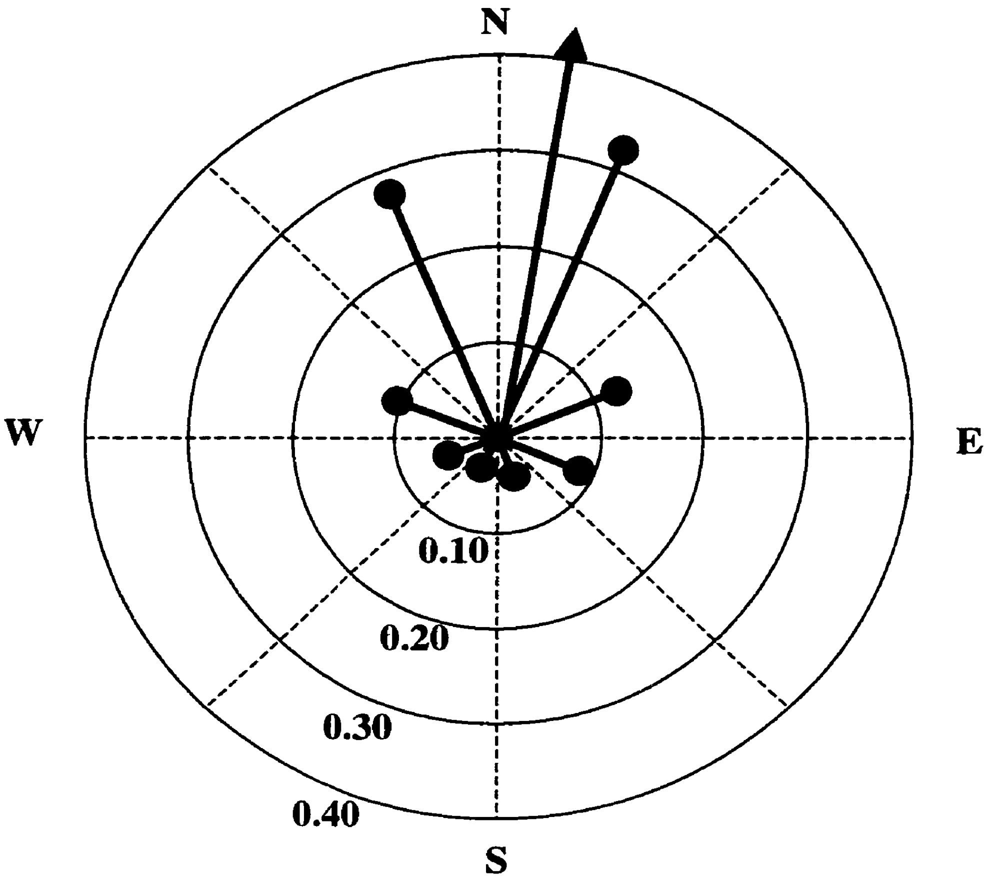


Figure 7.4. Frequency distribution of mean movement directions for tiger shark "moves" used to generate CRW random tracks. Tiger sharks tended to move in a northerly direction with a slight bias towards moving east. To avoid pseudoreplication, each individual contributed only a single set of proportions to the overall mean. The arrow indicates the mean movement direction (10.7°).

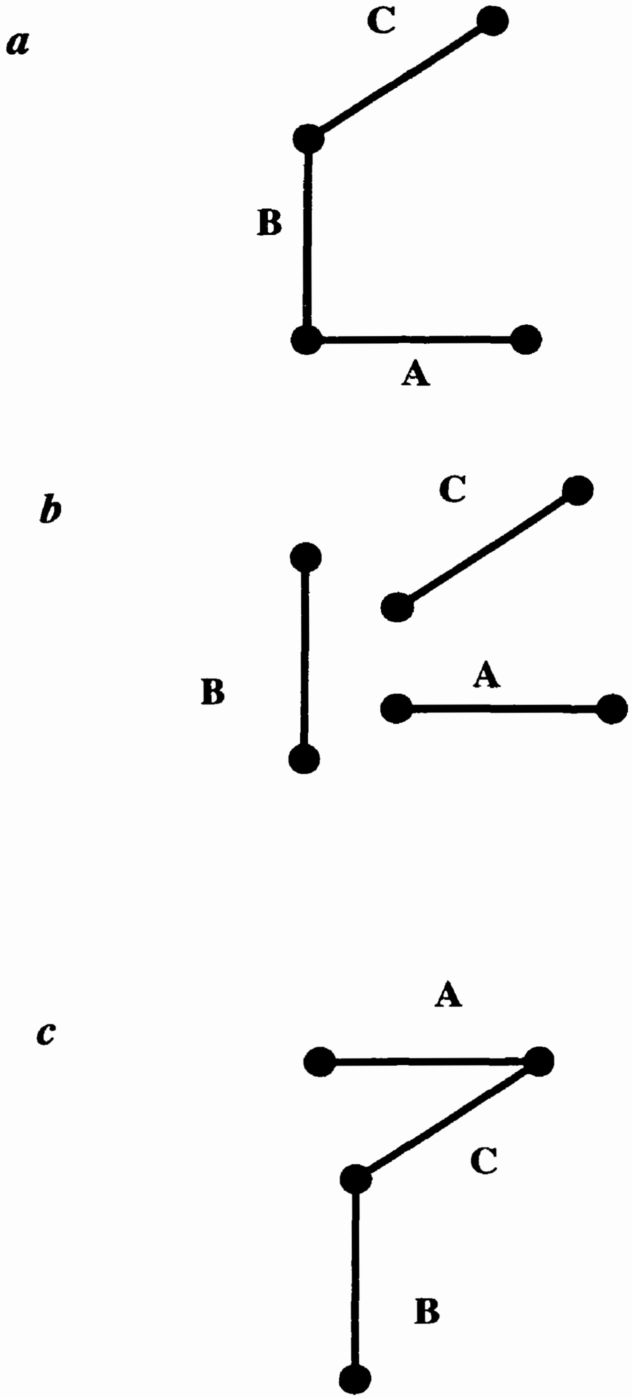


Figure 7.5. Schematic diagram of randomization (RZ) method. *a*) The original track is divided into component moves defined by the direction and distance moved between successive five-minute position fixes. *b*) The moves are separated, but the direction and distance traveled are maintained. *c*) The moves are reassembled in random order to generate a new track based on random movement. Closed circles indicate the location of hypothetical position fixes.

and I recorded the number of random tracks in which the observed proportion of fixes in a) shallow habitats, or b) deep habitats was greater than the observed track. If fewer than 5% of random tracks used a particular habitat more than the observed track, this individual was considered to exhibit a significant habitat preference (Heithaus and Hamilton in review).

The above methods are useful in different situations. The RZ method is the most conservative and assumes that the animal can only make moves of the directions and distances observed. Thus, if the observed track was generally directional, the random tracks cluster tightly along the observed track (Figure 7.6c). Therefore, if an animal moves in a straight line through a preferred habitat, it is likely to be wrongly identified as having no habitat preference because there is no variation in movement angle to allow the animal to select another habitat. In the CRW method a "bubble" of tracks surrounds the original track (Figure 7.6e). However, if an animal makes moves that are more directional than predicted based on a CRW, this method may not provide an accurate reflection of expected habitat use with no habitat preference. Because the RZ and CRW methods are both conservative (i.e. likely to detect no preference even if one exists), a habitat preference detected by either method is likely to be biologically significant. Although RZ and CRW methods did not always both detect a significant habitat preference for an individual, in no cases did they detect opposite preferences.

Several analyses were carried out to determine the overall pattern of habitat use by tiger sharks. Using individuals as single data points, G-tests were conducted comparing the observed habitat use to the expected habitat use based on 1) habitat availability (HA) within the study area, and 2) the overall proportion of "fixes" from random tracks for each individual, for both RZ and CRW techniques. G-tests can be used to show a deviation from no habitat preference, but are not ideal for identifying a specific habitat preference of a sample since deviations in either direction (i.e., shallow preference or deep preference) add to the significance level of the test. To circumvent this problem, an overall sample randomization (SR) was conducted (Heithaus and Hamilton in review). In this procedure, the order, direction, and distance of all moves was conserved for each track, and tracks were randomly reallocated among observed starting positions of all tracks. For each iteration (n = 500) the mean proportion of fixes in each habitat was

Figure 7.6. GIS maps of *a, b*) example original tracks (C5, C2), and random tracks based on this original for the c, *d*) randomization (RZ) method, and *e, f*) correlated random walk (CRW) method. Each dot represents a position fix from a random track. Notice that for C5 the RZ method tends to retain the inherent directionality of the track while the CRW method generates tracks with much greater geographic spread. Both methods generate tracks with similar spread for C2, which made more turns, but only the RZ method retained the general trend for southward movement in the original track.

recorded using each track as a single data point. The observed mean proportion of fixes in each habitat was compared to the distribution of means obtained from the randomizations. If less than 5% (n = 25) of iterations generate a mean use of a habitat greater than the observed mean use, a significant habitat preference is indicated (Heithaus and Hamilton in review).

Average shark speed was the distance (measured by GIS) along an entire track divided by total track time. Displacement rate was the straight-line distance between the start and end points of the track divided by total track time. Observed net squared displacements (km) were compared to the net squared displacements predicted by the CRW model using a paired t-test to determine if overall shark movements could be described as a correlated random walk or if they were more directional. Net squared displacement increases linearly with track duration under a CRW; if the observed net squared displacement increases faster than predicted, animals are moving more directionally than predicted (Turchin 1998, Bergman et al. 2000).

7.3.2.6 Foraging Behavior

Tiger shark foraging behavior and prey responses to tiger sharks were investigated using 22 Crittercam deployments (49 video hours). Not all Crittercam deployments could be used for foraging analyses as some provided a view adequate only for measuring habitat use. A behavior was considered to be definite foraging when 1) a food item was ingested, 2) a potential prey item was encountered within 30 seconds of an obvious change in direction ("inspection") or during a burst swim , 3) a potential prey item was pursued, 4) audio from the Crittercam revealed that the shark had bitten prey, 5) biting motions followed a burst swim, or 6) animal material was expelled from the gills after a biting motion or burst swim. Possible foraging behavior was noted when sharks engaged in burst swims but prey could not be seen (often due to a poor camera angle) or there was no bite after a burst swim. Based on these definitions, this study probably underestimates the foraging rate of tiger sharks.

7.4 RESULTS

7.4.1 Prey Availability

All potential tiger shark prey species that were surveyed were found in greater density in shallow seagrass habitats than in deep ones in all years (Table 7.1). Sea snakes and dugongs were 3 - 4 times more abundant in shallow habitats than in deep ones. The relative abundance of sea birds (almost exclusively pied cormorants, *Phalacrocorax varius*) and sea turtles (both green sea and loggerhead, *Caretta caretta*) were more variable. Sea birds were 4.5 - 8.4 times and sea turtles 1.7 – 2.9 times more abundant in shallow habitats.

7.4.2 Tiger Shark Movements and Habitat Use

Tracks of 45 tiger sharks revealed a general pattern of northward movement (Figure 7.4). Although several sharks remained in a restricted area for several hours and made many turns (Figure 7.7), most sharks made relatively straight movements (Figure 7.8). Net squared displacements of tiger sharks were significantly greater than predicted by a correlated random walk (paired t-test, $t = 2.8$, $df = 44$, $P < 0.01$; Figure 7.9) indicating directional movements. Backwards stepwise linear regression omitted gender and water temperature as factors influencing speed or displacement, but shark length was positively correlated to both speed (Linear Regression, $y = 0.0063x + 0.6902$, $r^2 = 0.29$, $F = 14.4$, $P < 0.001$) and displacement (Linear Regression, $y = 0.0079x + 0.802$, $r^2 = 0.16$, $F = 9.7$, $P < 0.01$). However, little of the variation in displacement per hour was explained by size variation.

Table 7.1. Habitat-specific densities (sightings*km^{-2}) of tiger shark prey during months that tiger sharks were caught (Chapter 5). All species were sighted more frequently in shallow habitats in all years. χ^2 values were calculated by comparing observed counts in shallow and deep transects to expected counts based on survey effort and area in each habitat.

	Shallow	Deep	χ^2	P
Dugongs				
1997	0.53	0.12	80.5	< 0.0001
1998	0.28	0.06	20.3	< 0.001
1999	0.40	0.11	49.8	< 0.0001
Birds				
1997	45.2	10.0	270.5	< 0.0001
1998	42.9	5.1	417.1	< 0.0001
1999	41.7	6.3	805.5	< 0.0001
Turtles				
1997	5.5	2.4	12.4	< 0.001
1998	4.3	2.6	5.4	< 0.05
1999	8.3	2.9	88.0	< 0.0001
Sea Snakes				
1998	12.8	4.0	20.4	< 0.0001
1999	16.9	5.3	33.8	< 0.0001

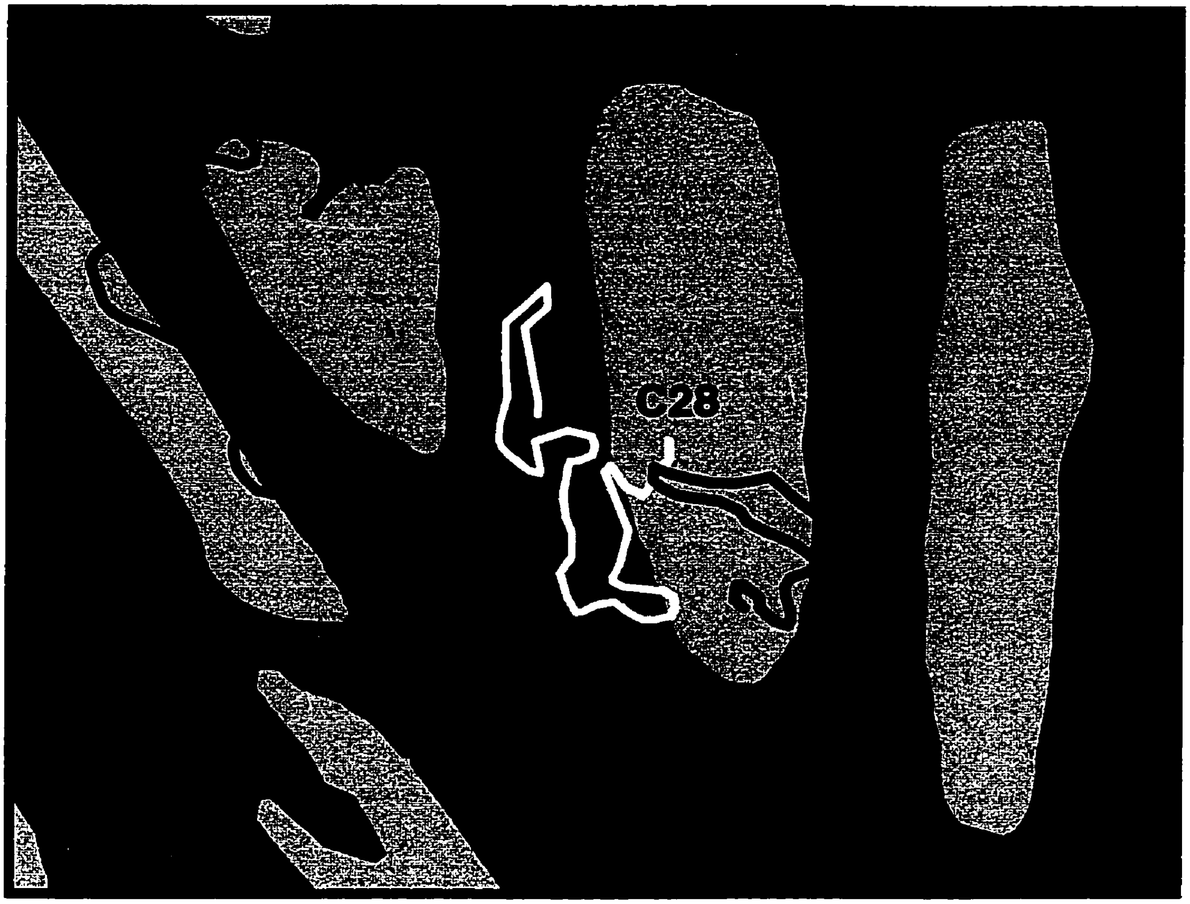


Figure 7.7. Example tracks for three tiger sharks that remained in a restricted area throughout a tracking session. The shark identifications are at the beginning of the track.

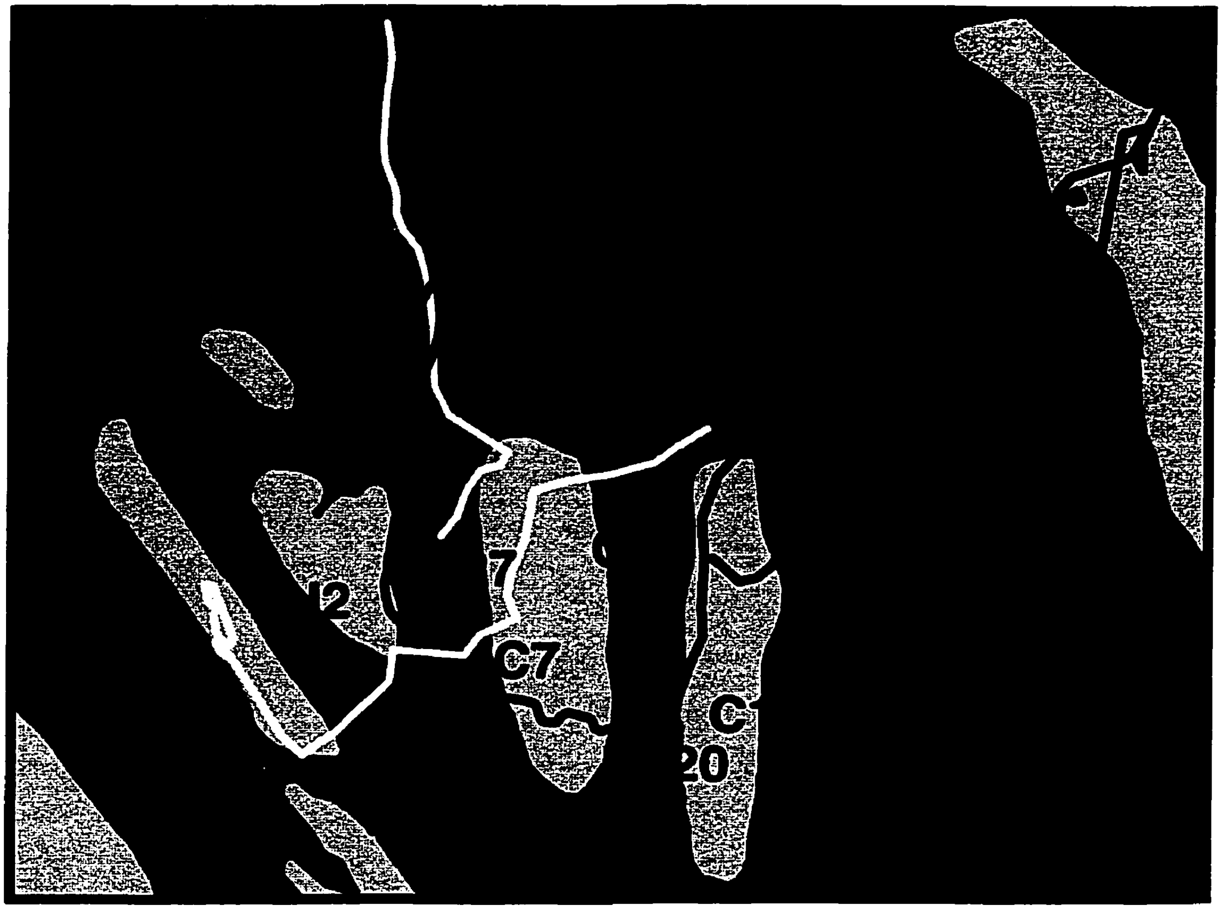


Figure 7.8. Example tracks for seven tiger sharks that made generally straight line movements. The shark identifications are at the beginning of the track. Notice that despite starting in different areas, the tracks of many individuals follow similar paths (e.g. C27, C20, C7).

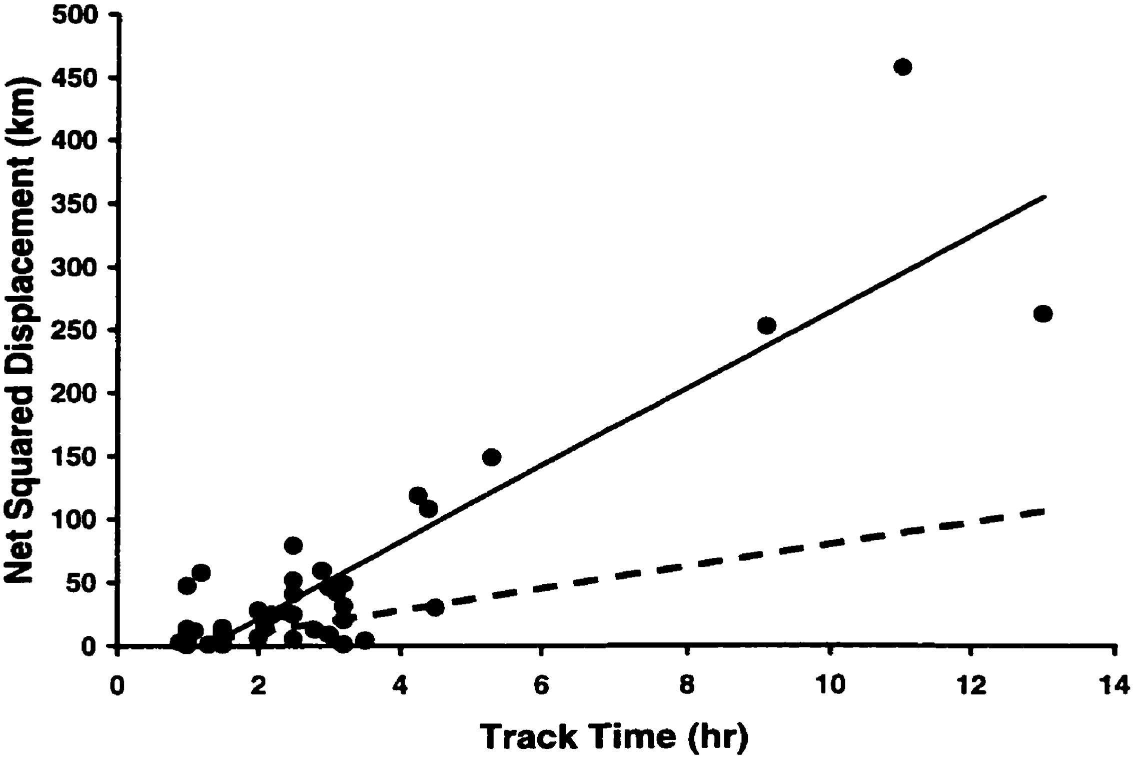


Figure 7.9. Net squared displacements of tiger sharks. Observed net displacements were significantly greater than expected values (dashed line), indicating directional movement.

Tiger sharks exhibited a preference for shallow habitats (Figure 7.10). On average, tiger sharks were found to spend approximately 36% of their time in shallow habitats, which is significantly more often than expected based on habitat availability (HA, 16%, $G = 325.3$, $P < 0.0001$) and on predictions generated by the RZ (21%, $G = 246.9$, $P < 0.0001$) and CRW (27%, $G = 268.0$, $P < 0.0001$) techniques. The sample randomization also showed a significant preference for shallow habitats: none of the 500 iterations had a greater mean use of shallow habitats than was observed.

There was individual variation in habitat use by tiger sharks (Figure 7.11). Based on RZ, there was no habitat preference detected for 23 sharks, 19 preferred shallow habitats, and 3 preferred deep habitats. Results were almost identical for CRW (Figure 7.11, Appendices 1, 2). Habitat use was not influenced by shark size (ANOVA, $F = 0.6$, df = 43, NS) or gender ($t = 0.6$, df = 43, NS).

7.4.3 Vertical Movements

All tiger sharks for which swimming depth data were obtained ($n = 37$ from Crittercam, $n = 2$ from internal transmitters) exhibited a stereotypical swimming pattern I refer to as "bouncing" (Figure 7.12). Bouncing involves a short period of swimming at a shallow depth (< 2 m) followed by a relatively rapid descent ($\bar{x} = 0.16$ m/s, sd = 0.03) then a period of swimming at depth before a slower ascent ($\bar{x} = 0.10$ m/s, sd = 0.02, $t = 10.1$, $P < 0.001$). At the bottom of most bounces, the shark swims within a few cm of the substrate, but not all bounces involve a descent to the substrate. Bounces last an average of 4.3 min (sd = 0.87) and sharks bounce an average of 14.0 times/hr (sd = 3.3). Sharks exhibited the bouncing swimming pattern even when over shallow habitats (Figure 7.12). During the descent phase, all tiger sharks continued power-swimming and did not glide.

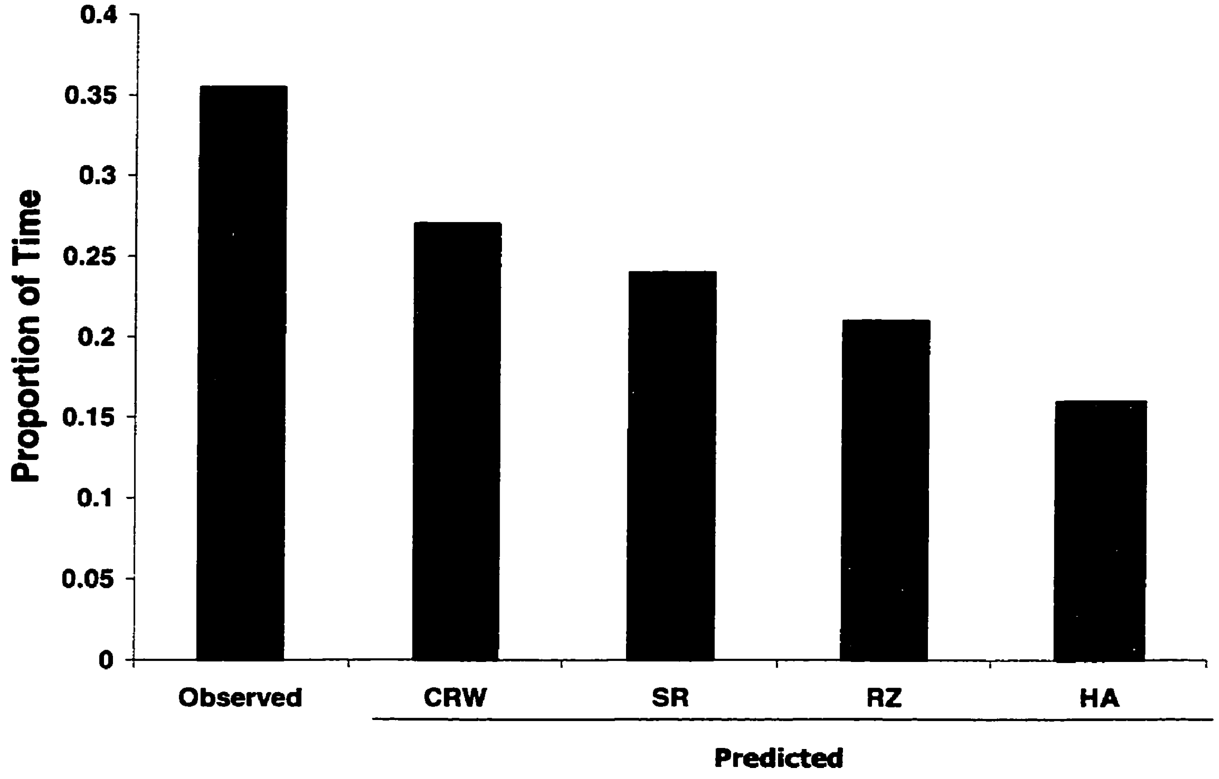


Figure 7.10. Average shallow habitat use by tiger sharks. Tiger sharks use shallow habitats significantly more often than expected based on all measures of habitat use. RZ = randomization, SR = sample randomization, CRW = correlated random walk, HA = Habitat availability.

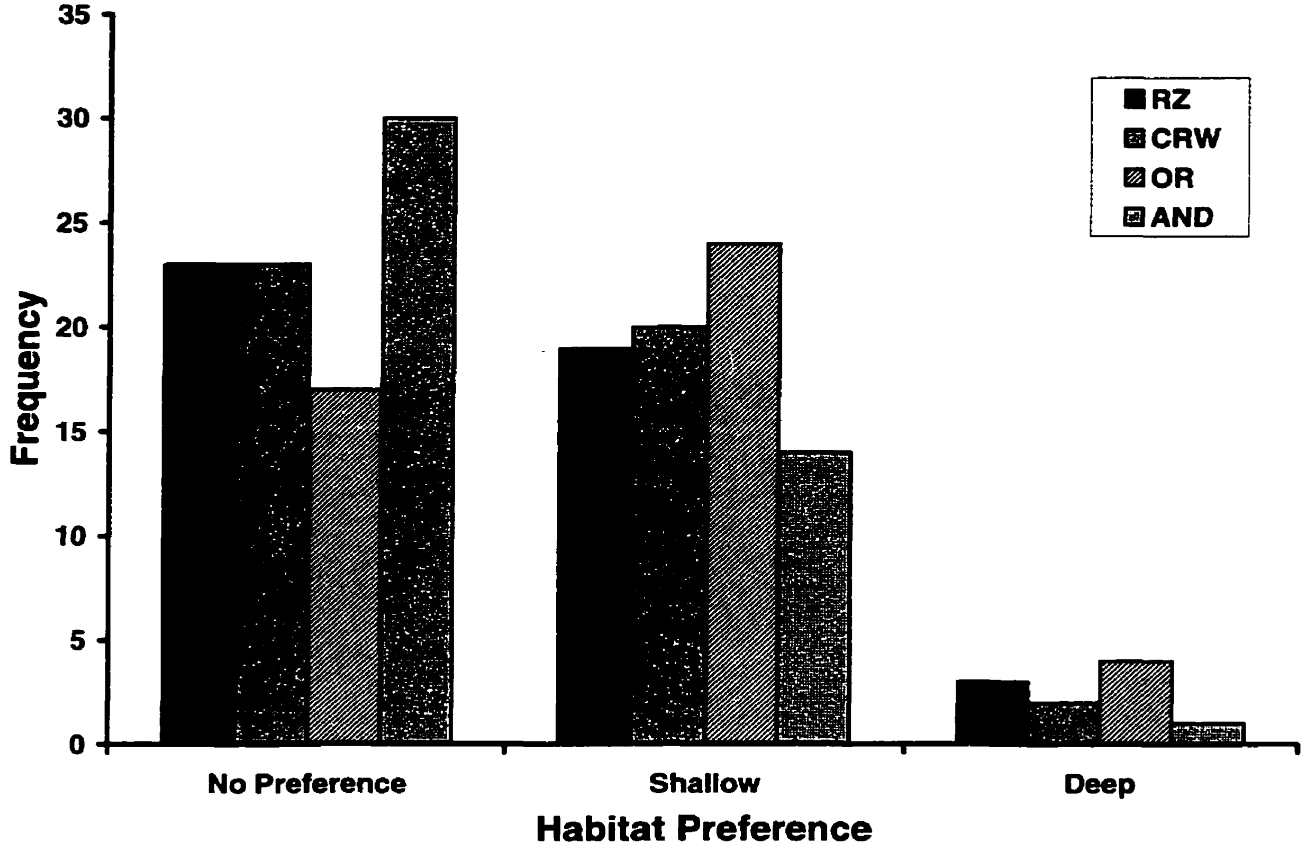


Figure 7.11. Individual variation in habitat use by tiger sharks based on RZ and CRW techniques. Bars represent the number of individuals that showed a significant preference for a habitat ($P < 0.05$) or did not significantly differ from expected habitat use with no preference ($P > 0.05$). OR = individuals were considered to have a habitat preference if *at least* one method showed a significant preference. Individuals were only considered to use habitats randomly if *both* methods showed random use. AND = individuals were considered to have a habitat preference only if both methods showed a significant preference. Individuals were considered to use habitats randomly if *either* method showed random use.

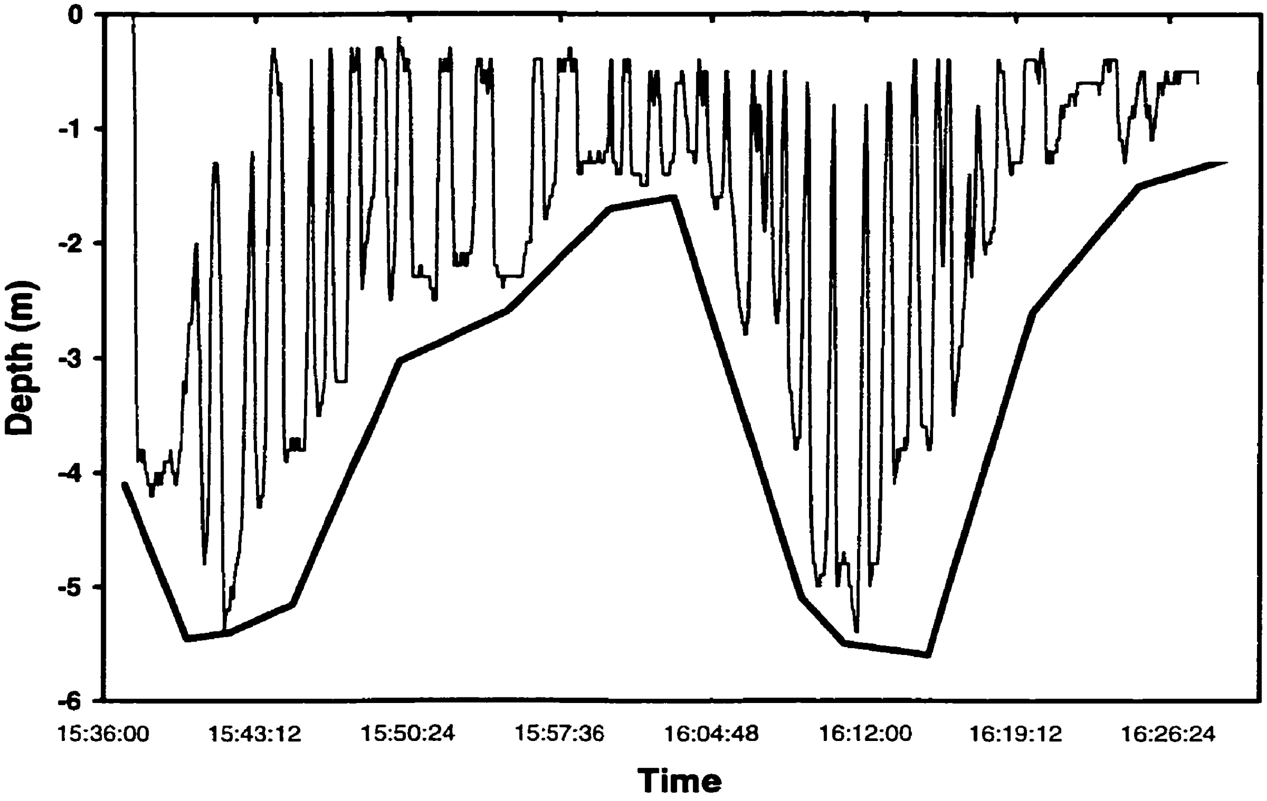


Figure 7.12. Vertical movements of tiger shark C2. The thick line indicates the bottom.

7.4.4 Foraging Behavior

Foraging behavior was observed in 12 of 22 tiger sharks (54.5%, Table 7.2). At least five sharks successfully captured prey and one (C37) also scavenged. Benthic foraging was observed in two sharks, and burst swims (usually < 5 sec) definitively associated with foraging were observed in 3 sharks (Table 7.2). In C5, 16 burst swims were observed, all on descents from the surface. At least two resulted in prey captures (flesh and blood were extruded from the gills within 2 - 4 seconds of a bite), and two appeared unsuccessful. In one of these, a shovelnose ray (Rhinobatidae) was seen escaping.

Nine sharks encountered 19 identifiable potential food items, but very few encounters resulted in predation attempts (Table 7.3). Sharks did not attack vigilant prey (head up and directed towards the approaching shark) and did not initiate or continue attacks after prey began to flee.

When descending from the surface, sharks were able to approach benthic prey closely before eliciting responses. One large teleost and three rays that were encountered by a descending shark did not respond until the shark was within approximately 2 m.

Table 7.2. Foraging behavior of tiger sharks. Bold text indicates definite foraging events and italics indicate possible foraging. Burst swims were always followed by bites in definite foraging events. However, Bite was only scored if it did not follow a burst swim, and usually involved lunges towards prey. INS = Prey inspection, SUC = successful attempt, UNS = unsuccessful attempt, UNK = success unknown

	Burst Swim			Bite		Benthic	INS
Shark	SUC	UNS	UNK	SUC	UNK	SUC	(see Table 7.3)
C4					*5*	**1**	
C5	**2**	**2**, *7*	**5**				**2**
C8	**3**	**1**	*14*				
C15							**1**
C17							**1**
C19					*2*		**2**
C20				**2**			**2**, *1*
C29			*3*				
C34							**1**
C37	**1**					**1**	**3**
C38							**1**
C39			*1*		*4*		

Table 7.3. Tiger shark encounters with potential food items. Inspection is defined as a shark altering its course in order to approach a potential food item. SB = shark behavior upon detecting prey. PB = prey behavior at time of detection.

Shark	Prey	SB	PB	Prey Response	Shark Response
C5	Shovelnose ray	Inspect	Rest, vigilant	Flight	Turn away
C5	Baldchin groper	Inspect	Stationary	Flight	None
C15	Shovelnose ray	Attack	Unknown	Flight	Stop attack
C15	Green turtle	Inspect	Swim, vigilant	None	Turn away
C17	Ray	Inspect	Rest, vigilant	None	Turn away
C17	Sea snake	Straight swim	Swim, vigilant	None	None
C19	Black stingray	Inspect	Rest, vigilant	Flight	None
C19	Shovelnose ray	Inspect	Rest, vigilant	Flight	Turn away
C20	Potato cod	Inspect	Vigilant	Turn towards	Turn away
C20	Green turtle	Inspect	Rest, vigilant	None	Reinspect, Turn away
C34	Mackerel	Straight swim	Swim vigilant	Move away	None
C34	Loggerhead turtle	Inspect	Rest, vigilant	None	None
C37	Ray	Inspect	Rest, vigilant	None	None
C37	Mackerel	Straight swim	Swim	None	None
C37	Dead teleost	Inspect	-	-	Consume
C37	Bait on line	Inspect	-	-	Consume
C38	Garfish	Straight swim	Swim, vigilant	Flight	None
C38	Turtle	Inspect	Rest, vigilant	None	None
C41	Mackerel	Straight swim	Swim	None	None

7.5 DISCUSSION

7.5.1 Prey Availability

Tiger shark prey species were more abundant in shallow habitats. This is not surprising as the majority of seagrass, the primary food of dugongs and green sea turtles, is found in such areas. Teleosts, the principle prey of sea birds and sea snakes and another potential prey item for tiger sharks, are also more common in shallow seagrass habitats, which contain approximately three times more teleost biomass than do deep habitats (Chapter 8, Chapter 9). Bottlenose dolphins are another potential prey item, but are rarely consumed (Heithaus in press a, Simpfendorfer et al. in press). During months that tiger sharks are present, dolphins are most abundant in deep habitats (Chapter 9).

7.5.2 Foraging Behavior

The high rate of foraging behavior observed in this study is surprising. Calculations of white shark (*Carcharodon carcharias*) energetic requirements suggest that large sharks may be able to survive for periods of weeks without feeding (Carey et al. 1982). In this study, however, 10 feeding events were recorded in only 49 hours of video footage (27 hr from foraging sharks), and this is likely an underestimate as prey items (especially those swallowed whole) could have been consumed without being seen. Such a high rate of foraging may be due to the bias associated with catching hungry sharks which may be more likely to attack baits than sharks that have full stomachs.

Another interesting result was the relatively low frequency of fast chases after prey and the lack of attacks on prey items that were inspected (sometimes within 2 m). The lack of attacks may be due to vigilant prey or the initiation of flight. That sharks would not chase prey once they have been detected is not surprising. Despite the strong burst-swimming capabilities of tiger sharks (Compagno 1984), they have limited maneuverability (M. Heithaus, personal observation), making a successful attack unlikely once detected. Thus, the tactic used by tiger sharks appears to be one of stalking and attacking unwary prey. Stealth is a foraging tactic also used by other sharks (e.g. white sharks, Klimley 1994, Strong 1996, Goldman and Anderson 1999; sevengill sharks, *Notorynchus cepidianus*, Ebert 1991).

Tiger sharks' reliance on stealth as a foraging tactic may help explain the high frequency of air-breathing animals in the tiger sharks' diets in Western Australia (e.g. Simpfendorfer 1992, Heithaus 2000, Simpfendorfer et al. 2000). Reduced vigilance during breathing and light attenuation make it difficult for animals at the surface to visually detect a predator below (Strong 1996), and the countershading and vertical stripes along the tiger sharks' flanks provide excellent camouflage, especially when swimming over seagrass. Furthermore, a tiger shark attacking from below reduces the number of escape routes for air-breathing prey (see Strong 1996), and by swimming near the bottom, tiger sharks would increase their search area of surface waters and their ability to visually detect silhouettes of air-breathing animals, a tactic thought to aid other marine predators (e.g. Weddell seals, *Leptonychotes weddelli*, Davis et al. 1999, blue sharks, *Prionace glauca*, Carey and Scharold 1990; white sharks, Strong 1996, Goldman and Anderson 1999).

While swimming near the bottom would be appropriate for hunting prey at the surface, tiger sharks also feed on benthic prey, including rays and air-breathing prey (e.g. dugongs, sea turtles, sea snakes) that spend most of their submerged time near the bottom (Simpfendorfer 1992, Heithaus in press a, Simpfendorfer et al. in press). When swimming along the bottom, tiger sharks are probably more likely to be detected by benthic prey. Moving into surface waters may reduce this problem as foraging benthic prey are likely to suffer reduced search areas of surface waters. Thus, the bouncing swimming pattern observed in Shark Bay tiger sharks may allow detection and capture of both benthic and air-breathing prey.

There are several alternate hypotheses for the observed tiger shark vertical movements, including enhanced olfactory detection. Detection of oils from floating or submerged carcasses may be an important way of locating scavenging opportunities, and tiger sharks may move between the surface and the bottom to detect vertically stratified scents. However, they would not be expected to bounce in shallow habitats, where water is well-mixed, and should move either against or across currents to maximize the probability of detecting scents. Tiger sharks do not conform to either of these predictions. Bouncing may also represent an adaptation for minimizing the energetic costs of swimming. A bouncing swimming pattern, with a gliding descent and powered ascent, may result in an energetic savings of 50% by negatively buoyant animals like sharks (Weihs 1973). Although such a swimming pattern has been found in both teleost fishes (e.g. yellowfin tuna, *Thunnus albacares*, Block et al. 1997) and a variety of marine mammals (Marshall 1998, Williams et al. 2000), Crittercam revealed that tiger sharks power-stroke as they descend, making the energetic-savings hypothesis unlikely as the sole explanation for this behavior. Also, if tiger sharks were engaging in vertical movements purely to save energy, bouncing should occur in other locations, but tiger sharks in Hawaiian waters < 100 m deep swim primarily along the bottom, rarely ascending (Holland et al. 1999). Sharks may still realize some energetic saving with a powered descent and future empirical study and theoretical modeling efforts may provide further support for the hypothesis that bounce-swimming by tiger sharks represents a foraging tactic.

7.5.3 Movements and Habitat Use

I found that tiger shark movements were primarily directional. Such movements are generally considered to be evidence for avoidance of an area (Turchin 1998, Bergman et al. 2000). Despite the apparent avoidance of the study area, tiger sharks return to it (Heithaus in press a, Chapter 5) indicating that it may be part of their home ranges. Thus, generally straight-line movement detected in most tiger sharks may be due to sizeable home ranges, which are common for large predators. Straight-line swimming has also been observed in scalloped hammerhead sharks (*Sphyrna lewini*; Klimley 1993) and in tiger sharks in Hawaii (Holland et al. 1999). In these studies, directional swimming was associated with round-trip excursions away from and back to a seamount (hammerhead sharks) and from coastal waters to an offshore bank (tiger sharks). In this study, tiger sharks were not followed long enough to determine whether movements were oriented towards a specific site. Future studies will be required to investigate long-term movements of tiger sharks in Shark Bay.

It is curious that sharks seldom moved to the south. This may be due to hypersaline waters (sometimes above 60 ppt) several kilometers south of the study area (Walker 1989), which may represent poor habitat for tiger sharks.

Tiger sharks used shallow seagrass habitats significantly more often than expected by all analysis methods despite the different biases associated with each method. This result supports the hypothesis that tiger shark distribution is influenced by prey availability, which is greater in shallow waters. There are several theoretical models that may explain this pattern. First, the ideal free distribution (IFD, Fretwell and Lucas 1970) predicts that the proportion of animals in a habitat will match the proportion of food available there. However, the basic IFD assumes that prey do not move among habitats in response to predation risk, which is unlikely in Shark Bay since tiger shark prey are highly mobile and should be able to switch among habitats. Theoretical models with mobile prey predict that the predators should be distributed proportional to the food of their prey (Hugie and Dill 1994, Sih 1998). In Shark Bay, such a model would also predict that tiger sharks should be most abundant over shallow seagrass habitats. The results of this study qualitatively support both hypotheses, but it is impossible to test whether these models are appropriate descriptions of this system without experimental manipulation.

The above models assume that frequency-dependent exploitation competition among sharks drives their habitat use, but the observed pattern may not require such frequency-dependence. As a shark spends more time in one habitat, prey may become more vigilant or leave the habitat (see Brown et al. 1999 for a discussion of the "ecology of fear"). Thus, an individual shark would improve its foraging success by switching among habitats. It is also possible that sharks would prefer to spend all their time in shallow habitats, but must cross deep habitats to access these areas. This seems unlikely given deep habitat preference exhibited by some individuals.

Another possibility is that tiger shark distribution is not influenced by the distribution of their prey, but by some unaccounted for and unmeasured factor. Water is well-mixed among habitats and temperatures are identical (Heithaus in press a) arguing against thermal differences influencing habitat use. Reproductive or social considerations are also unlikely explanations for the observed tiger shark habitat use patterns. There were no differences in habitat use by sharks of different sizes and genders and tiger sharks were not observed interacting with conspecifics during Crittercam deployments. Second, the study area does not appear to be an important mating area. Tiger sharks in other locations, like Hawaii, appear to be heavily scarred during mating attempts (e.g. Holland et al. 1999), but no such scars were observed during this study despite 270 shark captures. Finally, predation risk may influence habitat use (e.g. Lima and Dill 1990). However, the sharks tracked in this study were all large and there are no potential predators of large tiger sharks in the Eastern Gulf of Shark Bay. Thus, there is no support for these alternate hypotheses for the tiger shark's preference for shallow habitats.

Changes in prey availability have been proposed as an important factor influencing the large-scale movements of some shark species. For example, seasonal movements of tiger sharks in Shark Bay appear to be linked to changes in water temperature and prey availability, primarily sea snakes and dugongs (Heithaus in press a). Temperature and prey shifts may also be the cause of seasonal onshore - offshore movements of blue sharks (Tricas 1979). At a more restricted geographic scale, basking sharks (*Cetorhinus maximus*) have been shown to concentrate their foraging effort in areas of high plankton abundance (Sims and Quayle 1998). This study is the first to show that shark habitat use is associated with prey availability.

Tiger sharks may be at the apex of a trophic cascade in Shark Bay (Heithaus in press a, Simpfendorfer et al. in press) as well as a mediator of behaviorally mediated indirect interactions. Bottlenose dolphins are an occasional prey item of tiger sharks (Simpfendorfer et al. 2000), and dolphin habitat use is influenced by their food availability and the risk of predation from tiger sharks (Chapter 9). Therefore, since tiger shark habitat use appears to be determined by the distribution of their principal prey species (i.e., dugongs, sea snakes, sea turtles) the habitat use decisions of these species indirectly affect those of dolphins through their shared predator, the tiger shark. This situation provides a behavioral analog to the population-level process of apparent competition (Holt 1977, 1984) and stresses the importance of identifying the factors influencing habitat use decisions of top predators. Future studies in Shark Bay on the factors influencing habitat use decisions of turtles, sea snakes, and dugongs should begin to elucidate the complex behaviorally mediated indirect interactions in this community. Given the complexity of many communities (e.g. Polis 1991, Polis and Strong 1996), both marine and terrestrial, behaviorally mediated indirect interactions may be a common feature of communities and should be further investigated.

I have shown that using a variety of field techniques and appropriate methods for analyzing tracking data it is possible to gain insights into the factors influencing the spatial distribution of elusive top predators. Such insights are extremely valuable in elucidating the complex set of behavioral interactions within communities and provide a basis for making appropriate conservation decisions (e.g. Mills and Gorman 1997). Furthermore, I have shown that Crittercam is a valuable tool for studying marine top predators and will eventually allow us to gain a better understanding of the role of such predators in marine environments. Such studies are particularly important as many coastal marine ecosystems are being altered at an alarming rate, and proper conservation strategies may require a functional knowledge of the foraging behavior and habitat use decisions of top predators.

7.6 ACKNOWLEDGEMETNS

I thank Colin Simpfendorfer and Rory McAuley for their help in initiating the shark study by providing bait, fishing gear and advice. Chris Lowe, Peter Klimley, Larry Dill, Birgit Buhleier, Greg Marshall, Richard Connor, Bernie Crespi, Bernie Roitberg, David Lank, the crew of the R/V Flinders, and members of the Dill lab also provided advice. Funding and support were provided by National Geographic Expeditions Council, National Geographic Special Projects, Australian Geographic, NSERC Canada grant A6869 to LMD, Monkey Mia Wildlife Sailing, the PADI Foundation, the Columbus Zoo, the Dolphins of Shark Bay Research Foundation, Mercury Marine, Shakespeare Electronics, Humminbird, the Burghardt family, Fisheries WA, Kodak Australia, Monkey Mia Dolphin Resort, Singapore Airlines, Eurocom Computers, and public donations. Field assistance was provided by Justin McLash, Jenny Burghardt, Hugh Finn, Kym Collins, Patrick Greene, Colby Genrich, Lynne Barre, Alex Dent, Ian Hamilton, Fernando Bretos, and Seana Buchanan. Special thanks go to Birgit Buhleier, Greg Marshall, Derrik Cheung, Medhi Bakhtiari, and the NGS Special Projects team for providing Crittercam technical assistance and advice throughout the project. Logistical support was given by Brad Barton, David Charles, Ron Swann, Jo Heymans, Richard

Holst, the University of Western Australia Department of Anatomy and Human Biology, Monkey Mia Dolphin Resort, and the Shark Bay Fish Factory. Ian Hamilton provided helpful statistical advice. Thanks to Larry Dill, Ian Hamilton, Bernie Roitberg, and Bernie Crespi for comments on previous versions of this chapter. This research was conducted under the authority of Fisheries WA permit 69/97, Department of Conservation and Land Management permits SF002347 and NE001808, and Simon Fraser University Animal Care permit.

7.7 LITERATURE CITED

Arthur, S. M., B. F. J. Manly, L. L. McDonald and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77: 215-227.

Bergman, C. M., J. A. Schaefer and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123: 364-374.

Block, B. A., J. E. Keen, B. Castillo, H. Dewar, E. V. Freund, D. J. Marcinek, R. W. Brill and C. Farwell. 1997. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. Marine Biology 130: 119-132.

Brown, J. S., J. W. Laundré and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. Journal of Mammalogy 80: 385-399.

Carey, F. G., J. W. Kanwisher, O. Brazier, G. Gabrielson, J. G. Casey and H. L. Pratt Jr. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982: 254-260.

Carey, F. G. and J. V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. Marine Biology 106: 329-342.

Compagno, L. J. V. 1984. FAO species catalogue. Vol 4. Sharks of the world. Part 2 - Carchariniformes: FAO Fisheries Synopsis 125: 250-655.

Davis, R. W., L. A. Fuiman, T. M. Williams, S. O. Collier, W. P. Hagey, S. B. Kanatous, S. Kohin, and M. Horning. 1999. Hunting behavior of a marine mammal beneath the Antacrtic fast ice. Science 283: 993-996.

Ebert, D. A. 1991. Observations of the predatory behaviour of the sevengill shark *Notorynchus cepidianus*. South African Journal of Marine Science 11: 455-465.

Fretwell, S. D. and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16-36.

Goldman, K. J. and S. D. Anderson. 1999. Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. Environmental Biology of Fishes 56: 351-364.

Heithaus, M. R. in press a. The biology of tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes.

Heithaus, M. R. in press b. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. Marine Mammal Science

Heithaus, M. R. and I. M. Hamilton. in review. Assessing animal habitat use from tracking data.

Heithaus, M. R., G. Marshall, B. Buhleier and L. M. Dill. in press. Employing Crittercam to study the behavior and habitat use of large sharks. Marine Ecology Progress Series.

Holland, K. N., B. W. Wetherbee, C. G. Lowe and C. G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134: 665-673.

Holt, R. D. 1977. Predation, apparent competion and the structure of prey communities. Theoretical Population Biology 12: 197-229.

Holt, R. D. 1984. Spatial heterogeeity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45 (Suppl. A): 151-169.

Klimley, A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Marine Biology 117: 1-22.

Klimley, A. P. 1994. The behavior and feeding ecology of the white shark. American Scientist 82: 122-133.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lowe, C. G., B. M. Wetherbee, G. L. Crow and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Enironmental Biology of Fishes 47: 203-211.

Marshall, G.J. 1998. Crittercam: an animal-borne imaging and data logging system. Marine Technology Society Journal 32: 11-17.

Mills, M. G. L. and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11: 1397-1406.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138: 123-155.

Polis, G. A. and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147: 813-846.

Porter, W. F. and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. Journal of Wildlife Management 51: 681-685.

Randall, J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). Australian Journal of Marine and Freshwater Research 43: 21-31.

Sih, A. 1998. Game theory and predator-prey response races. Pages 221-238 *in* L. A. Dugatkin and H. K. Reeve, editors. Game Theory and Animal Behavior. Oxford University Press: Oxford.

Simpfendorfer, C. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. Australian Journal of Marine and Freshwater Research 43: 33-43.

Simpfendorfer, C. A., A. B. Goodreid and R. B. McAuley. in press. Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes.

Sims, D. W. and V. A. Quayle. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393: 460-464.

Stirling, I., D. Andriashek, and W. Calvert. 1993. Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. Polar Record 29: 13-24.

Strong, W. R. Jr. 1996. Shape discrimination and visual predatory tactics in white sharks. Pages 229-240 *in* A. P. Klimley and A. D. Ainley, editors. Great White Sharks: The Biology of Carcharodon carcharias. Academic Press: New York.

Tricas, T. C. 1979. Relationships of blue sharks, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fishery Bulletin, US 77: 175-182.

Turchin, P. 1998. Quantitative Analysis of Movement. Sunderland: Sinauer Associates

Walker, D. I. 1989. Regional studies – seagrass in Shark Bay, the foundation of an ecosystem. Pages 182-240 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, editors. Biology of Seagrasses. Elsevier: New York.

Weihs, D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. Journal of Marine Research 31: 194-209.

Williams, T. M., R. W. Davis, L. A. Fuiman, J. Francis, B. J. Le Boeuf, M. Horning, J. Calambokidis and D. A. Croll. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. Nature 288: 133-136.

Appendix 7.1. Tiger sharks tracked using internal transmitters and their habitat preferences based on correlated random walk (CRW) and randomization (RZ) methods. S= shallow, D = deep, NP = no preference detected, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

Track	Date	TL (cm)	Sex	Hours	CRW	RZ
IN1	8 Dec 97	349	F	4.5	S****	S****
IN2	17 Mar 98	338	M	13.0	NP	NP
IN3	13 Mar 99	360	M	2.0	S**	S**
IN4	10 Apr 99	356	F	2.0	NP	NP
IN5	11 Apr 99	324	M	1.5	S*	S**
IN6	17 Apr 99	348	M	1.0	NP	NP
IN7	21 Apr 99	398	F	4.25	S***	S***
IN8	10 Jul 99	367	F	5.3	NP	NP

Appendix 7.2. Tiger sharks tracked and recorded using Crittercam (sharks tracked or recorded for > 1.0 hour, 74.9 total recording hours) and their habitat preferences based on correlated random walk (CRW) and randomization (RZ) methods. TH = tracking hours, RH = video hours recorded, S= shallow, D = deep, NP = no preference detected, * $P < 0.05$, **, $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

Crittercam #	Date	TL (cm)	Sex	TH	RH	CRW	RZ
C1	12 Nov 97	320	M	1.5	1.5	NP	NP
C2	19 Nov 97	376	F	1.0	1.0	S*	S**
C3	23 Nov 97	350	M	1.0	1.0	NP	S*
C4	24 Nov 97	352	F	3.0	3.0	NP	S****
C5	25 Mar 98	358	M	2.5	2.5	NP	NP
C6	30 Mar 98	285	M	3.0	3.0	NP	NP
C7	4 Apr 98	319	M	3.2	3.0	NP	NP
C8	9 Apr 98	344	M	2.2	2.2	NP	S****
C9	10 Apr 98	339	M	2.8	2.8	NP	NP
C11	25 Apr 98	334	M	2.1	2.1	S*	S**
C12	26 Apr 98	380	F	3.1	1.7	NP	D***
C13	2 May 98	340	M	2.5	2.5	S**	S**
C14	4 May 98	285	F	9.1	3.0	NP	NP
C15	5 May 98	340	F	3.2	3.0	NP	NP
C16	6 May 98	393	F	1.0	0.3	S****	S****
C17	21 May 98	345	F	11.0	3.0	NP	NP
C18	24 May 98	230	F	3.0	3.0	S*	S****
C19	31 May 98	401	F	4.4	3.0	NP	D*
C20	24 Aug 98	294	F	3.2	3.0	S***	NP
C21	27 Aug 98	291	F	2.9	3.0	S**	S****
C23	16 Feb 99	310	F	1.0	1.0	NP	NP
C24	23 Feb 99	300	M	1.0	1.0	S*	S****
C25	23 Feb 99	331	F	1.5	1.5	NP	NP
C27	25 Feb 99	349	M	2.4	0.6	NP	S**
C28	27 Feb 99	271	F	3.2	0.0	D*	D**
C29	3 Apr 99	320	M	2.5	4.0	D*	NP
C30	4 Apr 99	310	F	1.0	0.0	NP	NP
C31	7 Apr 99	300	F	2.1	2.1	S*	NP
C32	12 Apr 99	280	F	1.1	2.0	NP	NP
C33	5 May 99	392	F	1.0	3.0	NP	NP
C34	10 May 99	370	F	1.5	1.5	S*	S*
C36	16 May 99	378	F	1.2	2.5	S*	S**
C37	23 May 99	302	F	1.5	1.5	S*	NP
C38	8 Jun 99	256	M	1.3	1.3	S**	S****
C39	24 Jun 99	289	F	2.5	2.9	NP	S****
C40	26 Jun 99	300	M	2.5	0.0	S****	NP
C41	8 Apr 00	309	F	3.5	3.5	S****	NP

CHAPTER 8

Fish Communities of Seagrass Meadows and Associated Habitats in Shark Bay, Western Australia

8.1 ABSTRACT

Seagrass habitats support some of the most productive marine communities and provide critical habitat for many fish species, including some of commercial importance. Previous studies have shown that, in most cases, fish communities of seagrass meadows are more diverse than those in adjacent habitats. However, most studies of fish communities in seagrass habitats have been conducted in very shallow waters and generally used seining methods to collect fish, which selects for small species and size classes. I used Antillean–Z style fish traps to study the fish communities of seagrass and associated habitats in the relatively undisturbed Eastern Gulf of Shark Bay, Western Australia. Overall, more species were caught in shallow seagrass habitats than in shallow unvegetated habitats, or in deep habitats both with and without seagrass. The number of species, individuals and biomass captured per trap was higher in vegetated areas. The structure of fish communities varied with the presence or absence of seagrass and an interaction between season and physical habitat (i.e., shallow shoal, channel, embayment plane). Unlike previous studies, a small number of species numerically dominated fish trap catches, most notably, striped trumpeters, *Pelates sexlineatus*, and to a lesser extent western butterfish, *Pentapodus vitta*. The dominance of *P. sexlineatus* led to lower Shannon-Weiner diversity in seagrass habitats than unvegetated areas despite higher species richness. The factors that influenced the abundance of particular species, including season, physical habitat, and seagrass cover, were identified and varied with species.

8.2 INTRODUCTION

Seagrass meadows are among the most productive ecosystems in the world and they provide critical habitat for many species of fishes by providing protection from predators as well as abundant food resources (Bell and Pollard 1989; Connolly 1994a). Seagrass ecosystems are under increasing pressure and many seagrass habitats are being destroyed rapidly (Shepherd et al. 1989). In order to understand and protect these critical habitats it is important to document the communities supported by undisturbed seagrass ecosystems and understand the factors that influence the distribution and abundance of associated species. The seagrass beds of Shark Bay, Western Australia are not under threat of human destruction, owing largely to Shark Bay's remote nature, relatively low commercial fishing pressure, and its listing as a United Nations World Heritage area in 1991. Thus, Shark Bay provides an opportunity to investigate the fish communities of seagrass beds in a relatively undisturbed ecosystem.

Fish communities in seagrass habitats are usually both more diverse and contain more individuals than adjacent unvegetated areas (Black et al. 1990, Ferrell and Bell 1991, Connolly 1994b, Gray et al. 1996), but this pattern is not universal (Hanekom and Baird 1984). Most studies on fishes in seagrass habitats have been carried out in very shallow waters (e.g. <1.5 m, Ferrell and Bell 1991, Gray et al. 1996). And although differences in species composition and abundance have been found between deep and shallow seagrass beds (Bell et al. 1992), the generality of these results is unclear. In addition, sampling techniques have been limited largely to seining, which tends to be selective for small size classes (Ferrell and Bell 1991, Gray et al. 1996, de Troch et al. 1996). Fish traps have been used successfully to sample fish communities in tropical estuaries (e.g. Sheaves 1992, 1995), and may provide insights into the fish communities of seagrass habitats different from those obtained by seining methods because they capture larger individuals and can readily be used in a variety of water depths.

In this study, I used Antillean-Z fish traps to investigate the structure and diversity of fish communities as well as the distribution and abundance of particular fish species in seagrass habitats and associated unvegetated areas of both shallow and deep habitats. The goals of this study were to 1) describe the fish communities of the Eastern Gulf of Shark Bay, 2) determine the patterns of species richness and diversity among different habitats and seasons, 3) determine the factors that influence the distribution and abundance of common fish species, and 4) investigate seasonal changes in the size distribution of common species.

8.3 METHODS

8.3.1 Study Site

The study was conducted 1997 - 1999 in the Eastern Gulf of Shark Bay, Western Australia (approximately 25°45'S, 113°44'E, Figure 8.1). Shark Bay is a large, semi-enclosed bay with extensive shallow seagrass beds (< 4 m depth), channels (6 - 12 m), and broad expanses of deeper waters (embayment planes, 6 - 15 m). The boundaries between habitats are generally distinct. To further minimize edge effects, areas 4 - 6 m deep were not included in analyses. Shallow habitats are predominantly covered by seagrasses (primarily monospecific stands of *Amphibolis antarctica* and occasionally *Posidonia australis*) but also contain large patches of sand. In contrast, deep habitats (generally >7.5 m) are covered largely by sand or silt with some isolated seagrass patches. The habitats in this study were classified by two factors: physical habitat (shallow, channel, embayment plane) and cover (seagrass, no seagrass).

Shark Bay is situated at the boundary between tropical and temperate waters and both warm - and cold-water fish species are present (Hutchins 1990). Seasonal fluctuations in water temperatures are found in the study site (Heithaus in press). During warm months surface water temperatures are generally above 20° C but drop to a minimum of 14° C in the winter months. Due to the mixed species composition of the bay, these seasonal fluctuations in water temperature may influence the abundance of some species. For the purposes of this paper, seasons are defined as "warm" (September-May) or "cold" (June-August) based on both changes in water temperature and in the community present in the study area (Chapter 5).

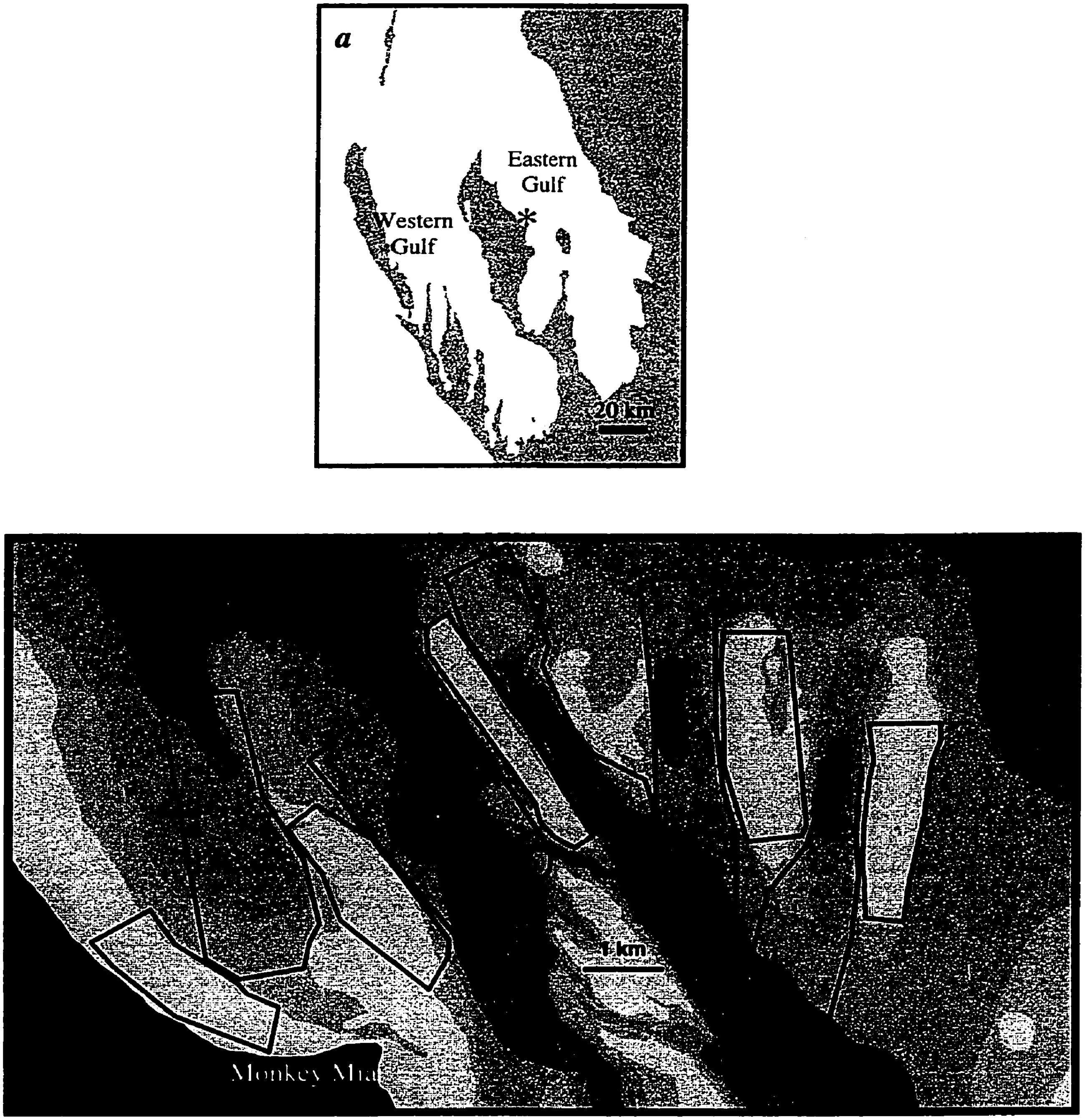


Figure 8.1. *a*) Shark Bay, Western Australia. The study site was located in the Eastern Gulf and is indicated with an asterisk. Land is gray. *b*) The study area was divided into eleven sampling zones for fish trapping, indicated with polygons. The lightest color represents shallow water (< 2m at MSLW) and successively darker colors represent waters 2-5 m, 5-7 m, 7-9 m, and >9 m. Land is black.

8.3.2 *Field Methods*

Fish were captured with Antillean-Z fish traps. Traps were approximately 1.1 m long, 0.6 m tall, and 0.6 m wide and had straight, conical entrances (see Sheaves 1992 for a detailed description of trap design). Traps were covered with either a small (12 mm) square wire mesh or a larger (35 mm) hexagonal mesh. Traps were baited with approximately 250 g of cut pilchards (*Sardinops neopilchardus*) placed in a bait capsule hung from the ceiling of the trap. The bait capsules were made of PVC pipe capped at both ends with numerous 10 mm holes to allow water to flow easily through the capsule while preventing bait removal by fishes in the trap.

Up to ten traps were set concurrently from an 11 m catamaran. In most cases, traps were set simultaneously in both deep and shallow habitats to avoid biases caused by tidal or diel movements of fishes. In addition, an equal proportion of small- and large-mesh traps were placed in each habitat to remove potential biases of mesh size on catches (Sheaves 1995). The location of the initial trap in a habitat was haphazard but further traps were placed along a line, spaced at least 80 m apart (usually over 150 m) to avoid overlap in catch radii, which are generally less than 40 m (Sheaves 1992). Traps were "soaked" for approximately two hours to maximize catch rate and minimize trap saturation (Sheaves 1995). When traps were recovered, the fork length (FL) of every fish was measured and a sample of individuals of each species were weighed using an Ohaus electric balance (Model LS2000, 2000 g capacity, 1.0 g accuracy). All individuals were returned to the water alive. For those species in which many individuals were occasionally caught in a single trap, length-weight relationships (Table 8.1) were used to determine biomass without weighing all individuals. Sharks were omitted from biomass analyses due to their disproportionately large size.

Table 8.1. Length (mm) – weight (g) relationships of 11 species used to generate biomass estimates.

Species	N	Equation	R^2
Amniataba caudovittatus	18	$Y = 2.9659e^{0.0195x}$	0.91
Apogon ruppelli	16	$Y = 0.2259e^{0.0452x}$	0.92
Choerodon rubescens	6	$Y = 2.9889e^{0.0182x}$	0.91
Chrysophrys auratus	68	$Y = 6.6011e^{0.0164x}$	0.96
Lethrinus laticaudis	23	$Y = 1.7954x - 20.715$	0.92
Monacanthus chinensis	12	$Y = 0.3691x - 20.215$	0.94
Pelates sexlineatus	252	$Y = 3.3898e^{0.0167x}$	0.93
Pentapodus vitta	168	$Y = 1.523e^{0.0221x}$	0.95
Psammoperca waigiensis	30	$Y = 4.2952e^{0.016x}$	0.97
Rhabdosargus sarba	28	$Y = 12605x - 113.16$	0.95
Saurida undosquamis	12	$Y = 3.8252e^{0.0128}$	0.94

8.3.3 Statistical Methods

The structure of fish communities was described with principal components analysis. To improve the quality of this analysis, only species with more than 90 individuals were included and all capture data were log (x+1) transformed prior to analysis (Clarke and Green 1988). Only principal components with eigenvalues over 1.0 were included in subsequent analyses (Tabachnick and Fidell 1983). Species were considered to be an important factor of a principal component if their loading value was greater than 0.55 or less than -0.55 (Tabachnick and Fidell 1983).

Community diversity was quantified using the Shannor-Wiener index (H') using species represented by at least 10 individuals. Because one species dominated fish trap catches and might mask underlying patterns of abundance and diversity (cf. Ferrell and Bell 1991), index values were also calculated excluding this species. H' is an underestimate of actual species diversity, but becomes less so as sample size increases (Zar 1984). Therefore, I also used the average number of species caught per trap as an estimate of diversity.

Analyses of variance (ANOVA) were used to investigate the influences of season, physical habitat, and seagrass cover on the number of species and individuals captured per trap, biomass per trap, and catch rates of each of the ten most common species. Season, physical habitat, and cover were all treated as class variables and fixed effects. Data were log (x+1) transformed and checked for homogeneity of variances using Bartlett's test, B_C (Zar 1984). Non-significant interactions were removed from analyses. If two factors showed a significant interaction, the factors involved were not considered as main effects regardless of significance level. Tukey's test, which corrects for multiple comparisons, was used to determine significant differences among means in the case of interactions.

The influences of season, physical habitat, and cover on community structure were determined with MANOVA on principal component scores for each trap set that captured fish. As with ANOVAs, factors were considered fixed effects and non-significant interaction terms were removed from the analysis. Also, I do not consider factors involved in interactions as main effects regardless of significance level. I used contrasts in JMP IN 4.0.3 (SAS Institute Inc.) to determine significant differences among means in the case of interactions, and F-tests to determine which factors had significant effects on individual principle components. All P-values from both contrasts and F-tests were Bonferroni corrected for multiple comparisons.

8.4 RESULTS

8.4.1 Community Structure

Overall, 684 traps were set for approximately 1,368 hours. Traps were set in vegetated shallow (n = 233), unvegetated shallow (n = 40), vegetated channel (n = 14), unvegetated channel (n = 322), vegetated embayment plane (n = 22), and unvegetated embayment plane (n = 97) habitats. Of these sets, 293 were during warm months and 391 during cold months. A total of 13,734 individuals representing 31 fish species from 23 families were captured (Table 8.2). Additionally, 5 bar-bellied sea snakes (*Hydropis elegans*) were caught. *Pelates sexlineatus* numerically dominated the catch (76.8%) followed by *Pentapodus vitta* (13.0%). *Chrysophrys auratus* (1.7%), *Amniataba caudovittatus* (1.4%), and *Rhabdosargus sarba* (1.2%) were the only other species to contribute over 150 individuals to the catch (Table 8.2). Together these five species represent over 93% of the fishes captured.

There were both qualitative and quantitative differences in community composition among habitats. Although *Pelates sexlineatus* and *Pentapodus vitta* dominated all habitats, the relative abundance of *P. sexlineatus* was far greater in seagrass habitats of shallows, channels and embayment planes than in unvegetated habitats (Figure 8.2). In unvegetated habitats of both shallows and channels, *P. vitta* was dominant. *P. sexlineatus* was dominant in unvegetated areas of embayment planes, but this may be due to the sparse stands of seagrass found throughout this habitat that may not have been noted during trap deployments. In general, either *P. vitta* or *P. sexlineatus* dominated traps set in unvegetated areas of embayment planes; few contained both species.

Four principal components (each defining a group of species that tend to covary) had eigenvalues over 1.0. Together, they explained 59% of the variation in fish communities (Table 8.3). Only nine species were identified as significant factors in principal components. PC1 was characterized by the presence of *Rhabdosargus sarba*,

Table 8.2. Overall catches and occurrences of fish species caught in fish traps. Ch = channel, P = embayment plane, S = shallow, Y = seagrass present, N = seagrass absent. Habitat and cover type in bold represent the most common occurrence.

Scientific Name	Common Name	N	Habitat	Cover
Apogonidae				
Apogon ruppelli	Gobbleguts	100	Ch, **S**	**Y**, N
Carangidae				
Selaroides leptolepis	Smooth Tailed Trevelly	41	**P**	**N**
Carcharhinidae				
Carcharhinus amblyrhychos	Grey Reef Shark	1	**S**	**Y**
Centropomidae				
Psammoperca waigiensis	Sand Bass	91	Ch, **S**	**Y**, N
Chaetodontidae				
Chelmon marginalis	Marginated Coralfish	1	**P**	**N**
Congridae				
Unidentified		1	**S**	**Y**
Gerreidae				
Gerres subfasciatus	Roach	1	**S**	**Y**
Harpadontidae				
Saurida undosquamis	Large-Scaled Grinner	8	Ch, **P**	**N**
Hemiscyllidae				
Chilioscyllium punctatum	Grey Carpet Shark	7	**S**	**Y**
Labridae				
Choerodon schoenleinii	Bluespotted Tuskfish	16	**S**	**Y**
Choerodon rubescens	Baldchin Groper	10	Ch, **S**	**Y**
Halichoeres brownfieldi	Brownfield's Wrasse	1	**S**	**Y**
Lethrinidae				
Lethrinus laticaudis	Blue-Spotted Emperor	92	Ch, **S**	**Y**, N
Lutjanidae				
Lutjanus erythropterus	Stripey Seaperch	6	**Ch**	**N**
Monacanthidae				
Monacanthus chinensis	Fan-Bellied Leatherjacket	102	Ch, **P**, **S**	**Y**, N
Scobinichthys granulatus	Rough Leatherjacket	16	Ch, **P**, **S**	**Y**, N
Mugiloididae				
Parapercis multiplacata	Red Banded Grubfish	9	Ch, **P**	**N**
Mullidae				
Upeneus tragula	Bartailed Goatfish	6	**Ch**, P, S	Y, **N**
Nemipteridae				
Pentapodus vitta	Western Butterfish	1,782	**Ch**, P, S	Y, **N**
Orectolobidae				
Orectolobus ornatus	Banded Wobbegong	1	**S**	**Y**
Pseudochromidae				
Labracinus lineata	Lined Dottyback	34	Ch, **S**	**Y**, N
Platycephalidae				
Cymbacephalus nematophthalmus	Fringe-eyed Flathead	1	**S**	**Y**
Scorpaenidae				

Apistops sp	Waspfish	1	**Ch**	**N**
Sparidae				
Rhabdosargus sarba	Tarwhine	161	Ch, P, **S**	**Y**, N
Chrysophrys auratus	Pink Snapper	240	**Ch**, P	Y, **N**
Teraponidae				
Amniataba caudovittatus	Yellowtail Trumpeter	198	**S**	**Y**
Pelates sexlineatus	Striped Trumpeter	10,548	Ch, P, **S**	**Y**, N
Pelates quadrilineatus	Trumpeter	144	P, **S**	**Y**
Tetraodontidae				
Torquigener pleurogramma	Banded Toadfish	73	**Ch**, P, S	Y, **N**
Torquigener parcuspinus	Orange-Spotted Toadfish	40	Ch, **P**, S	Y, **N**
Lagocephalus sceleratus	Silver Toadfish	2	P, S	Y, N

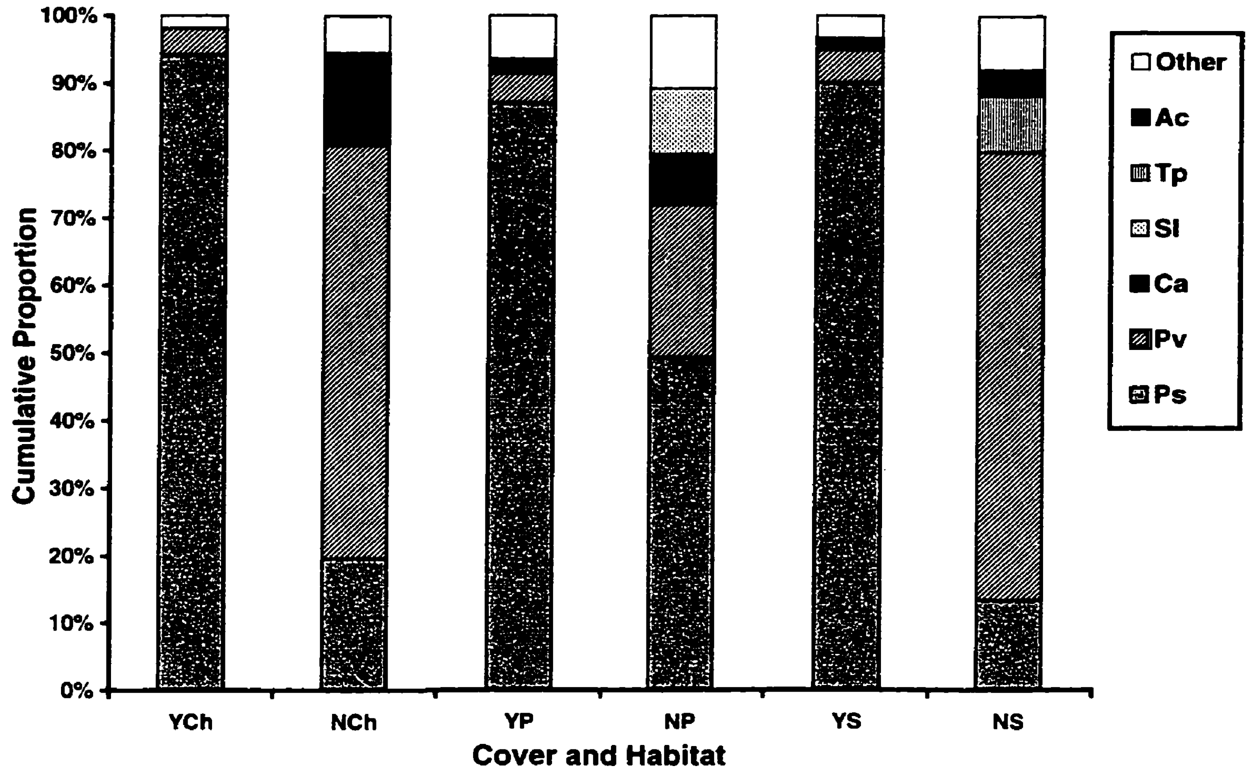


Figure 8.2. Variation in community composition among habitats and cover types. Communities are more similar among locations with similar cover rather than similar physical habitats. Y = seagrass, N = no seagrass, Ch = channel, P = embayment plane, S = shallow, TP = *Torquigener pleurogramma*, Sl = *Selaroides leptolepis*, Pv = *Pentapodus vitta*, Ca = *Chrysophrys auratus*, Ac = *Amniataba caudovittatus*, Ps = *Pelates sexlineatus*.

Table 8.3. Factor loadings (with varimax rotation) of principal components with eigenvalues greater than 1.0.

	PC1	PC2	PC3	PC4
Proportion of total variance	0.17	0.15	0.14	0.13
Eigenvalue	2.1	1.3	1.2	1.2
Species				
Pelates sexlineatus		0.81		
Rhabdosargus sarba	0.57			
Amniataba caudovittatus		0.80		
Psammoperca waigiensis				0.87
Lethrinus laticaudis			0.79	
Chrysophrys auratus			0.72	
Pentapodus vitta	0.66			
Apogon ruppelli				0.73
Pelates quadrilineatus	0.76			

Pentapodus vitta, and *Pelates quadrilineatus* and PC2 was driven primarily by *Pelates sexlineatus* and *Amniataba caudovittatus* . *Lethrinus laricaudis* and *Chrysophrys auratus* were the significant species in PC3 while PC4 was characterized by *Psammoperca waigiensis* and *Apogon rupelli.*

Community structure (i.e., principal component scores) was influenced by seagrass cover and an interaction between season and physical habitat (Table 8.4). Cover was a main effect for both and PC2 and PC4 with higher values found in seagrass habitats (Table 8.5, Figure 8.3). PC2 values were also affected by season with higher values during cold months. PC1 was influenced by season with higher values during cold months (Table 8.5). Physical habitat had a main effect on PC2 and values were higher in shallow physical habitats than both deep physical habitats (Table 8.5). PC3 values were high in channels during both seasons and shallow habitats during warm months, and low in shallow habitats during cold months (Figure 8.4a). Finally, PC4 values were only high in shallow habitats during warm months (Figure 8.4b).

8.4.2 Community Diversity and Fish Abundance

In general, more species were caught in shallow physical habitats than deeper ones and a more species were caught in areas covered by seagrass than in unvegetated areas (Table 8.2, Table 8.5). Nine species represented by more than a single individual were restricted to one cover type. Five species were found only over seagrass and four were found only over unvegetated areas.

The number of species caught per trap set was influenced by an interaction between physical habitat and cover (ANOVA, $F = 23.7$, $df = 1,653$, $P < 0.001$) and an interaction between season and cover (ANOVA, $F = 13.8$, $df = 1,653$ $P < 0.001$). More species were caught in seagrass habitats and shallows and seagrass covered areas during warm months (Figure 8.5). Despite higher species richness in shallow seagrass-covered habitats, diversity (H') was lower in seagrass areas than in unvegetated portions of all habitats (Table 8.6) and unvegetated regions had higher species evenness. This result could not be explained entirely by sample size differences among habitats. Lower H' diversity in seagrass covered areas almost entirely due to the dominance of *Pelates sexlineatus* in these areas, and when *P. sexlineatus* was removed from the calculations,

Table 8.4. MANOVA table showing the influence of season, physical habitat, and seagrass cover on community structure described by four principal components.

Factor	Wilks Lamda	approximate F	df	P
Cover	0.937	8.4	4,496	< 0.001
Physical habitat	0.831	12.0	8,992	< 0.001
Season	0.970	3.9	4,496	< 0.005
Season:Physical habitat	0.949	3.3	8,992	< 0.001

Table 8.5. Summary of F-Tests showing factors that had a significant effect on values of the four principal components. The season, cover type or physical habitat with the highest values are given. Results of independent contrasts are shown in Figure 8.4. *P < 0.05, **P < 0.01, P < 0.001.

Factor	PC1	PC2	PC3	PC4
Season	Cold**			
Cover		Seagrass**		Seagrass**
Physical habitat		Shallow*		
Physical habitat:Season			Figure 8.4a*	Figure 8.4b***

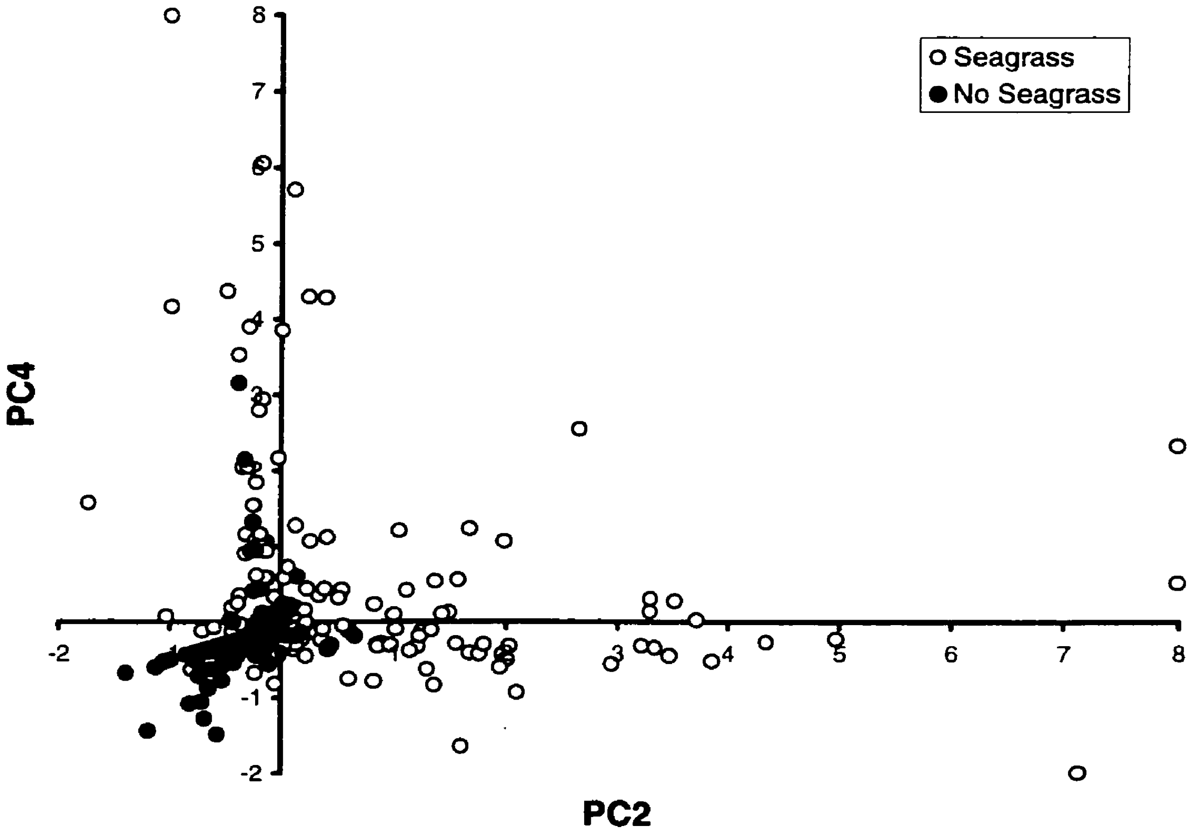


Figure 8.3 Plot of PC2 and PC4 relative to seagrass cover. Seagrass habitats had significantly higher scores for both principal components than did unvegetated habitats.

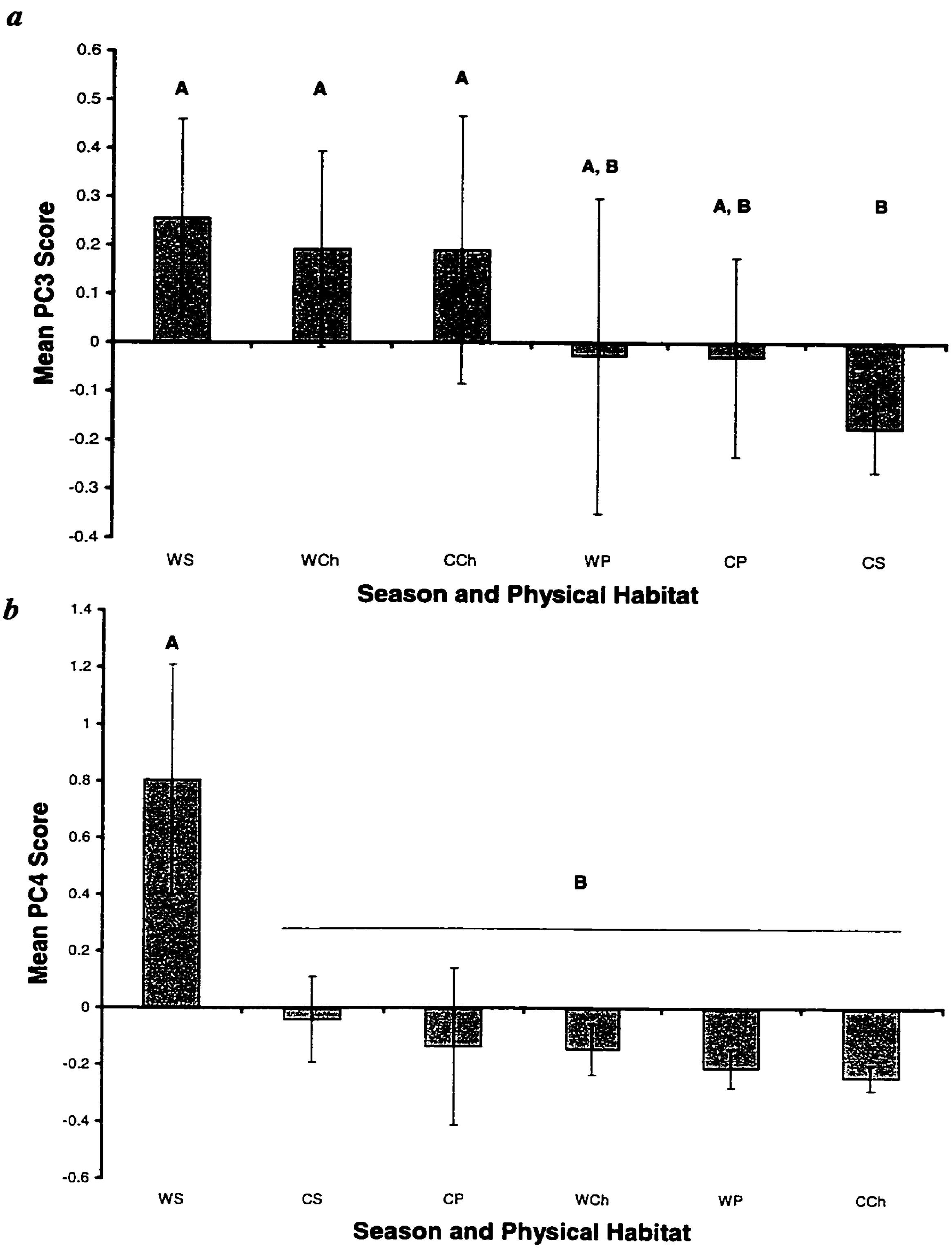


Figure 8.4. Differences in principal component scores for all combinations of season and physical habitat a) PC3, b) PC4. W = warm, C = cold, S = shallow, Ch = channel, P = embayment plane. Bars labeled with the same letter are not significantly different from each other at $P < 0.05$. Error bars represent 95% confidence intervals.

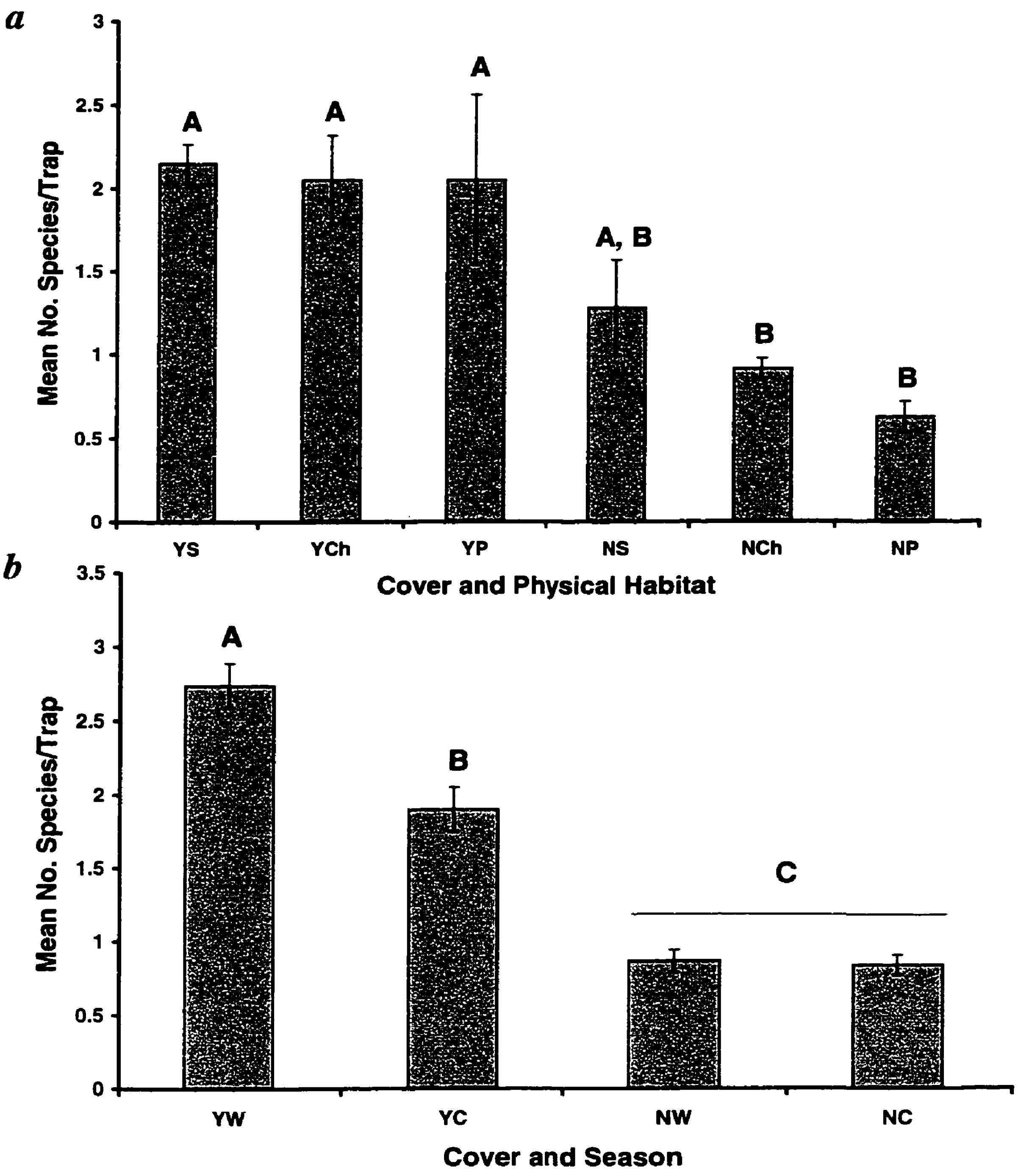


Figure 8.5. Influence of a) physical habitat and cover and b) season and cover on the number of species caught in each trap set. Bars labeled with the same letter are not significantly different at $P < 0.05$. Y = seagrass, N = no seagrass, Ch = channel, P = embayment plane, S = shallow, W = warm, C = cold. Error bars represent 95% confidence intervals.

Table 8.6. Diversity measures for the six habitats sampled. Notice that results change considerably with the removal of ***Pelates sexlineatus*** from calculations. Y = seagrass, N = no seagrass, Ch = channel, P = embayment plane, S = shallow, (-) = ***P. sexlineatus*** removed from calculations, S = Species Richness, AI = average number of individuals caught per trap, H' = Shannon-Wiener diversity index, J' = Evenness.

	S	AI	AI (-)	H'	H' (-)	J'	J' (-)
YCh	8	27.2	1.8	0.31	1.23	0.15	0.69
NCh	17	4.6	3.7	1.18	0.86	0.46	0.34
YP	9	27	3	0.50	1.58	0.24	0.76
NP	14	4.1	2	1.32	1.38	0.60	0.63
YS	22	41.1	4.9	0.59	1.90	0.22	0.71
NS	9	5.6	5.1	1.19	0.91	0.54	0.41

diversity was higher in vegetated regions, especially in shallow habitats (Table 8.6).

The number of individuals caught in each trap was only influenced by cover with significantly more individuals captured in seagrass beds ($\bar{x}$ = 39.2 individuals, s = 83.5, n = 249 trap sets) than in areas without seagrass ($\bar{x}$ = 5.8 individuals, s = 11.6, n = 398 trap sets; ANOVA, F = 32.1, df = 1,646, P < 0.001). Neither season nor physical habitat had a significant effect (ANOVA, F = 2.0, df = 1,653, NS, and F = 2.8, df = 2,653, NS, respectively). Biomass per trap was significantly higher in sets over seagrass ($\bar{x}$ = 1932.2 g, s = 3137.4 g, n = 249) than those over unvegetated areas ($\bar{x}$ = 417.6 g, s = 798.2 g, n = 398, ANOVA, F = 18.9, df = 1,646, P < 0.001), and physical habitat was also a significant main effect with average biomass higher in shallow habitats ($\bar{x}$ = 1859.0 g, s = 3150.8 g, n = 237) than channels ($\bar{x}$ = 547.5g, s = 1036.1 g, n = 292) or embayment planes ($\bar{x}$ = 321.2, s = 978.2 g, n = 118, ANOVA, F = 10.7, df = 2,646, P < 0.01). There was no influence of season on biomass per trap (ANOVA, F = 2.7, df = 1,646, NS).

8.4.3 Species-Specific Abundance

The catch rates of the ten most common species varied with a variety of factors (Table 8.7). The number of individuals captured per trap of *Amniataba caudovittatus*, *Apogon rupelli*, *Rhabdosargus sarba*, *Pelates quadrilineatus* and *P. sexlineatus* was higher in seagrass covered areas than unvegetated ones. *Amniataba caudovittatus* was also found exclusively in shallow physical habitats. The abundance of *Chrysophrys auratus* varied only in relation to physical habitat. Individuals were captured in both deep physical habitats and never in shallow areas. *Lethrinus laticaudis* catch rates differed according to an interaction between season and cover (Figure 8.6), and were higher in shallow and channel habitats than in embayment planes. Catches were highest over seagrass, but only during warm months. *Monocanthus chinensis* abundance was highest in seagrass areas and in shallow areas during warm months (Figure 8.7). *Pentapodus vitta* was caught most often during cold months and was caught less often in seagrass areas and embayment planes (Figure 8.8). *Psammoperca waigiensis* capture rate was highest in shallow habitats during warm months (Figure 8.9).

Table 8.7. Factors influencing the catch rates of the ten most common species based on ANOVA. For main effects, the preferred cover, physical habitat, or season is given in parentheses. Bracketed factors indicate an interaction of factors. Asterisks indicate significance level of ANOVAs for a particular factor or interaction. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Factor
Amniataba caudovittatus	Cover (seagrass)***, Physical habitat (shallow)*
Apogon ruppelli	Cover (seagrass)***
Chrysophrys auratus	Physical habitat (channel, embayment plain)*
Lethrinus laticaudis	[Season:Cover]***, Physical habitat (shallow, channel)**
Monacanthus chinensis	[Season:Physical habitat]**; Cover (seagrass)**
Pelates quadrilineatus	Cover (seagrass)**
Pelates sexlineatus	Cover (seagrass)***
Pentapodus vitta	[Physical habitat:Cover]**; Season (cold)**
Psammoperca waigiensis	[Season:Physical habitat]***
Rhabdosargus sarba	Cover (seagrass)***

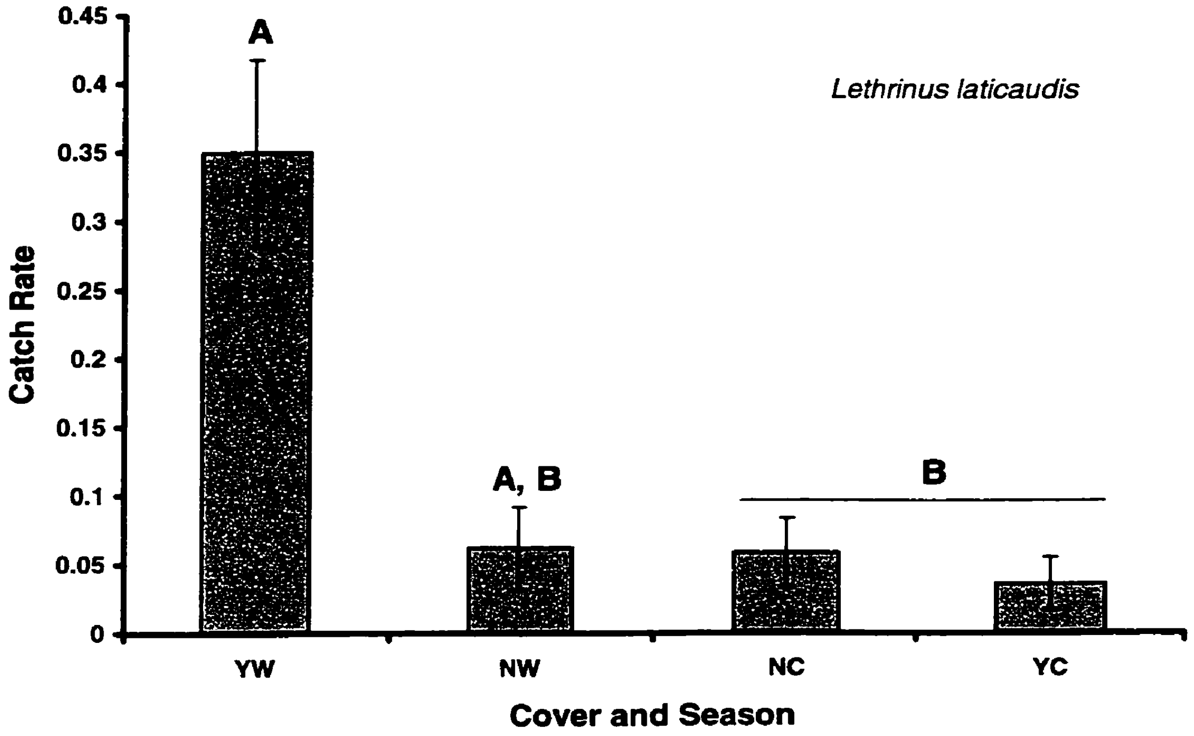


Figure 8.6. Influence of the interaction between season and cover on catch rates of *Lethrinus laticaudis*. Bars labeled with the same letter are not significantly different at $P < 0.05$. W = warm, C = cold, Y = seagrass, N = no seagrass. Error bars represent 95% confidence intervals.

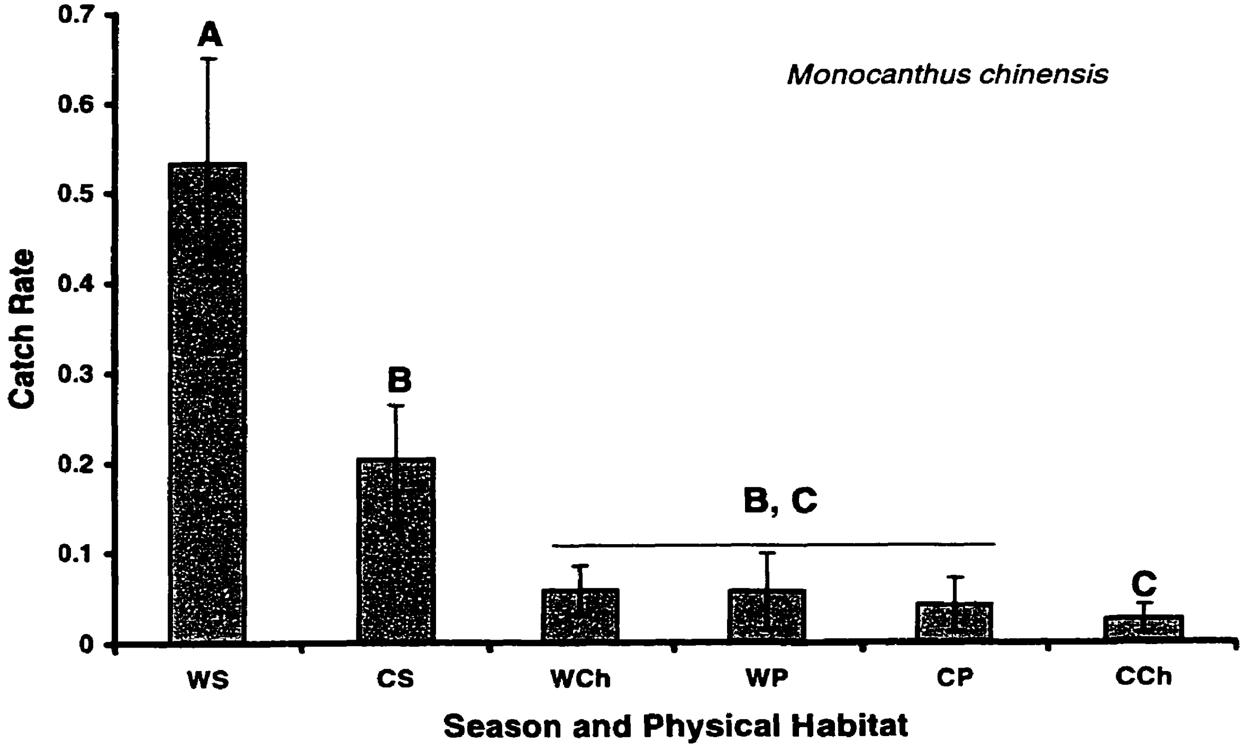


Figure 8.7. Influence of the interaction between season and physical habtiat on catch rates of *Monocanthus chinensis*. Bars labeled with the same letter are not significantly different at $P < 0.05$. Y = seagrass, N = no seagrass, Ch = channel, P = embayment plane, S = shallow. Error bars represent 95% confidence intervals.

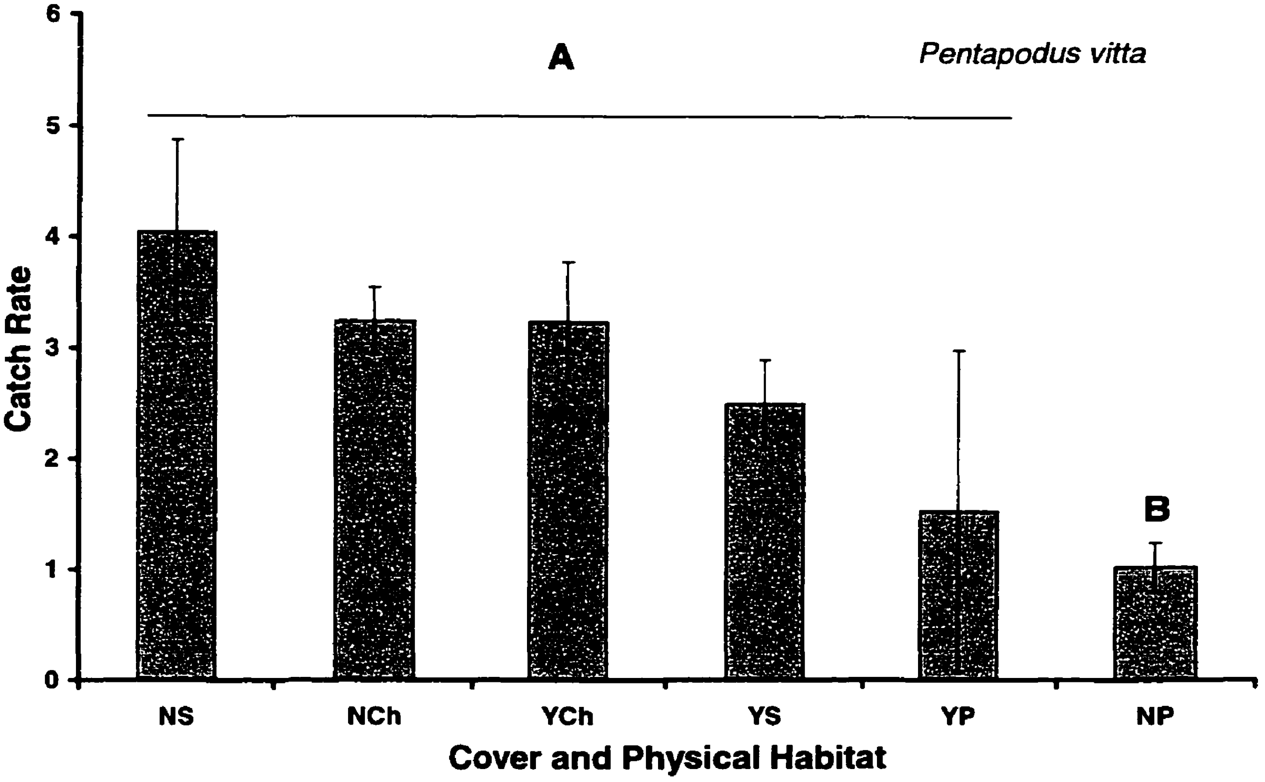


Figure 8.8. Influence of the interaction between physical habitat and cover on catch rates of *Pentapodus vitta*. Bars labeled with the same letter are not significantly different at $P < 0.05$. Ch = channel, P = embayment plane, S = shallow, Y = seagrass, N = no seagrass. Error bars represent 95% confidence intervals.

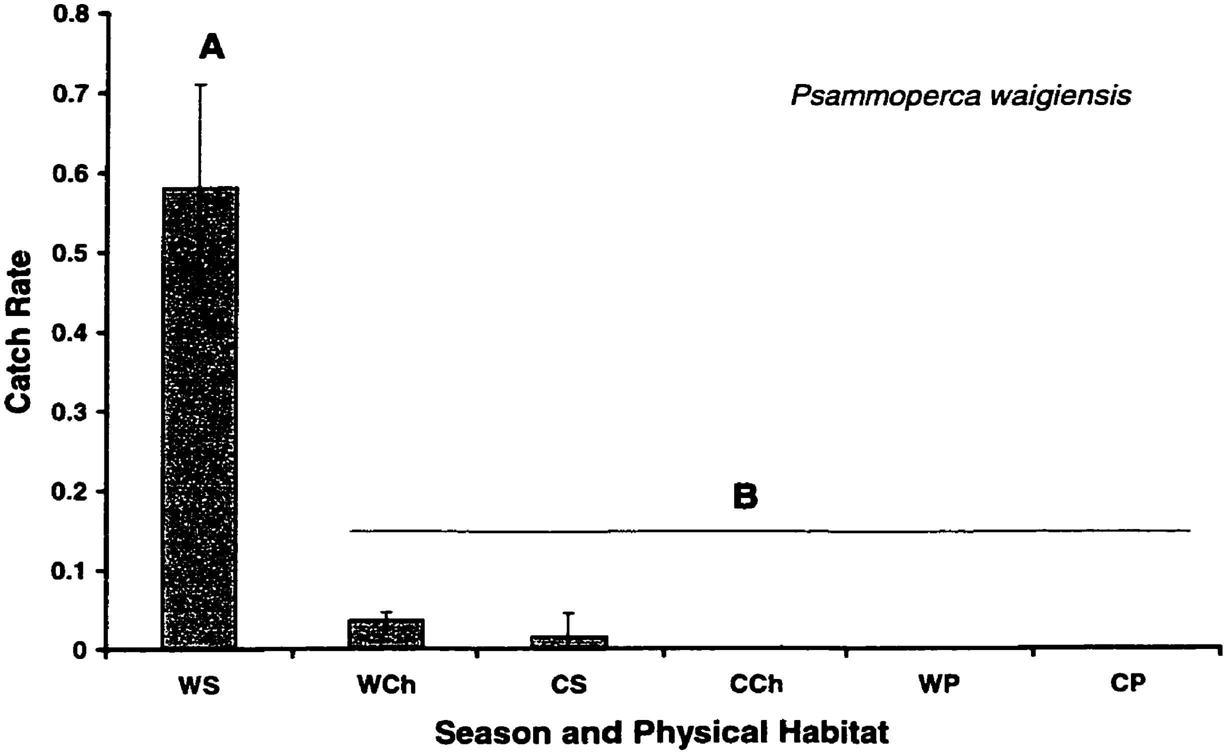


Figure 8.9. Influence of the interaction between season and physical habitat on catch rates of *Psammoperca waigiensis*. Bars labeled with the same letter are not significantly different at $P < 0.05$. W = warm, C = cold, S = shallow, Ch = channel, P = embayment plane. Error bars represent 95% confidence intervals.

8.4.4 Seasonal Changes in Size Distribution

The size distributions of the 10 most common species are shown in Figure 8.10. Seven of the 10 most common species showed significant seasonal changes in mean size (Table 8.8). *Amniataba caudovittatus*, *Apogon ruppelli*, *Lethrinus laticaudis*, *Monacanthus chinensis*, and *Rhabdosargus sarba* were all larger, on average, in warm months. In contrast, the mean size of *Chrysophrys auratus* and *Pelates sexlineatus* was greater in cold months. There were no seasonal changes in the size of *Pelates quadrilineatus*, *Pentapodus vitta*, and *Psammoperca waigiensis*. However, due to the very low catches of *P. waigiensis* in cold months it is unlikely that a difference in mean size would be detected.

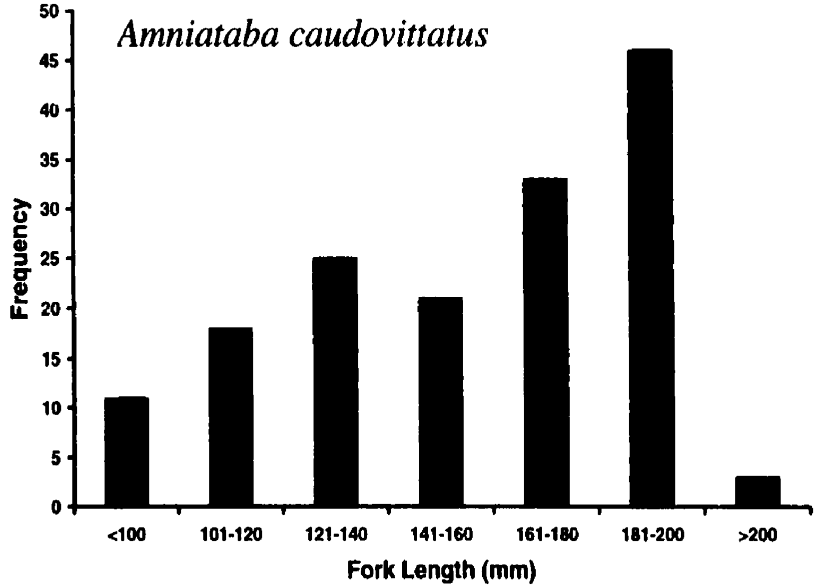
8.5 DISCUSSION

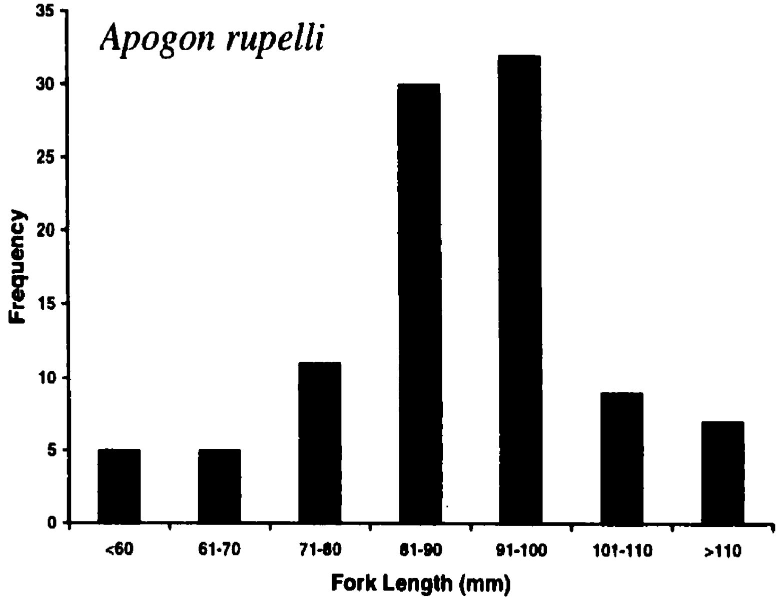
The shallow seagrass habitats of Shark Bay support fish communities with more species and individuals caught per trap than adjacent unvegetated areas. This is consistent with many other studies of fish communities in seagrass habitats (Bell and Pollard 1989, Ferrell and Bell 1991, Gray et al. 1996). However, I found that although species richness was higher, the fish communities of vegetated areas of all physical habitats were less diverse (as measured by the Shannon-Wiener index) than unvegetated areas due to the dominance of a single species. This result contrasts with previous studies, including another in the Eastern Gulf of Shark Bay, which found that fish communities of shallow seagrass meadows were more diverse than those in adjacent unvegetated regions and were not dominated by a single species (Hanekom and Baird 1984; Black et al. 1990; Connolly 1994b). Other studies have found that relatively few species can make up over 90% of captures in seagrass ecosystems of southeastern Australia (Robertson 1980, Bell et al. 1992, Gray et al. 1996), but unlike Shark Bay, the most common species are often found in roughly equal abundance. The difference in the patterns of species diversity found in this and previous studies may be due to variation in sampling methods. Other studies generally have used hand-pulled seines, which are unlikely to catch large, fast-moving individuals, like the most common size classes of *Pelates sexlineatus* and *Pentapodus vitta*. Conversely, the fish traps are unlikely to capture very small individuals that are common in seine hauls. Also, fish

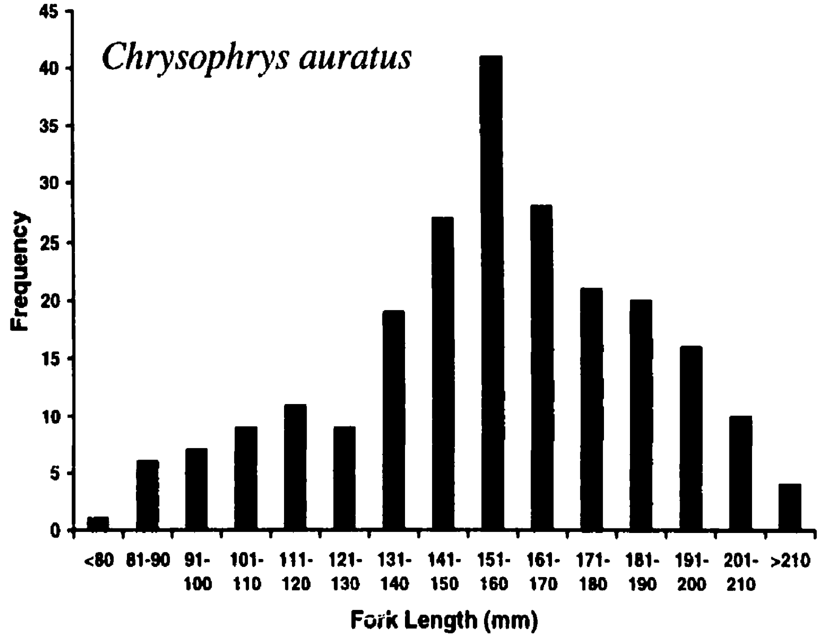
Table 8.8. Average FL (mm) during cold and warm months of the ten most commonly caught species. NS = not significant

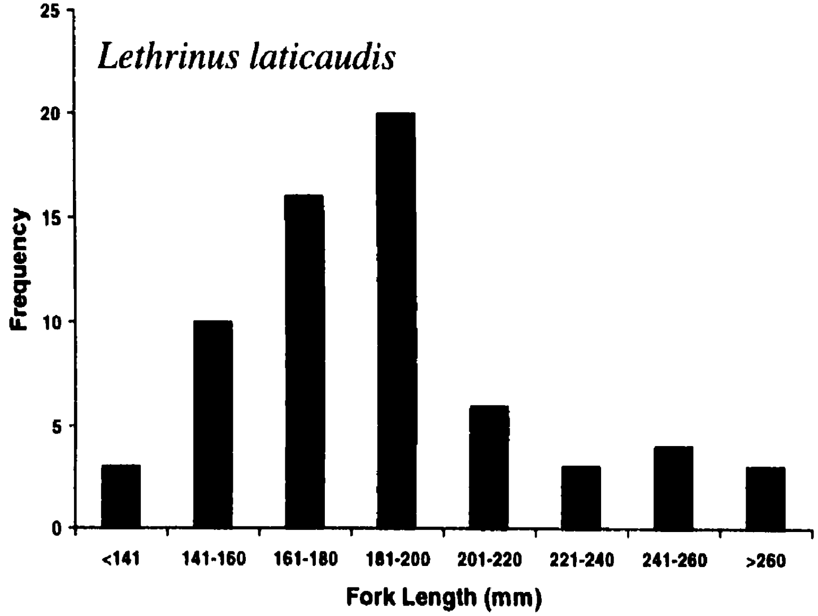
Species	Warm (n)	Cold (n)	t (df)	P
Amniataba caudovittatus	**171.5 (74)**	144.3 (83)	5.9 (155)	< 0.001
Apogon ruppelli	**94.6 (48)**	86.4 (51)	2.4 (97)	< 0.05
Chrysophrys auratus	145.4 (96)	**164.1 (133)**	4.5 (227)	< 0.001
Lethrinus laticaudis	**190.3 (51)**	167.8 (12)	2.1 (61)	< 0.05
Monacanthus chinensis	**104.6 (79)**	88.6 (31)	2.0 (108)	< 0.05
Pelates quadrilineatus	92.8 (14)	90.0 (39)	0.8 (51)	NS
Pelates sexlineatus	150.3 (5,410)	**157.3 (1,789)**	7.5 (7,196)	< 0.001
Pentapodus vitta	160.8 (529)	160.4 (1,219)	0.2 (1,746)	NS
Psammoperca waigiensis	189.5 (67)	206 (2)	0.8 (66)	NS
Rhabdosargus sarba	**138.0 (33)**	126.6 (71)	3.2 (102)	< 0.01

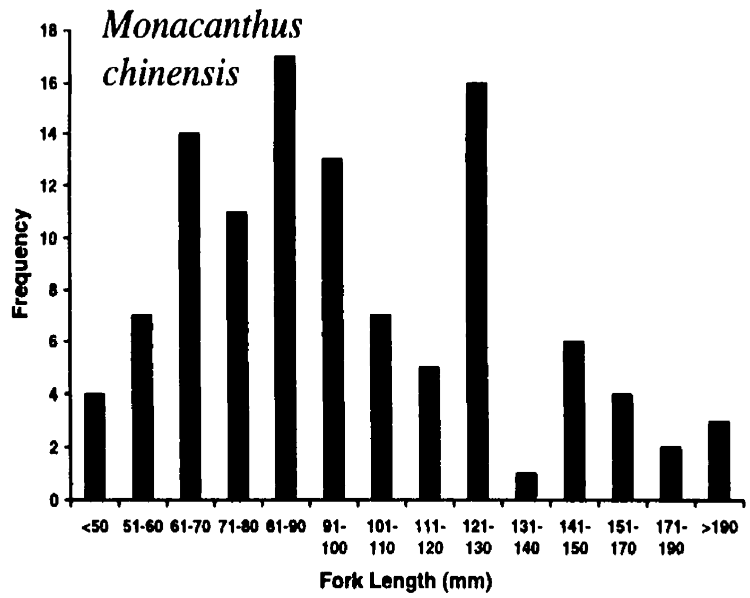
Figure 8.10. Size distributions of the 10 most common fish species.


Amniataba caudovittatus
Frequency
50
45
40
35
30
25
20
15
10
5
0
<100
101-120
121-140
141-160
161-180
181-200
>200
Fork Length (mm)

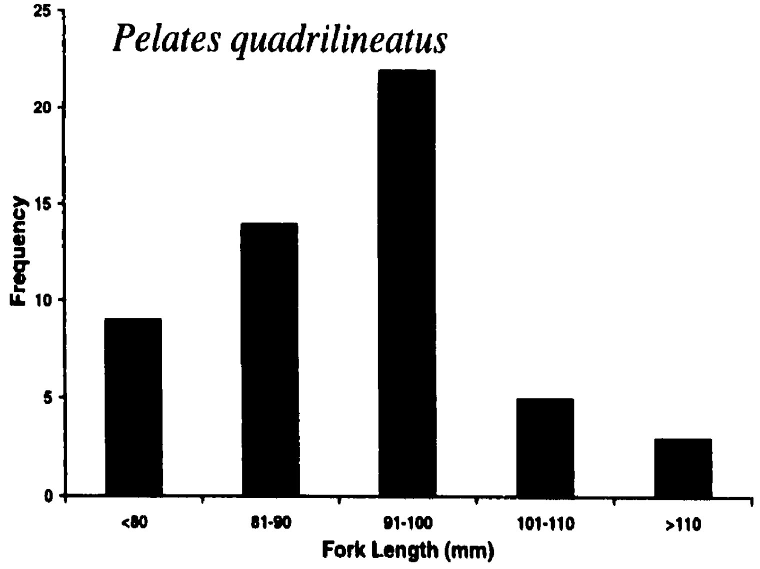

Apogon rupelli
Frequency
35
30
25
20
15
10
5
0
<60
61-70
71-80
81-90
91-100
101-110
>110
Fork Length (mm)


Chrysophrys auratus
Frequency
45
40
35
30
25
20
15
10
5
0
<80
81-90
91-100
101-110
111-120
121-130
131-140
141-150
151-160
161-170
171-180
181-190
191-200
201-210
>210
Fork Length (mm)

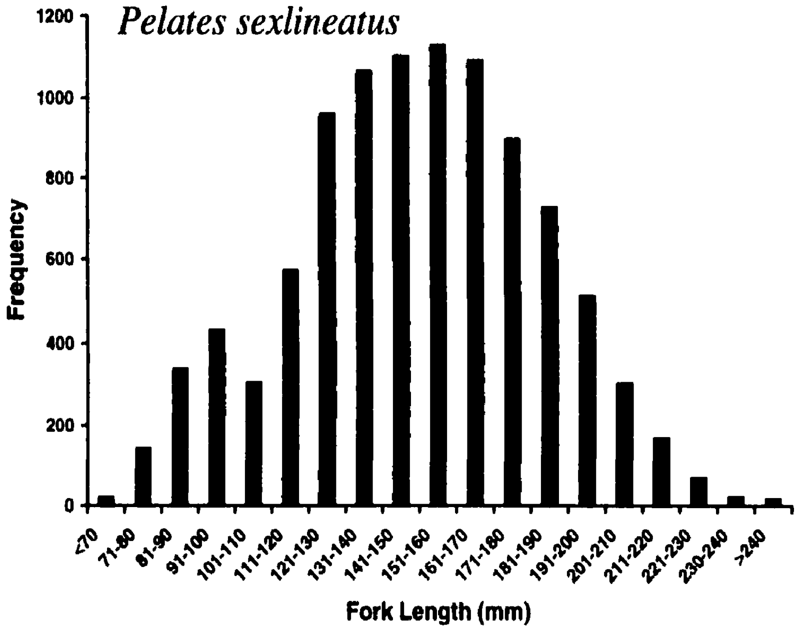

Lethrinus laticaudis
Frequency
25
20
15
10
5
0
<141
141-160
161-180
181-200
201-220
221-240
241-260
>260
Fork Length (mm)



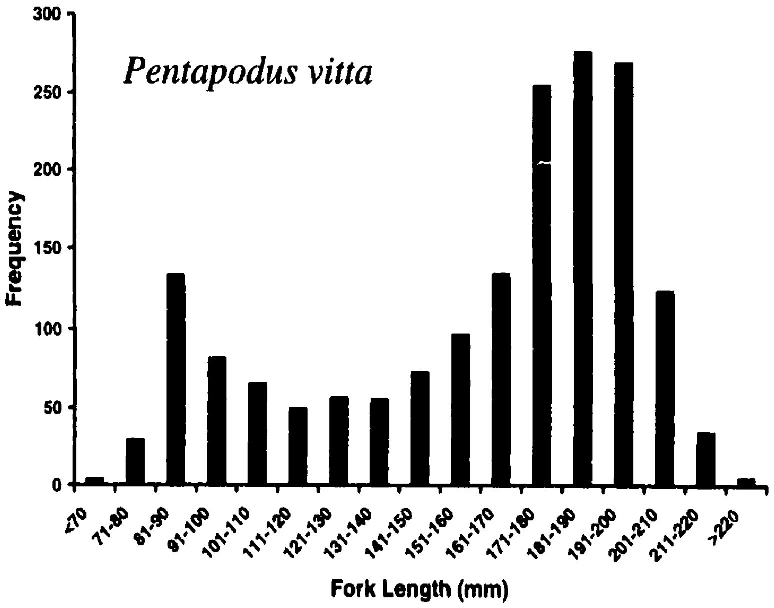
Monacanthus chinensis



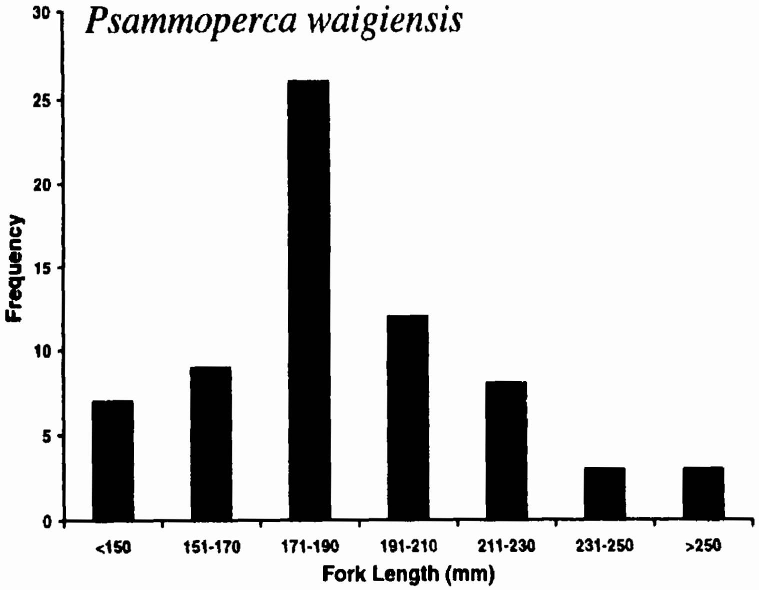
Pelates quadrilineatus



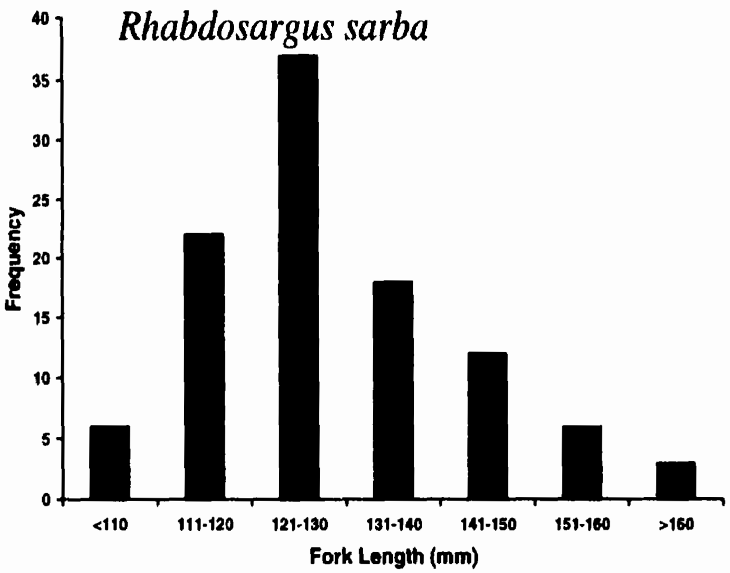
Pelates sexlineatus



Pentapodus vitta



Psammoperca waigiensis



Rhabdosargus sarba

traps are more likely to catch species with high long-term mobility (Robichaud et al. 2000) and the high catch rates of *Pelates sexlineatus* and *Pentapodus vitta* may be a result of this characteristic of fish trap sampling. However, qualitative underwater visual observations support the observed pattern of *Pelates sexlineatus* and *Pentapodus vitta* dominating fish communities of Shark Bay (personal observation). That the differences in results obtained is based at least in part on sampling methods is supported by the fact that, although Black et al. (1990) sampled within my study areas, there was almost no overlap in species composition of the catch. Given the biases of the sampling methods, fish traps probably understimate the number of species inhabiting seagrass habitats to a greater extent than seining, but fish traps may provide a more accurate assessment of the dominance of a small number of species in terms of both biomass and the number of individuals.

The dominance of *Pelates sexlineatus* masks the diversity found in vegetated regions of all habitats. When *P. sexlineatus* was removed from diversity calculations, although the species richness was decreased, shallow seagrass areas still had the highest catch rates of individuals and diversity indices were greater in vegetated regions than in unvegetated regions of the same physical habitat. This trend was minor in embayment planes where diversity in unvegetated regions was almost as high as vegetated regions, probably as a result of habitat misclassification. The catch biases of fish traps cannot explain the observed differences in fish abundance between vegetated and unvegetated areas. Catchability of fish traps is generally higher in habitats that are less complex structurally (Robichaud et al. 2000), so the catch rate should be higher relative to actual fish densities in unvegetated habitats than in structurally complex seagrass habitats. Therefore, higher fish abundance in seagrass areas of all physical habitats is not likely due to sampling bias.

Despite seagrass covered areas having higher species richness, individual abundance, and biomass, unvegetated habitats also supported relatively diverse communities. Over 70% of the species represented by more than 10 individuals were found in both vegetated and unvegetated areas and 11 species were found most often in unvegetated areas. This suggests that unvegetated habitats are also be important to populations of marine fish and deserve conservation considerations along with seagrass habitats.

Differences in the structure of fish communities have been found between seagrass habitats and adjacent bare sand areas (Ferrell and Bell 1991), between deep and shallow seagrass habitats (Bell et al. 1992), and among months (Ferrell et al. 1993). This study simultaneously investigated the influences of seagrass cover, depth (i.e., physical habitat), and season on the structure of fish communities. I found that seagrass cover had a main effect on community structure, but not on all components of the community. Fish communities were also influenced by an interaction between season and physical habitat. This shows that it is important to consider a variety of factors simultaneously to gain insights into the factors influencing the structure of fish communities in seagrass ecosystems. This finding is particularly important to conservation efforts for fish communities of shallow seagrass ecosystems and associated habitats. In order to understand possible anthropogenic effects on these marine communities, it is important to consider the many factors that may naturally influence these communities and how different community components are likely to respond to changes in various factors (e.g. destruction of seagrass).

The abundance of the ten most commonly caught species were correlated with different factors. For most species, the presence of seagrass was correlated with higher catch rates regardless of physical habitat or season. Similar affinities for seagrass and sand habitats were found in this study and that of Black et al. (1990) with the exception of *Pentapodus vitta*. I found no difference in use of vegetated and unvegetated shallow areas while Black et al. found that *P. vitta* was more common over shallow seagrass habitats than shallow unvegetated areas. As with community-level patterns, this is likely due to differences in the size classes of fish sampled. The size classes of *P. vitta* captured by fish traps show a bimodal distribution (Figure 8.10). While large size classes made up most of the catch and were found predominantly over sand, small size classes were most often captured in shallow, seagrass covered habitats. Thus, the differences in habitat use between this study and that of Black et al. (1990) probably reflect an ontogenetic shift in habitat use by *P. vitta*. Season and physical habitat (shallow, channel, or embayment plane) were also main effects on the catch rates of some species. In general, when there was a seasonal change in abundance, catch rates were higher during warm months. One particularly interesting result is that the species that made up specific principal components in the community analysis did not necessarily respond to the same factors when analyzed separately (e.g. PC4). These results suggest that conservation efforts must consider not only community-level patterns, but also take into account interspecific variation in the factors influencing spatial distributions and abundance.

Chrysophrys auratus, the pink snapper, is a species of both commercial and recreational importance in Shark Bay. There is a distinct breeding stock of *C. auratus* in the Eastern Gulf of Shark Bay (Johnson et al. 1986), which had been severely depleted, largely by recreational fishers outside of the current study area, by 1997 (G. Jackson, personal communication[1]). This drop in biomass resulted in a closure of the fishery in June 1998, which is projected to last until at least 2002 (G. Jackson, personal communication). In order to facilitate the recovery of this species, protecting juvenile habitats is critical. I found that unlike many other commercially important species, which are found in shallow seagrass habitats (Bell and Pollard 1989), *C. auratus* juveniles are found predominantly in deep habitats. Most individuals were caught in areas without seagrass cover, but analyses did not identify the presence or absence of seagrass as an influence on *C. auratus* abundance.

This study shows that fish traps can provide valuable data on the fish communities of seagrass habitats and complement data derived from seining methods. I found that although shallow seagrass habitats supported the most species, individuals, and biomass, these habitats were dominated by a single species. This study also shows that it is important to consider the influences of a variety of habitat characteristics and environmental factors, and the interactions among them, as catch rates of some species can be influenced by a suite of factors.

---

[1] Gary Jackson, Fisheries Western Australia

8.6 ACKNOWLEDGEMENTS

Financial support was provided by the American Museum of Natural History, Fisheries Western Australia, and NSERC Canada (grant A6869 to L.M. Dill). I thank G. Jackson, M. Moran, and C. Burton for providing logistical support, equipment loans, and advice throughout the study. The Dolphins of Shark Bay Research Foundation gave me access to the catamaran used throughout this work. J. McLash, J. Burghardt, I. Hamilton, C. Genrich, P. Greene, H. Finn, L. Barre, F. Bretos, L. Dill, and S. Buchannan provided field assistance. Thanks also to M. Sheaves and L. Dill for providing advice and A. Fraser, R. Swann, R. Holst, J. Heymans, and the Department of Anatomy and Human Biology (University of Western Australia) for logistical support. I. Hamilton provided statistical advice. I. Hamilton, R. Heithaus, L. Dill, Bernie Crespi and Bernie Roitberg provided helpful comments on previous versions of this manuscript. This work was conducted under the authority of Fisheries WA permit 67/97.

8.7 LITERATURE CITED

Bell, J. D. and D. A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. Pages 565-609 *in* Biology of Seagrasses. A. W. D. Larkum, A. J. McComb and S. A. Shepherd, editors. Elsevier, Amsterdam.

Bell, J. D., D. J. Ferrell, S. E. McNeil, and D. G. Worthington. 1992. Variation in assemblages of fish associated with deep and shallow margins of the seagrass *Posidonia australis*. Marine Biology 114: 667-676.

Black, R., A. I. Robertson, C. H. Peterson and N. M. Peterson. 1990. Fishes and benthos of near-shore seagrass and sandflat habitats at Monkey Mia, Shark Bay, Western Australia. Pages 245-261 *in* Research in Shark Bay. P.F. Berry, S.D. Bradshaw, and B.R. Wilson, editors. Western Australian Museum, Perth.

Clarke, K. R. and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecology Progress Series 46: 213-226.

Connolly, R. M. 1994a. Removal of seagrass canopy: effects on small fish and their prey. Journal of Experimental Marine Biology and Ecology 184: 99-110.

Connolly, R. M. 1994b. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Australian Journal of Marine and Freshwater Research 45: 1033-1044.

De Troch, M., J. Mees, I. Papadopoulos and E. O. Wakwabi. 1996. Fish communities in a tropical bay (Gazi Bay, Kenya): seagrass beds vs. unvegetated areas. Netherlands Journal of Zoology 46: 236-252.

Ferell, D. J. and J. D. Bell. 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Marine Ecology Progress Series 72: 15-24.

Ferrell, D. J., S. E. McNeil, D. G. Worthington, and J. D. Bell. 1993. Temporal and spatial variation in the abundance of fish associated with the seagrass *Posidonia australis* in south-eastern Australia. Australian Journal of Marine and Freshwater Research 44: 881-899.

Gray, C. A., D. J. McElligott and R. C. Chick. 1996. Intra- and inter-estuary differences in assemblages of fishes associated with seagrass and bare sand. Marine and Freshwater Research 47: 723-735.

Hanekom, N. and D. Baird. 1984. Fish community structures in Zostera and non-Zostera regions of the Kromme estuary, St. Francis Bay. South African Journal of Zoology 19: 295-301.

Heithaus, M. R. in press. The biology of tiger sharks (Galeocerdo cuvier) in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes.

Hutchins, J. B. 1990. Fish survey of South Passage, Shark Bay, Western Australia. Pages 263-278 *in* Research in Shark Bay. P.F. Berry, S.D. Bradshaw, and B.R. Wilson, editors. Western Australian Museum, Perth.

Johnson, M. S., S. Creagh and M. Moran. 1986. Genetic subdivision of stocks of snapper, Chrysophrys unicolor, in Shark Bay, Western Australia. Australian Journal of Marine and Freshwater Research 37: 337-345.

Robertson, A. I. 1980. The structure and organization of an eelgrass fish fauna. Oecologia 47: 76-82.

Robichaud, D., W. Hunte and M. R. Chapman. 2000. Factors affecting the catchability of reef fishes in Antillean fish traps. Bulletin of Marine Science 67: 831-844.

Sheaves, M. J. 1992. Patterns of distribution and abundance of fishes in contrasting habitats in a mangrove-lined tropical estuary as determined by fish traps. Australian Journal of Marine and Freshwater Research 43: 1461-1479.

Sheaves, M. J. 1995. Effect of design modifications and soak time variations on Antillean-Z fish trap performance in a tropical estuary. Buletin of Marine Science 56: 475-489.

Shepherd, S. A., A. J. McComb, D. A. Bulthuis, V. Neverauskas, D. A. Steffenson and R. West. 1989. Decline of seagrasses. Pages 346-393 *in* Biology of Seagrasses. A. W. D. Larkum, A. J. McComb and S. A. Shepherd, editors. Elsevier, Amsterdam.

Tabachnick, B. G. and L. S. Fidell. 1983. Using multivariate statistics. Harper and Row: New York.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall Inc: Englewood Cliffs, NJ.

CHAPTER 9

Food Availability and Tiger Shark Predation Risk Influence Bottlenose Dolphin Habitat Use

9.1 ABSTRACT

Although both food availability and predation risk have been hypothesized to affect dolphin habitat use and group size, no study has measured both factors concurrently to determine their relative influences. From 1997-1999, we investigated the effect of food availability and tiger shark (*Galeocerdo cuvier*) predation risk on bottlenose dolphin (*Tursiops aduncus*) habitat use and group size in Shark Bay, Western Australia. Food availability was measured by fish trapping, while predation risk was assessed by shark catch rates, acoustic tracks and Crittercam deployments. Dolphin habitat use was determined using belt transects. The biomass of dolphin prey did not vary seasonally and was significantly greater in shallow habitats than in deeper ones in all seasons. Predation risk varied with season and habitat as tiger sharks were virtually absent during cold months of 1997 and 1998, abundant in warm months of all years, and found at an intermediate density in the cold months of 1999. When present, shark density was highest in shallow habitats. Decreased echolocation efficiency in very shallow water and poor visual detection of tiger sharks (camouflaged over seagrass) probably further enhance the riskiness of such habitats, and the relative riskiness of shallow habitats is supported by the observation that dolphins select deep waters in which to rest. The observed dolphin group sizes were consistent with a food-safety tradeoff. Groups were larger in the more dangerous shallow habitats, larger during resting than during foraging and largest during resting in high-risk seasons. Foraging dolphins matched the distribution of their food when sharks were absent. However, during warm months, the distribution of foraging dolphins significantly deviated from that of their food, with fewer dolphins foraging in the productive (but dangerous) shallow habitats than expected by food alone. When shark density was intermediate, habitat use by foraging dolphins was intermediate, but more similar to seasons with high shark density than periods of low shark density. These results are consistent with the hypothesis that foraging dolphin distribution reflects a tradeoff between predation risk and food availability. Because the distribution and abundance of tiger sharks is influenced by species other than dolphins, the distribution of the tiger sharks' primary prey (sea snakes, dugongs, and sea turtles) may indirectly influence dolphin habitat use, suggesting that it is important to consider the community context in studies of habitat use.

9.2 INTRODUCTION

Understanding the spatial distribution of animals is a primary goal of ecologists, and determining the factors that are responsible for these distributions is critical to making predictions about how animals will respond to changes in their environment. Both the spatial distribution of food and habitat differences in predation risk may be important in determining animal habitat use (see Lima and Dill 1990 for a review of foraging under the risk of predation). Of particular interest are situations in which the habitats that have high food availability are also the most dangerous, so that animals may have to trade-off food and safety when selecting a habitat to occupy.

In some situations, animals may be distributed across habitats proportional to food productivity or availability (e.g. guppies, *Poecilia reticulata*, Abrahams and Dill 1989; armored catfish, *Ancistrus spinosus*, Oksanen et al. 1995). However, if predation risk varies among habitats, prey will not necessarily select habitats based solely on energetic return. Instead, individuals are likely to accept lower energetic returns in order to forage in habitats that are relatively safer. Both theoretical (e.g. McNamara and Houston 1990) and empirical studies have shown that this often results in animals undermatching the relative food availability in dangerous habitats (e.g. creek chubs, *Semotilus atromaculatus*, Gilliam and Fraser 1987; guppies, Abrahams and Dill 1989, coho salmon, *Oncorhynchus kisutch*, Grand and Dill 1997). The specific nature of food-safety tradeoffs may be influenced by the response of predators to the distribution of their prey (i.e., the foragers) (Hugie and Dill 1994, Sih 1998), the age-sex class of individuals (e.g. Cresswell 1994), and the community context of interactions (Heithaus in press a, Chapter 3). Although the importance of predation risk and food availability have been shown both theoretically and in the laboratory, relatively few field studies, especially those of large-bodied animals, have demonstrated tradeoffs between food and safety (but see Werner and Hall 1988, Cowlishaw 1997, Mills and Gorman 1997).

Tradeoffs between food and safety are also known to influence the size of animal groups. In general, forming larger groups can be advantageous for reducing the risk of predation, but intraspecific competition often selects for smaller groups sizes (e.g. Bertram 1978). For example, a balance of foraging costs (competition) and predation risk can explain group size in primates (Terborgh 1983, Janson and Goldsmith 1995, Hill and Lee 1998).

Risk of predation and food availability have both been hypothesized to influence dolphin habitat use and group size (e.g., Wells et al. 1980, 1987), but no studies have tested these hypotheses. This study investigates the role of tiger shark (*Galeocerdo cuvier*) predation risk and food (fish) availability in determining bottlenose dolphin (*Tursiops aduncus*) habitat use and group size in Shark Bay, Western Australia.

The population of bottlenose dolphins in Shark Bay provides an excellent field system for studying food – safety tradeoffs. The dolphins in this area are long-lived and are year-round residents within relatively restricted home ranges that encompass numerous habitat patches. Therefore, more than many species, dolphin individuals will have good knowledge of the food availability in various habitats. Furthermore, dolphins are frequently attacked by tiger sharks, and appear to face substantial risk of predation from them (Heithaus in press b, Chapter 4). These sharks are not present in the study area at all times (Heithaus in press c, Chapter 5) and thus dolphins are exposed to varying levels of predation risk. Finally, because dolphins have low locomotion costs (Williams et al. 1992) and there is no obvious aggression during foraging (personal observation) they should be able to move among habitats relatively freely in response to ecological conditions.

I set out to test the following hypotheses. 1) The distribution of foraging bottlenose dolphins will be determined primarily by the distribution of their food when risk is low, but dolphins will reduce their use of high-risk habitats, relative to food availability, when the risk of predation is increased. 2) Dolphins will select the safest habitats for resting, which is a particularly high-risk activity. 3) The size of dolphin groups will be larger during resting than during foraging. 4) The size of dolphin groups will be larger in dangerous habitats and during dangerous time periods. 5) Dolphin groups will be smaller in habitats with low food availability. In addition to testing these hypotheses, I investigated differences among dolphin age/sex classes in responsiveness to food availability and predation risk.

9.3 METHODS

9.3.1 Study Site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia. The study site was located in the Eastern Gulf, offshore of the Monkey Mia Dolphin Resort (approximately 25°45'S, 113°44'E, Figure 9.1a). It is relatively shallow throughout with extensive shallow seagrass banks (< 4 m depth) surrounded by deeper waters (6 - 12 m). For the purposes of this paper habitats have been classified as either shallow (< 4.0 m, 17% of study area) or deep (> 6.0 m). The boundaries between habitats are generally distinct and areas 4 - 6 m deep were omitted from analyses to avoid classification errors. Shallow habitats are predominantly less than 2.5 m deep with the bottom covered almost entirely by seagrasses (primarily *Amphibolis antarctica* and occasionally *Posidonia australis*) while deep habitats are primarily over 7.0 m and covered by sand or silt. Ten focal zones, representing replicates of these two habitat types, were defined for the purposes of this study (Figure 9.1b) and were mapped into a Geographic Information System (GIS, MapInfo Professional version 4.5, MapInfo Corporation).

Seasonal fluctuations in water temperature influence the community present in Shark Bay (Heithaus in press c, Chapter 5). Water temperatures during warm months (September-May) are generally above 20° C but drop rapidly in mid- to late-May to a minimum of 14° C in the winter months (June-August). Water temperatures begin to increase in late August. For the purposes of this paper, the data for "warm" (September-May) and "cold" (June-August) months are analyzed separately, and these periods were defined based on both changes in water temperature and in the abundance of many species which, along with dolphins, are prey of tiger sharks; these include dugongs (*Dugung dugon*), turtles (*Caretta caretta* and *Chelonia mydas*), and sea snakes (primarily *Hydrophis elegans*) (Heithaus in press c, Chapter 5). During the cold months of 1999 (June-July), patterns of dugong, turtle, and sea snake abundance were intermediate between those measured in warm months of all years and in cold months of 1997 and 1998 (Heithaus in press c, Chapter 5). There are no major differences in water temperature between habitats due to the relatively shallow nature of the bay and water mixing by wind and tidal movement (Heithaus in press c).

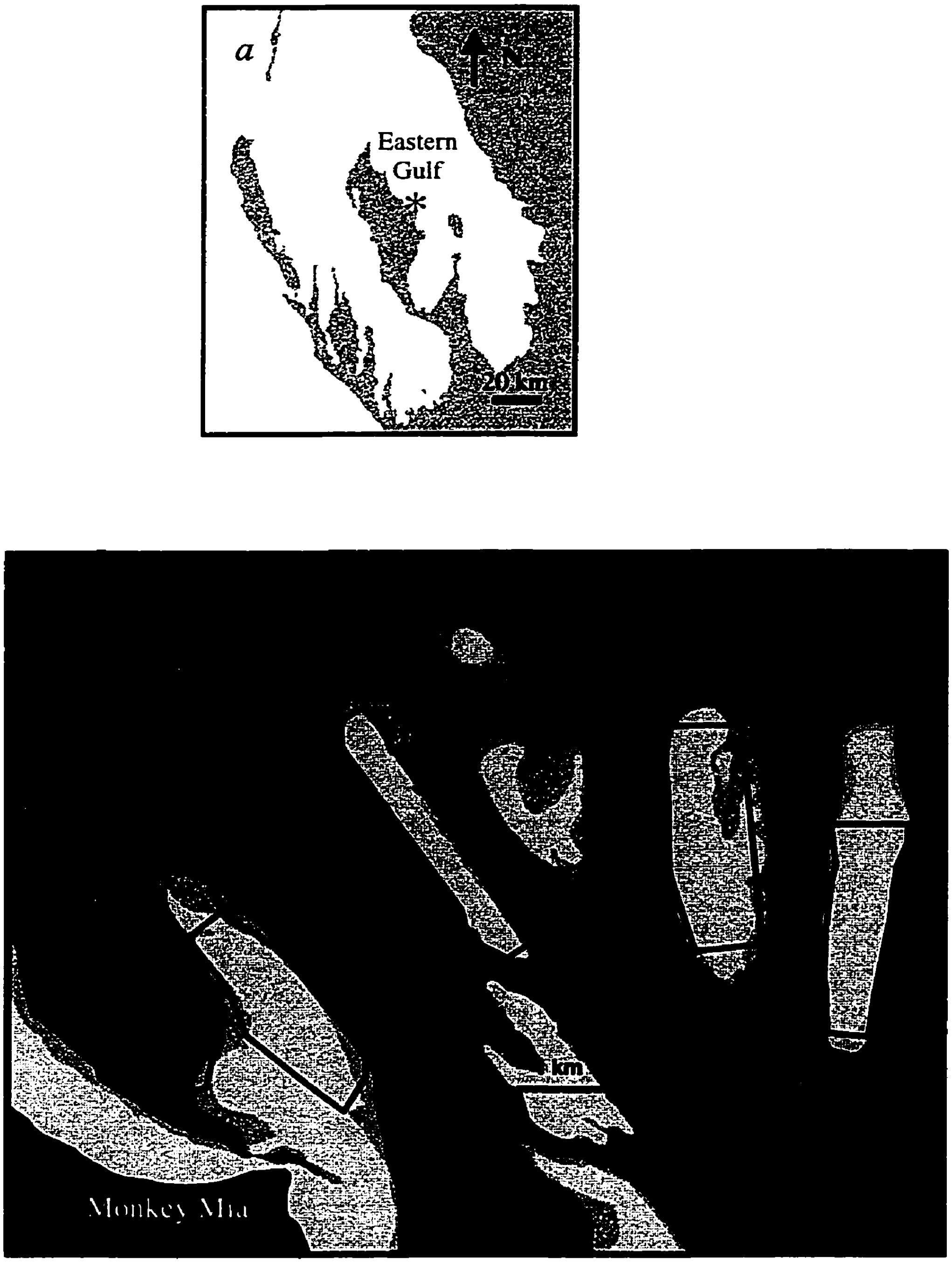


Figure 9.1. *a*) Shark Bay, Western Australia. Monkey Mia is indicated with an asterisk, *b*) Location of focal zones offshore of Monkey Mia. Lightest shading indicates waters < 2 m depth and darker shading indicates waters 2-4 m and >4 m. Land is black. Dolphin and fish work was conducted in all zones. Shark fishing did not occur in the two zones closest to Monkey Mia.

9.3.2 Food Availability

The abundance and biomass of dolphin prey (teleost fishes) were assessed with Antillean-Z fish traps. Traps were approximately 1.1 m long, 0.6 m tall, and 0.6 m wide, covered with wire mesh, and had straight, conical entrances (see Sheaves 1992 for a detailed description of trap design). Traps were baited with approximately 250 g of cut pilchards (*Sardinops neopilchardus*). Bait was placed in a PVC capsule that had numerous 10 mm holes and was capped at both ends, which allowed water to flow easily through the capsule while preventing bait removal by fishes in the trap. Up to ten traps were set concurrently from an 11 m catamaran. In most cases, traps were set simultaneously in paired transects (one deep, one shallow) to avoid biases caused by tidal or diel movements of fishes. Traps were spaced at least 80 m apart to avoid overlap in catch radii, which are generally less than 40 m (Sheaves 1992). Traps were set for approximately two hours to maximize catch rate and minimize trap saturation (Sheaves 1995).

When traps were recovered, the fork length (FL) of each fish was measured and a number of individuals of each species were weighed to generate length-weight relationships (Chapter 8) which were used to determine overall catch biomass. Biomass available to dolphins was calculated using all species that dolphins are known to consume. Fish < 10 cm FL were removed from biomass calculations since such small fish probably represent a relatively small proportion of dolphin diets. However, results for seasonal and spatial variation in food available to dolphins does not change with the inclusion of small size classes and all species (Chapter 8).

9.3.3 Predation Risk

There are three shark species found in the Eastern Gulf of Shark Bay that are potential dolphin predators: tiger (*Galeocerdo cuvier*), mako (*Isurus oxyrinchus*), and white sharks (*Carcharodon carcharius*) (Connor and Heithaus 1996, Heithaus in press c, d, Chapters 2, 5). Mako and white sharks are rare and probably not a major threat to the dolphins whereas tiger sharks are common in the study area (Heithaus in press c, Chapter 5). Shark bite scars are found on over 74% of adult dolphins in the study area and at least 11% of the dolphin population is attacked unsuccessfully each year (Heithaus in press b, Chapter 4). All attacks by sharks large enough to kill dolphins where a specific attacker could be identified were by tiger sharks. Therefore, analyses of predation risk focus on tiger sharks.

Seasonal changes in the risk of predation to dolphins were estimated from tiger shark catch rates, which appear to be an appropriate index of shark density (Heithaus in press c). Fishing was conducted in 8 focal zones (Figure 9.1). Up to 10 drum lines, baited with approximately 1.5 kg of Western Australian salmon (*Arripis truttaceus*), were set in at least 2 focal zones each fishing day. Lines were spaced approximately 0.7 km apart and were checked every 2-4 hours (see Chapter 5 for a detailed description of methodology). If bait was not present at a check, the bait was considered to be lost half way between the previous check and the time when loss was detected. Because not all size classes of sharks represent a predation risk to the dolphins (Heithaus in press b), three separate analyses were made for sharks: >300 cm TL, >275 cm TL, and all tiger sharks. These groupings correspond to the estimates of the sizes of sharks responsible for approximately 75%, 90%, and 100% of the bite scars and wounds observed on dolphins in the study area (Heithaus in press b).

Differences in catch rates among habitats are not appropriate for determining shark relative habitat use because of habitat-differences in bait removal by species other than tiger sharks and possible habitat-differences in the effectiveness of odor corridors (Heithaus in press c). Therefore, acoustic tracks of tiger sharks were used to estimate shark habitat use and habitat-specific risk to dolphins. Forty-four tiger sharks between 271 - 405 cm TL ($\bar{x}$ = 336 cm ± 33.2 cm SD) were tracked. Acoustic tracks were performed on sharks using either internally implanted acoustic transmitters (n = 8) or an integrated video/tracking package ("Crittercam," n = 36) attached to the dorsal fin with a temporary clamp or using a Floy tag (see Holland et al. 1999, Marshall 1998 and Heithaus et al. in press, Chapter 6 for descriptions of these techniques). Sharks were tracked from a 4.5 m research vessel using a directional hydrophone and acoustic receiver for periods ranging from 1-13 hours ($\bar{x}$ = 3.0 hrs ± 2.4 SD). Boat GPS location, habitat, depth, and estimated direction and distance to the shark were recorded every five minutes. For the purposes of this paper, tracks were truncated when sharks left the study area. Shark tracks were started in both shallow (n = 11) and deep habitats (n = 33). However, many sharks that started in shallow habitats (n = 6) switched habitats within the first ten minutes, and all sharks used multiple focal zones during tracks, so results regarding habitat use by sharks are not dependent on the starting point of tracks. Individual sharks were tracked only once.

9.3.4 Dolphin Habitat Use, Behavior, and Group Size

Dolphin habitat use and group size were investigated using belt transects and dolphin group surveys. Transects were positioned in the middle of focal zones and a sighting belt extended 500 m to either side of the transect except where the transect line was within 500 m of another focal zone or habitat (Figure 9.1b). Three observers drove along the transect in a 4.5 m boat at 6 - 9 km/hr. Transects were only included in analyses if they were conducted in Beaufort wind conditions of 2 or less, with the majority occurring in Beaufort 0 or 1 conditions. This was done to ensure that there was minimal variation in sighting efficiency with distance from the transect and among days. Beaufort 0 conditions refer to flat water with no wind rippling. Beaufort 1 conditions are those with flat water with slight ripples caused by wind, and Beaufort 2 includes those with wind-induced chop but with no whitecaps visible. The order and direction in which transects were driven was haphazard to minimize the influence of tidal and diel patterns on these data. A total of 795 transects was completed from 1997-1999 (Table 9.1).

Upon sighting a group of dolphins along a transect, the GPS position on the transect was marked, and I departed the transect line to survey the group. Data on group size, composition, and behavior were recorded along with environmental information. Individual identifications of dolphins were made using distinctive patterns

Table 9.1. Seasonal and habitat distribution of sample effort.

Fish Trap (sets)	Shallow	Deep
Warm	94	159
Cold 1997/1998	70	137
Cold 1999	91	93
Tiger sharks	Hours[1]	Tracks
Warm	3474	38
Cold 1997/1998	1808	1
Cold 1999	1044	5
Dolphin habitat use (transects)	Shallow	Deep
Warm	165	209
Cold 1997/1998	102	174
Cold 1999	57	88

[1] Hours refers to the number of hours baits were set during shark fishing.

of nicks and cuts out of the dorsal fin (e.g. Smolker et al. 1992). Once a survey was completed, I returned to the point of departure and resumed driving along the transect. The GPS locations of all dolphin groups were mapped into the GIS, and groups outside of focal zones were omitted from subsequent analyses.

Behavioral categories included foraging, resting, socializing, traveling, and unknown. Groups were defined by a ten-meter chain rule (Smolker et al. 1992) with all dolphins within ten meters of another dolphin considered to be part of a group. When not all individuals in a group were engaged in the same behavior, the number of dolphins in each behavioral state was recorded. Dolphins making multiple dives in the same location, surfacing rapidly when not interacting with other dolphins, engaging in rapid chases of fish or observed with a fish at the surface were considered to be foraging. Resting dolphins moved slowly, usually did not maintain a specific direction of travel, and often floated at the surface for several seconds to over a minute. Socializing was often observed in association with other behaviors with several dolphins in the group engaging in rubbing. Only groups engaged in intense social activity, which included aggressive behavior, sexual behavior, or chasing were classified as social groups. Dolphins were considered to be traveling only when they maintained a consistent heading at a speed greater than 2 km/hour. Dolphins traveling slowly could either be resting or foraging, and thus were classified as "unknown" to avoid errors. Analyses of activity-specific habitat use and group size were restricted to foraging and resting which were the least ambiguous behavioral states and the ones for which I have *a priori* predictions regarding predation risk-food availability tradeoffs (e.g. Heithaus in press d).

9.3.5 Statistical Methods

For most analyses data were combined for warm months and for cold months of 1997 and 1998 because environmental conditions and the abundance of tiger sharks and their primary prey species were similar (Heithaus in press c, Chapter 5). Data from the cold season of 1999 were analyzed separately from those of 1997/1998 because of both qualitative and quantitative differences in the abundance of tiger sharks and their primary prey species and water temperature (Heithaus in press c, Chapter 5). Tiger shark habitat use data were analyzed both 1) pooled to increase sample size and because most tracks occurred during warm months (Table 9.1), and 2) with warm months and cold months of 1999 separated. Dolphin group size data were lumped into warm and cold months, which increased sample sizes to allow comparisons of activity- and habitat-specific variation in group size. Data were analyzed using JMP IN® 4.0.3 (SAS Institute Inc. 2000).

Habitat and seasonal differences in the biomass of potential dolphin prey were investigated with ANOVA. Season and habitat were treated as fixed-effects and class variables. Data were log(x+1) transformed to homogenize variances, which were checked with Bartlett's test (Zar 1984). Non significant interactions ($P > 0.10$) were removed from analyses.

Seasonal changes in catch rates of tiger sharks for all three size-classes were analyzed using chi-square. This was accomplished by comparing the number of sharks captured in each season with the number expected based on fishing effort. The expected number of sharks for a season (i) was generated with the equation:

$$Expected_i = \frac{N * H_i}{H_T}$$

where N is the total number of sharks caught during the seasons being compared, H_i is the number of hours that baits were set during season i, and H_T is the total number of hours baits were set for all seasons in the comparison. Tiger sharks were rarely recaptured, and I only included the first capture of an individual in analyses.

Shark habitat use was tested by comparing the relative number of 5-minute location fixes inside each habitat type to the expected number of fixes based on relative availability of habitats in the study area. The first position fix of a track was excluded from analyses. Less than 5 fixes were expected in a particular habitat for some sharks, so a G-Test was used to test for a deviation from random habitat use. To avoid pseudoreplication, habitat use was measured using the number of fixes for each shark in a particular habitat as a single data point (Turchin 1998). Thus, the degrees of freedom were determined by the number of sharks tracked, not the overall number of five minute position fixes.

Tiger sharks exhibit a "bouncing" pattern of swimming through the water column during which they repeatedly move between the surface and the bottom (Chapter 7). It is possible that sharks would not detect prey throughout the entire water column when in deep habitats, but likely would be able to do so in shallow habitats. Therefore, in calculating the relative use of habitats by tiger sharks, habitat availability was determined in two manners: surface area and volume. Volume measurement assumed that deep habitats were only twice as deep as shallow ones on average. Since deep habitats are generally more than twice as deep as shallow ones, the availability of shallow habitats, to sharks, is likely overestimated and, thus, the relative use of shallow habitats is an underestimate in analyses using volume.

Since habitat area or volume may not be an appropriate measure of expected habitat use when animals have no habitat preference (see Chapter 7), I also conducted 500 iterations of the sample randomization procedure of Heithaus and Hamilton (in review, see Chapter 7 for a description). A significant habitat preference is indicated if less than 5% (n = 25) of iterations generate a mean use of a habitat greater than the observed mean use (Heithaus and Hamilton in review).

The effects of season and habitat on dolphin density were analyzed using ANOVA. Analyses were carried out separately for foraging and resting dolphins. Season and habitat were considered fixed effects and class variables. In order to avoid biases associated with variation in the number of passes along a transect in a season, data on dolphin densities were collapsed into a single mean density for each transect in each season. Therefore, dolphin density was calculated by dividing the number of dolphins sighted on a transect within a season by the total area of that transect that was surveyed. In order to measure foraging dolphin habitat use relative to food availability I calculated dolphin density in each transect relative to habitat area and fish abundance with

$$RelativeDensity_i = \frac{n_i}{P_i * A_i * F_i}$$

where n_i is the number of dolphins sighted on a transect in a particular season, P_i is the number of times the transect was sampled, A_i is the area of the transect (km^2), and F_i is the relative biomass of fish caught in the transect. F_i was calculated by dividing the average biomass of fish captured in a transect by the lowest mean biomass obtained in any transect. This measure of relative density assumes that, if food is the only factor influencing the distribution of foraging dolphins, they should be distributed across habitats relative to the standing stock of food resources. Although there is a theoretical basis for this prediction (Lessels 1995), it is not possible to determine if dolphins conform to all the assumptions of this model. However, this measure is still useful in providing a null model for comparing changes in dolphin distribution, relative to their food, with changes in the risk of predation. All data were $\log(x+1)$ transformed to homogenize variances, which were tested using Bartlett's test (Zar 1984). All non-significant interactions ($P > 0.10$) were removed from analyses. Tukey's test, which corrects for multiple comparisons, was used to determine significant differences among means in the case of interactions.

Although analyses included repeated sightings of the same individuals (see Results), this should not bias the results of this study. First, it is important to sample the same individuals in different seasons. Otherwise, any patterns observed might be due to sampling different sets of individuals rather than to a set of individuals shifting their habitat use. Within seasons, I sampled a large number of individuals with relatively few resightings of each ($\bar{x} = 1.9$ sightings/season for an individual each year) suggesting that independence assumptions of statistical tests are unlikely to be problematic. Also, to avoid non-independence problems, no individual dolphins were counted more than once in a single day. Samples of the same individual on separate days are relatively independent as most individuals move among focal zones several times within a single day, and group composition changes frequently throughout a day (Smolker et al. 1992, MRH unpublished data). Finally, analyses were also carried out on the number of groups in each habitat. All patterns were identical between analyses based on the number of groups and those based on individuals, so only analyses using the number of individuals are presented. However, the similarity of results suggests that non-random group formation by dolphins is not responsible for the habitat use patterns observed in this study.

Differences in habitat use among dolphin age-sex classes were investigated with contingency chi-square tests using the number of individuals sighted in deep and shallow habitats within a particular season. All P-values were Bonferroni corrected for multiple comparisons.

The effects of season, activity, and habitat on dolphin group size were investigated with ANOVA using the methods described above. Data were square-root transformed to normalize them and checked for homogeneity of variances as described above. Tukey's test was used to determine significant differences among means in the case of interactions.

9.4 RESULTS

9.4.1 Food Availability

Fish traps (n = 644) were set for 1,347 hours (Table 9.1). A total of 12,667 fish were captured, representing 31 species; dolphins were observed consuming 20 of these during survey observations. The biomass of potential dolphin prey was only influenced by habitat with significantly higher biomass per trap found in shallow habitats than in deep ones (ANOVA, n =644 sets, df = 1, 619, $F = 60.5$, $P < 0.001$; Figure 9.2). There was no significant effect of season on fish biomass (ANOVA, n = 644 sets, df = 2, 619, $F = 1.0$, NS).

9.4.2 Tiger shark abundance and habitat use

Shark baits were set for 6,326 hours (Table 9.1), resulting in 252 tiger shark captures. There were significant seasonal changes in catch rates within the study area for all three tiger shark size groupings. Shark abundance was extremely high during all warm seasons, very low during cold months of 1997 and 1998, and intermediate during cold months of 1999 (all: $\chi^2 = 124.6$, df = 2, n = 252, $P < 0.001$; >275 cm: $\chi^2 = 92.9$, df = 2, n = 163, $P < 0.001$; > 300 cm: $\chi^2 = 60.7$, df = 2, n =112, $P < 0.001$; Figure 9.3). There were significantly more sharks present during the 1999 cold months than those of 1997/1998 (all: $\chi^2 = 28.0$, df = 1, n = 22, $P < 0.001$; >275 cm: $\chi^2 = 12.9$, df = 1, n = 13, $P < 0.001$; > 300 cm: $\chi^2 = 8.1$, df = 1, n = 10, $P < 0.01$).

Acoustic tracking of 44 tiger sharks revealed a consistent overuse of shallow habitats (Figure 9.4). Tiger sharks were found in shallow habitats almost twice as often as expected based on habitat surface area and over four times more often than expected based on the volume of available habitats (surface area: G = 325.3, df = 43, $P < 0.001$; volume: G = 655.1, df = 43, $P < 0.001$). None of the 500 iterations had a higher mean use

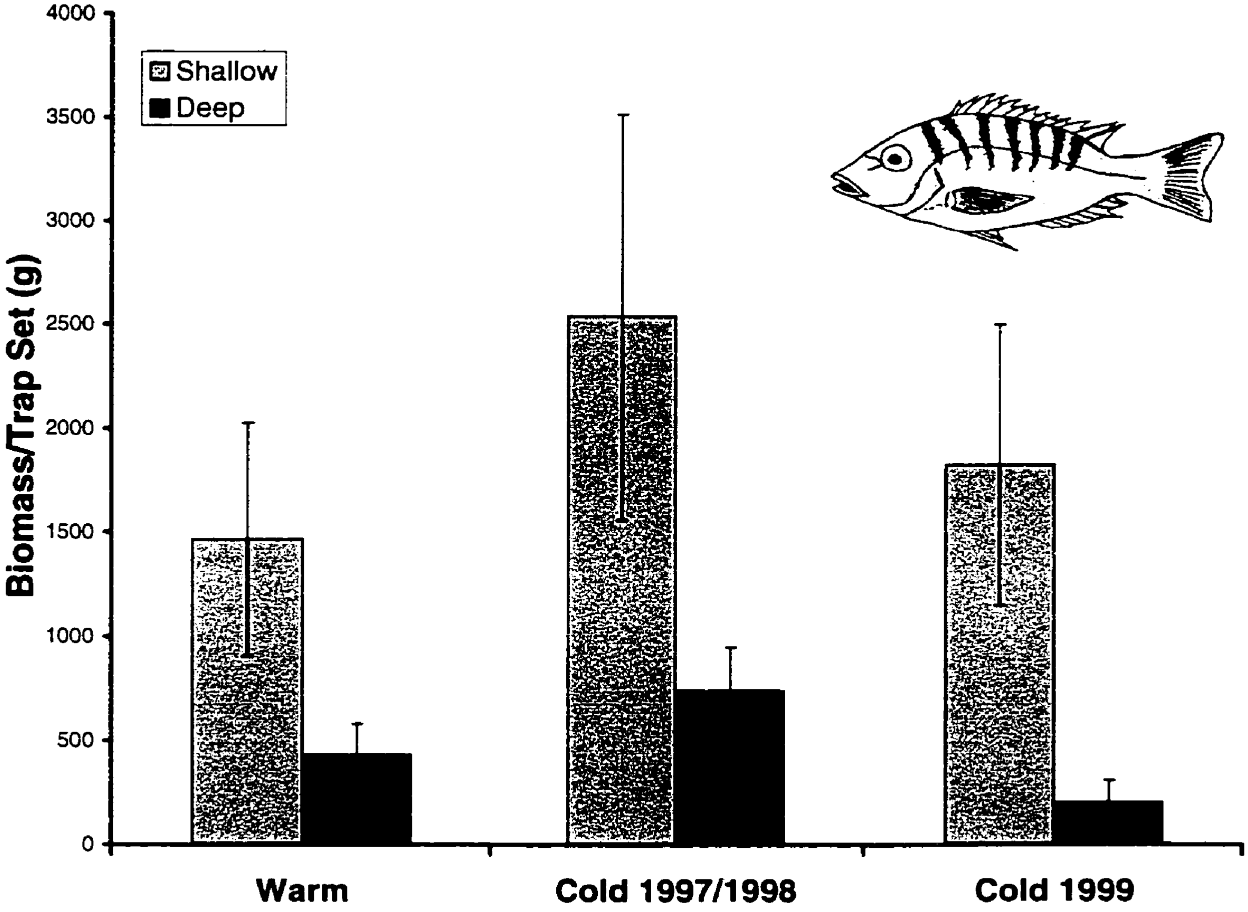


Figure 9.2. Distribution of fish biomass. Fish biomass per trap does not change seasonally, but is always greater in shallow habitats. Error bars represent 95% confidence intervals.

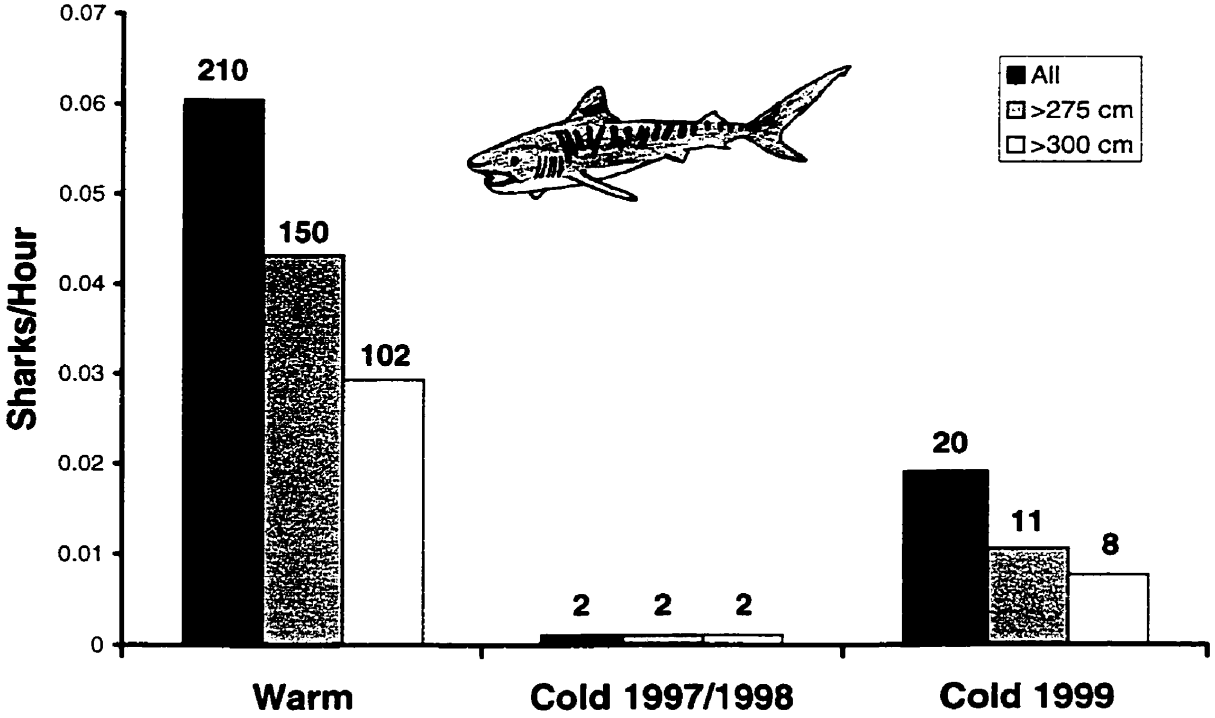


Figure 9.3. Seasonal changes in tiger shark catch rates. Note that the catch rate, and thus predation risk to dolphins, is high in warm months, very low in cold months of 1997/1998, and intermediate during the cold months of 1999. The numbers above the bars represent the numbers of sharks caught.

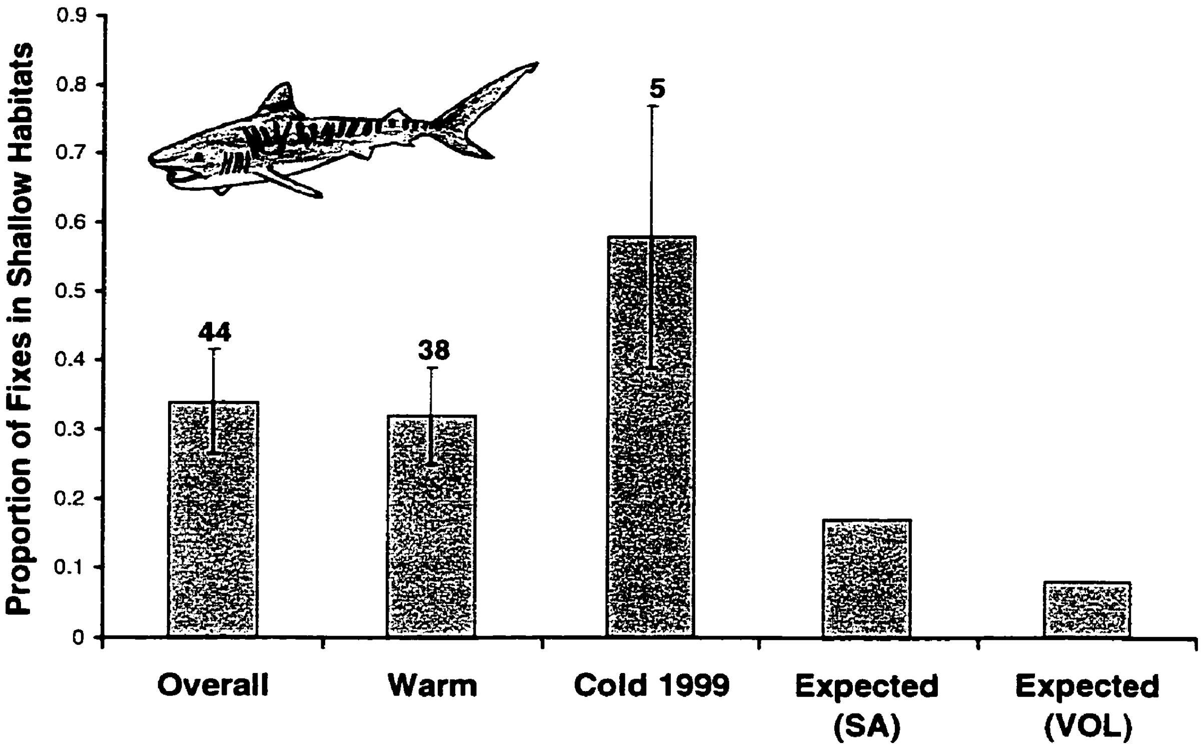


Figure 9.4. Tiger shark use of shallow habitats relative to the availability of these habitats based on surface area and volume. Tiger sharks are found in shallow habitats much more often than expected. Error bars represent 95% confidence intervals. The numbers above the bars represent the numbers of sharks tracked.

of shallow habitats than was observed. Tiger sharks were found in shallow habitats significantly more often than expected during both warm months (surface area: G = 250.2, df = 37, $P < 0.001$; volume: G = 517.3, df = 37, $P < 0.001$) and the cold months of 1999 (surface area: G = 74.3, df = 4, $P < 0.001$; volume: G = 137.8, df = 4, $P < 0.001$). There were insufficient data (n = 1) from cold months to address this question.

9.4.3 Dolphin Habitat Use

A total of 3,826 dolphins were sighted during transects. Of these 1,205 were foraging, 1,713 resting, 330 socializing, and 439 traveling. There were 300 known individuals sighted (3,493 sightings) and several unidentifiable individuals (333 sightings). Most individuals (232, 77.3%) were sighted during both warm and cold seasons and those sighted in only one season were rare.

Dolphin habitat use was activity-specific and changed seasonally. The density of foraging dolphins was influenced by an interaction between season and habitat (Table 9.2). Dolphin density was highest in shallow habitats during the cold months of 1997/1998 and lowest in shallow habitats during warm months (Figure 9.5). The density of foraging dolphins relative to the biomass of potential prey was also influenced by an interaction between season and habitat (Table 9.3). In this case, the density of foraging dolphins relative to food was the same in shallow and deep habitats during the cold months of 1997/1998 (Figure 9.6). In contrast, the density of dolphins relative to food was significantly higher in deep habitats than in shallow ones during warm months and the cold months of 1999 (Figure 9.6).

The density of resting dolphins was influenced by an interaction of season and habitat, but there was a strong effect of habitat (Table 9.4). During all seasons, the density of resting dolphins was significantly higher in deep habitats. The lowest densities of resting dolphins were found in shallow habitats during warm seasons (Figure 9.7).

There was only one significant difference among age-sex classes in foraging habitat use during warm months. Juvenile males were found foraging in shallow habitats more often than were adults ($\chi^2 = 6.0$, df = 1, n = 67, $P < 0.05$). In cold months, there were no significant differences in habitat use between adult males and adult females accompanied by calves, adult males and females without calves, or between adult females

Table 9.2. Analysis of variance of the effect of season and habitat on the density of foraging dolphins. The analysis is based on 1,205 dolphin sightings from 795 transect passes.

Factor	df	*F*	*P*
Season	2	8.1	< 0.001
Habitat	1	5.2	< 0.05
Season:Habitat	2	8.6	< 0.001
Error	52		

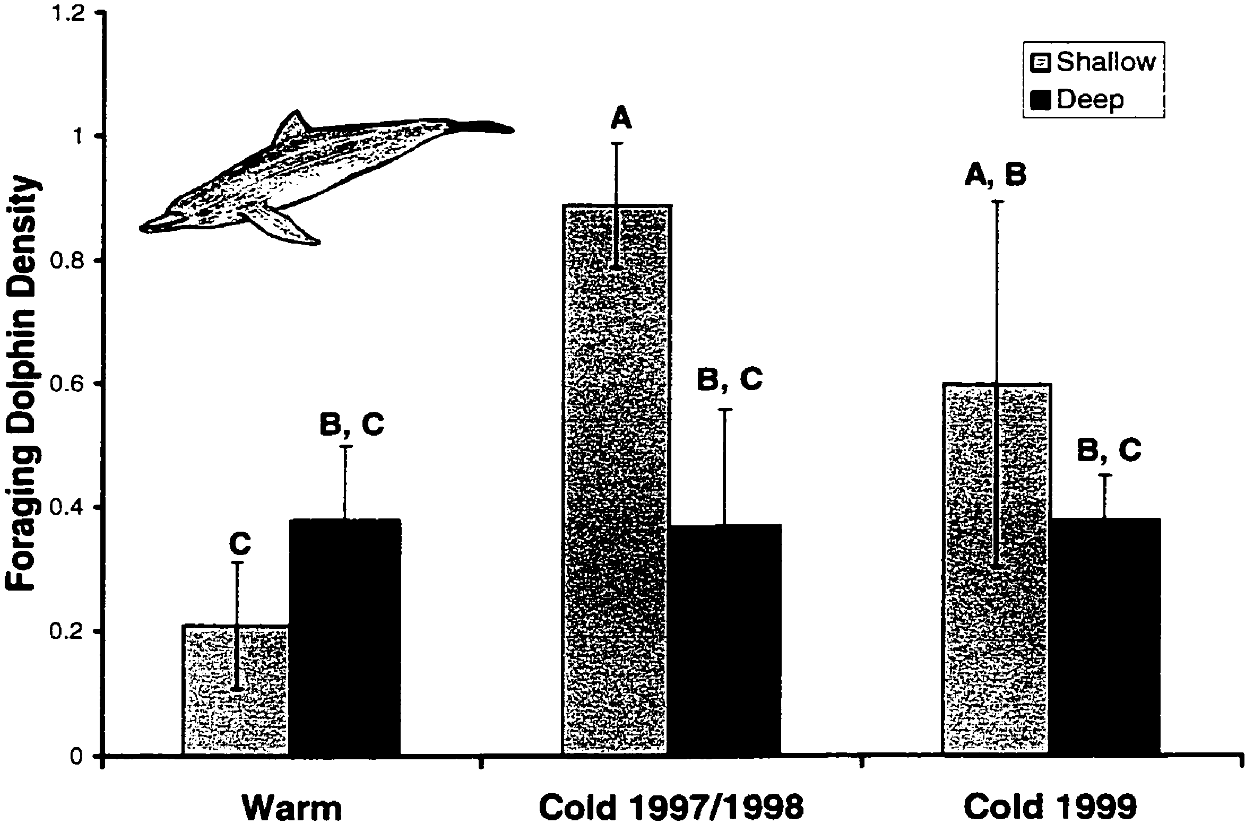


Figure 9.5. Seasonal changes in habitat use of foraging dolphins. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on log (x+1) transformed data. Error bars represent 95% confidence intervals.

Table 9.3. Analysis of variance of the effect of season and habitat on the density of foraging dolphins relative to fish biomass. The analysis is based on 1,205 dolphin sightings from 795 transect passes.

Factor	df	*F*	*P*
Season	2	0.3	0.73
Habitat	1	20.5	< 0.001
Season:Habitat	2	5.1	< 0.01
Error	52		

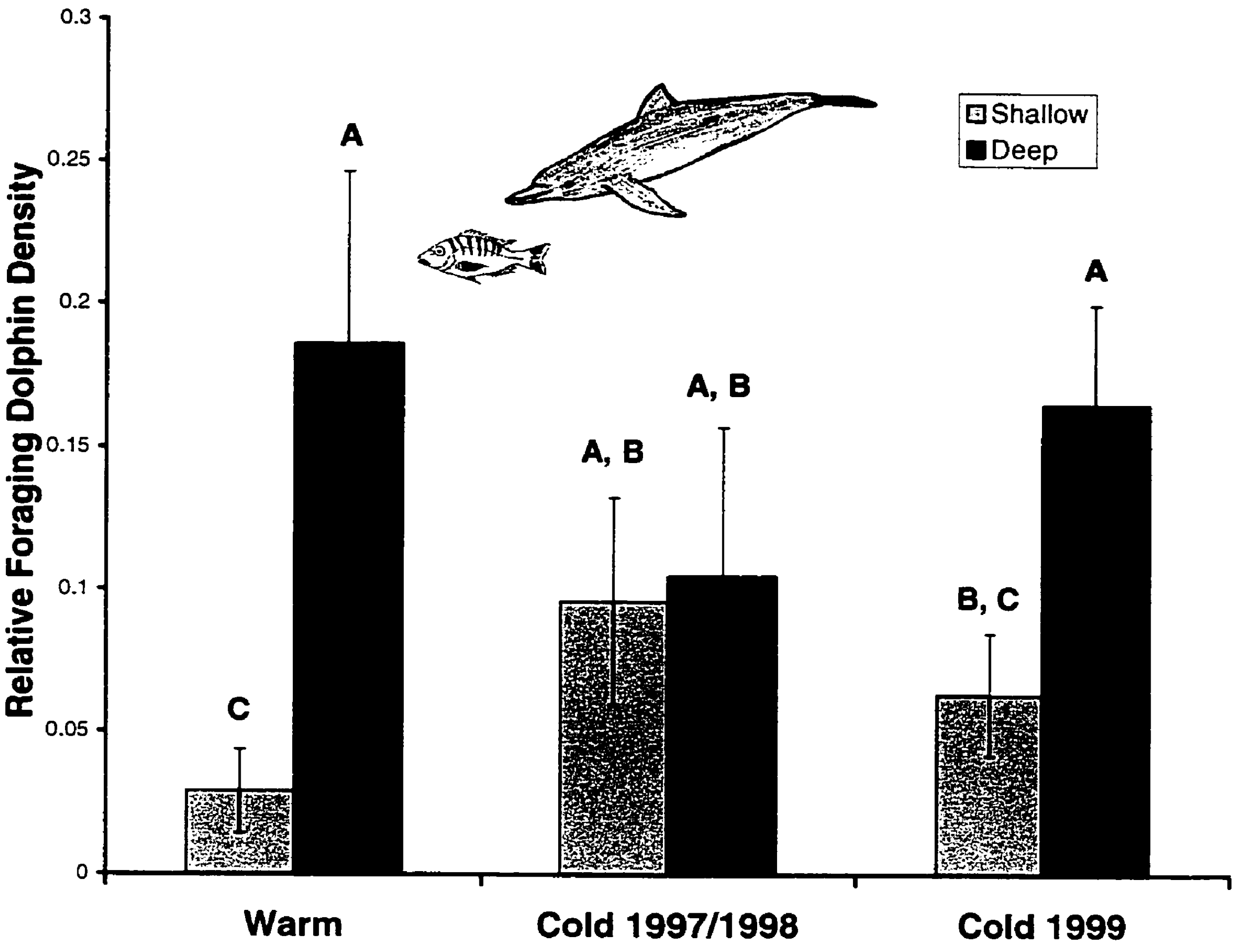


Figure 9.6. Seasonal changes in habitat use of foraging dolphins relative to food availability. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on log (x+1) transformed data. Error bars represent 95% confidence intervals.

Table 9.4. Analysis of variance of the effect of season and habitat on the density of resting dolphins. The analysis is based on 1,713 dolphin sightings from 795 transect passes.

Factor	df	*F*	*P*
Season	2	0.7	0.51
Habitat	1	45.9	< 0.001
Season:Habitat	2	4.8	< 0.025
Error	52		

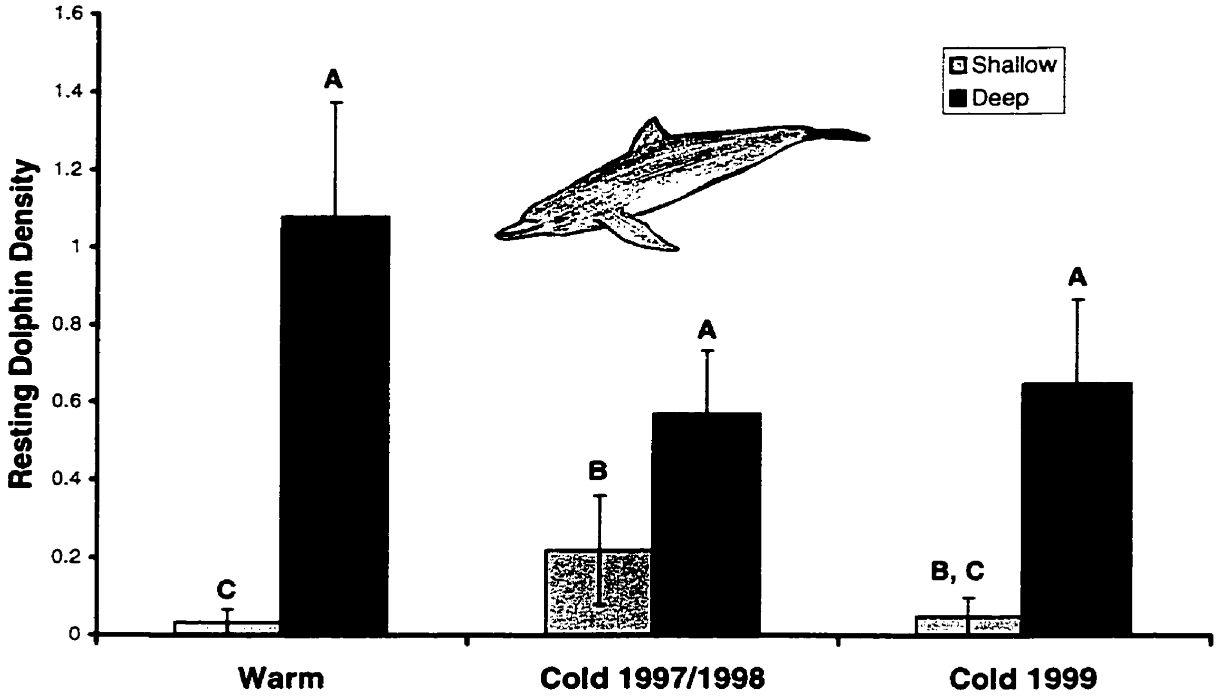


Figure 9.7. Habitat use of resting dolphins. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on log (x+1) transformed data. Error bars represent 95% confidence intervals.

with and without calves. However, juvenile males were found foraging in shallow habitats more often than adults ($\chi^2 = 7.6$, df = 1, n = 107, $P < 0.05$) and juvenile females ($\chi^2 = 11.9$, df = 1, n = 88, $P < 0.01$).

9.4.4 Dolphin Group Size

Dolphin group size was significantly influenced by habitat with significantly larger groups found in shallow habitats (n = 222, $\bar{x} = 3.40 \pm 0.16$ SE) than in deep ones (n = 813, $\bar{x} = 2.91 \pm 0.07$ SE; Table 9.5). Group size was also significantly affected by an interaction of season and activity (Table 9.5, Figure 9.8). Regardless of season, resting groups were larger than foraging groups (Figure 9.8). There was no significant difference in the size of foraging groups found in warm and cold months, but the size of resting groups was significantly larger in warm months (Figure 9.8). Within cold months, foraging groups in shallow habitats (n = 158, $\bar{x} = 2.1 \pm 0.10$ SE) were larger than those in deep habitats (n = 241, $\bar{x} = 1.4 \pm 0.08$ SE; t = 4.42, df = 398, $P < 0.001$).

9.5 DISCUSSION

I found that bottlenose dolphins faced spatial and temporal variation in predation risk and spatial variation in the abundance of food resources. The biomass of potential dolphin prey was higher in shallow habitats during all seasons and did not vary significantly with season. However, tiger sharks were abundant during warm months, almost absent during the cold months of 1997 and 1998 and caught at intermediate rates in the cold months of 1999. When sharks were present, shark density, and thus predation risk to dolphins was higher in shallow habitats. And although less volume must be scanned for sharks in shallow habitats (e.g. Norris and Dohl 1980a), they are likely to be intrinsically riskier than deeper ones. First, tiger sharks are better camouflaged when swimming over the seagrass characterizing much of the shallow habitats than when swimming over the light sandy bottoms of the deep habitats. Therefore, visual detection of predators would be more difficult in the shallows than in deeper water despite slightly lower light levels in the latter. Second, dolphin echolocation is likely to be less efficient in very shallow waters due to the scattering of the clicks off the surface and bottom.

Table 9.5. Analysis of variance of the effect of season, habitat and activity on the size of dolphin groups. The analysis is based on 1,035 groups.

Factor	df	*F*	*P*
Season	1	5.3	< 0.05
Habitat	1	9.0	< 0.01
Activity	1	668.8	< 0.001
Season:Activity	1	4.2	< 0.05
Error	1030		

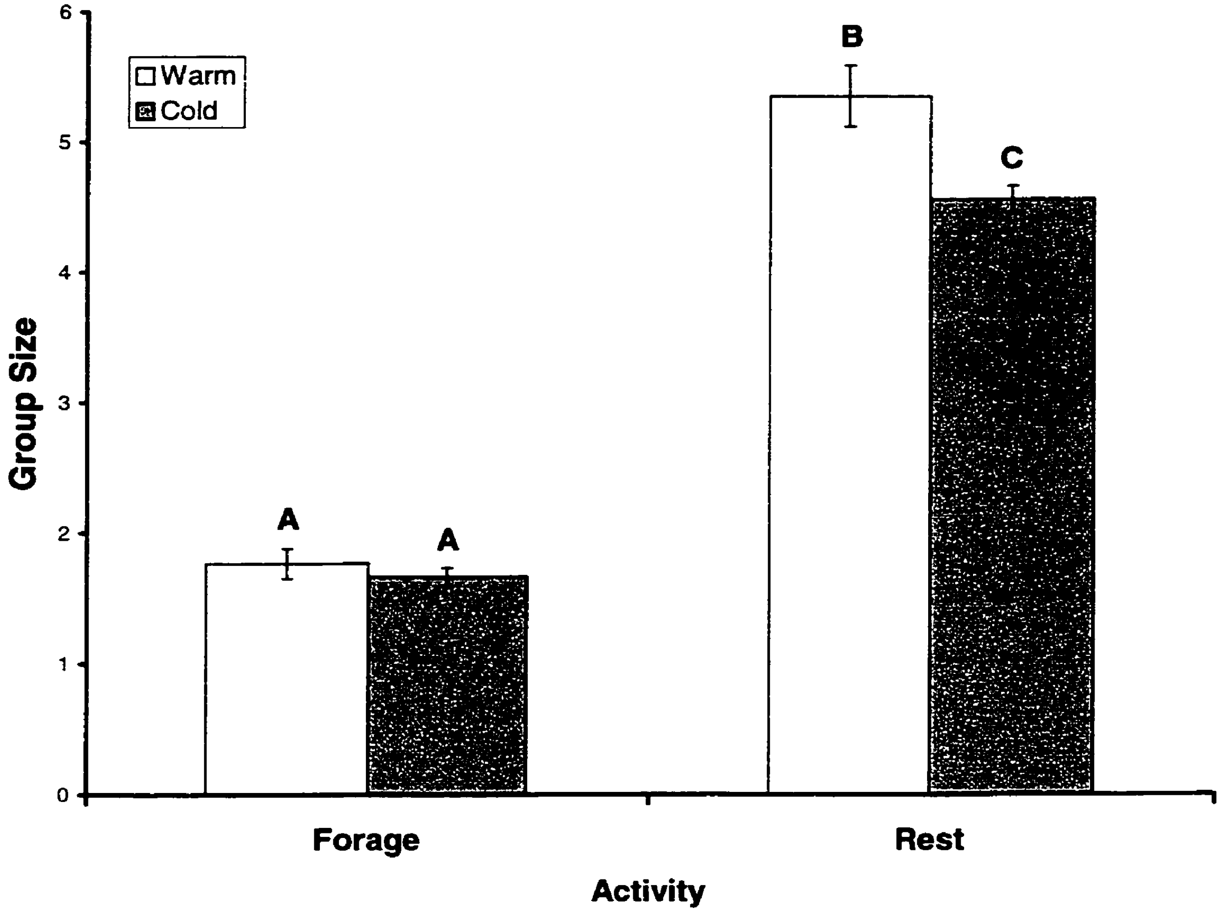


Figure 9.8. Average size of dolphin groups engaged in resting and foraging during both warm and cold months. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on square root transformed data. Error bars represent 95% confidence intervals.

Also, biological noise (e.g. sounds produced by snapping shrimp) is more frequent and louder in shallow habitats than deep habitats (MRH personal observation), which could further reduce echolocation efficiency (Au 1993). Thus, acoustic detection of predators may be more difficult in shallow habitats than in deep ones. Finally, the probability of dolphins escaping a shark attack is probably greater in deep habitats because there are more potential escape routes than in shallow habitats.

Dolphin behavior supports our conclusions regarding spatial and temporal variation in the risk of predation. Resting is probably the most dangerous activity that dolphins engage in because of reduced vigilance at this time (Würsig et al. 1994, Connor and Heithaus 1996, Heithaus in press d) and the lack of a refuge from predators. Since dolphins have low travel costs (Williams et al. 1992), and there is no benefit to staying in dangerous areas, dolphins should rest in the safest habitats (Heithaus in press d), especially during seasons when predators are common. Such activity-specific habitat use has been observed in other species. For example, desert baboons (*Papio cynocephalus ursinus*) avoid all habitats but the safest while resting (Cowlishaw 1997), and Hawaiian spinner dolphins (*Stenella longirostris*) move into shallow coves with white sand bottoms to rest during the day, probably to avoid shark predators (Norris and Dohl 1980a). Dolphins in this study rested almost exclusively in deep waters suggesting that these are perceived as the safer habitats. Despite underuse of shallow habitats for resting in all seasons, the observation that dolphins increase their use of shallow habitats for resting in cold months suggests that there are no intrinsic reasons, other than risk, for dolphins to avoid shallow waters for this activity.

Both food availability and the risk of predation from tiger sharks influence habitat use by foraging dolphins in Shark Bay. During cold months, when tiger sharks are largely absent, the habitat use of foraging dolphins appears to be driven primarily by food distribution. Foraging dolphins were found in the food-rich shallow habitats much more often than in deep habitats and the proportion of dolphins in deep and shallow habitats matched the proportion of fish biomass in those habitats.

Both theoretical and empirical studies (e.g. Abrahams and Dill 1989, McNamara and Houston 1990, Hugie and Dill 1994, Heithaus in press a, Chapter 3) lead to the prediction that dolphins should decrease their use of dangerous (i.e. shallow) habitats relative to food availability during high risk seasons if they trade-off food and safety. Indeed, when tiger sharks were present in the study area, dolphins did not match the distribution of their food quantitatively or qualitatively. During warm months dolphins were found in dangerous shallow habitats much less often than expected from food availability indicating that predation risk is an important determinant of dolphin habitat use.

There are several alternative hypotheses for the shift in dolphin habitat use during warm months. Dolphins may reduce their use of shallow habitats during warm months to avoid high water temperatures associated with shallow habitats, or habitat shifts may be due to seasonal peaks in reproductive activities (e.g. Connor et al. 1996, Mann et al. 2000). Neither of these hypotheses is supported. First, water temperatures do not differ between deep and shallow habitats during warm months, and few habitat use data were collected during the peak season of dolphin births. Also, the cold months of 1999 provide a natural experiment to test whether dolphins trade-off food and safety. While food availability, and presumably other factors (i.e. dolphin reproductive cycles), during the cold months of 1999 were similar to previous cold seasons, there were tiger sharks in the study area presenting a regime of predation risk more similar to previous warm seasons. Dolphins increased their use of shallow habitats relative to warm months, but habitat use by foraging dolphins relative to the distribution of food resources during the cold months of 1999 more closely resembled that of warm seasons and was different from that of other cold seasons. This provides strong support for the conclusion that differences in habitat use among seasons are due to a food-safety tradeoff rather than to some unmeasured variable, and that dolphins are able to adaptively modify their habitat use patterns in response to changes in tiger shark abundance.

Previous studies have hypothesized a role of both predation risk and prey availability in shaping patterns of dolphin habitat use. For example, habitat use of Atlantic bottlenose dolphins (*Tursiops truncatus*) in Sarasota, Florida has been hypothesized to reflect a tradeoff between food availability and predation risk, with dolphins selecting shallow habitats to avoid encounters with bull sharks (*Carcharhinus leucas*) (Wells et al. 1980, 1987). Ours is the first study to show that both predation risk and food availability play a significant role in determining the distribution of an odontocete cetacean. Furthermore, this study shows that dolphins may adaptively switch their habitat use patterns with changes in the level of risk.

Despite abundant laboratory evidence, few field studies have shown that animals trade-off predation risk and food availability, especially in systems where direct experimental manipulations are not possible. Experimental work has shown that small mammals stop foraging in risky habitats at higher remaining food availability than they do in safe habitats (e.g. Brown et al. 1992), and ontogenetic habitat shifts in bluegill sunfish (*Lepomis macrochirus*) are influenced by foraging rate and the density of predatory largemouth bass (*Micropterus salmoides*) (Werner and Hall 1988). Several observational field studies have also shown food-safety tradeoffs. Desert baboons appear to trade-off food availability and predation risk, and they spend less time foraging in high-risk and high-food habitats than expected from food availability alone (Cowlishaw 1997). In South Africa, wild dogs (*Lycaon pictus*) are found in low densities in areas with high food availability (small ungulates) but high predator (lion, *Panthera leo*) density (Mills and Gorman 1997). Wild dogs are found in the highest densities in areas with low predator density and lower food abundance.

Theoretical models suggest that the presence of alternative resources for top predators can have a substantial influence on the habitat use of their prey, resulting in indirect behavioral effects between prey species that do not compete with each other (Heithaus in press a, Chapter 3). This applies in the Shark Bay ecosystem. Tiger sharks in this area consume primarily dugongs, sea snakes and sea turtles, but also include rays, sea birds, and teleosts in their diet (Simpfendorfer et al. in press, Heithaus in press c, Chapter 5). Dolphins are a minor component of the sharks' diets despite being attacked frequently (Heithaus in press b). Tiger shark seasonal abundance and habitat use are linked to both water temperature and temporal and spatial variation in the availability of their main prey (Heithaus in press c, Chapters 5, 7). Therefore, dolphin habitat use is at least partially influenced by seasonal movements and habitat use decisions of species with which they do not interact directly but share a common predator (i.e. decisions made by dugongs, sea snakes, and sea turtles which influence the distribution of tiger sharks; e.g. Heithaus in review). This situation provides a behavioral analog to apparent competition (Holt 1977, 1984).

Complex trophic interactions characterize many food webs (e.g. Polis 1991, Polis and Strong 1996), and indirect behavioral effects on habitat use, like those described for dolphins, may be common. For example, wild dog distribution appears to be indirectly affected by the distribution of large ungulates, which influence the distribution of their shared predator, lions (Mills and Gorman 1997). Such indirect behavioral effects may function in a similar manner to trophic cascades (e.g. Pace et al. 1999). Because of the possibility of "behaviorally mediated indirect interactions" in many communities that contain top predators with diverse diets, field studies of animal habitat use may benefit from taking community and food web structure into account. The possibility of behaviorally mediated indirect interactions in Shark Bay and other communities is an intriguing possibility that warrants further investigation.

Juvenile male dolphins were found to enter shallow habitats more often than other age-sex classes during both warm and cold months, suggesting that juvenile males are more willing to accept higher predation risk to obtain higher energy intake rates. A similar age class difference in risk-taking behavior while foraging has been found in redshank (*Tringa totanus*) where juveniles attempt to maximize energy intake by foraging in high-risk areas of salt marshes where energy intake rate is high while adults are found in low-risk mussel bed habitats with low energy intake rates (Cresswell 1994). Risk-taking by juvenile redshank may facilitate early breeding (Creswell 1994) and juvenile male dolphins may also gain fitness benefits from risk-taking. In Shark Bay, adult males form alliances that aggressively maintain consortships with reproductive females (Connor et al. 1992, 1999). Foraging in the energetically profitable shallow habitats may increase the growth rate of juvenile males relative to those foraging in deeper waters. Increased growth rates and larger body size may facilitate earlier alliance formation or increase ability to compete for access to females at a relatively young age. Further studies will be required to test this hypothesis.

Reproductive success of female bottlenose dolphins in Shark Bay is negatively correlated with water depth, as females found, on average, in shallow waters have more calves survive until weaning (Mann et al. 2000). Mann et al. (2000) proposed that this trend may be a result of shallow water providing some protection from predatory sharks through increased detection and avoidance. That cetaceans obtain protection from predators in shallow waters has been proposed several times (Norris and Dohl 1980a, Wells et al. 1987), but the relationship between water depth and risk is unclear (e.g. Heithaus in press d, Chapter 2). If predation risk were reduced in shallow habitats of Shark Bay, female dolphins with calves should be found predominantly in shallow habitats during both foraging and resting in high-risk months, but this is not the case. Instead, female dolphins accompanied by calves avoid shallow waters during months of high shark density, suggesting that higher female reproductive success in shallow habitats in Shark Bay is not due to reduced predation risk. A more likely explanation for the trend in female success is that females found, on average, in shallower water would be able to take advantage of much higher food availability in shallow habitats during foraging, but then move into deeper and safer habitats during rest. Such adaptive switching between habitats based on activity would allow individuals to benefit from low predation risk in deeper habitats and high energy intake in shallow ones when required. Females found exclusively in deep waters are perhaps less likely to meet the energetic demands of lactation and thus have higher calf mortality rates. Also, if energy intake by mothers inhabiting deep habitats is low, this may lead to an increased predation rate on their calves. To fully understand the reasons for differential female reproductive success it will be necessary to determine the relative frequency of the causes of calf mortality.

A fission-fusion social organization, like that of bottlenose dolphins in Shark Bay (Smolker et al. 1992), allows individuals to select their group size based on ecological conditions and activity. Predation risk has been hypothesized to be the primary reason for group formation in dolphins (Norris and Dohl 1980b), but food availability may also be important. Group size of bottlenose dolphins in Sarasota appears to represent a trade-off between energy intake and risk (Wells et al. 1980, 1987) and group size data from Shark Bay are generally consistent with expectations based on such a tradeoff. As predicted, resting groups were larger than foraging groups suggesting that dolphins must form smaller groups during foraging to reduce competition. Also consistent with predictions, the sizes of resting groups were responsive to changes in predation risk, as resting groups were larger in the more dangerous warm months than in the safer cold months. Dolphin group sizes in Shark Bay also appear to be responsive to food availability. In low-risk months, foraging group size was higher in the more productive shallow habitats.

However, this result is also consistent with the hypothesis that groups were larger because of higher risk in shallow waters, even though overall shark density was low.

This study has several important implications for the conservation of nearshore odontocete cetaceans. Dolphins and porpoises are increasingly having to contend with human disturbance in the form of habitat alteration, reductions in prey species populations, and boating activity. This study suggests that human disturbance that changes the habitat use of species that share a common predator with dolphins may change dolphin habitat use through a behaviorally mediated indirect interaction. Also, human disturbances or activities that dolphins perceive as predation risk have the potential to alter dolphin habitat use and reduce population size, as observed in other species. For example, human disturbance of pink-footed geese (*Anser brachyrhynchus*) results in an underuse of available resources and diminishes the number of individuals a disturbed habitat supports (Gill et al. 1996). If human disturbance, like boating activity (e.g. Allen and Read 2000), is greatest in high productivity habitats, it is possible that dolphins will not make full use of their food resources, effectively reducing the carrying capacity of the environment. Such disturbance may also cause shifts in dolphin habitat use that increase their encounter rates with natural predators and thus increase mortality rates.

This study is the first to show that both food availability and predation risk influence dolphin habitat use. Dolphins adaptively reduce their use of high-risk high-food habitats based on the presence of tiger sharks. Future studies on dolphins, in areas which differ from Shark Bay in food distribution and predation risk, can incorporate the framework and methods developed during this study to elucidate the role of predation risk and food availability in the evolution of sociality and behavior of small odontocetes.

9.6 ACKNOWLEDGEMENTS

I would like to thank C. Simpfendorfer and R. McAuley for their help in initiating the shark study by providing bait, fishing gear and advice. L. Dill, C. Lowe, R. Connor, B Crespi, B. Roitberg, D. Lank, G. Marshall, B. Buhleier, the crew of the Fisheries WA R/V Flinders, and the Dill lab also provided helpful advice. L. Barre, J. Burghardt, J. McLash, C. Genrich, S. Buchannan, F. Bretos, P. Greene, S. Burghardt, I. Hamilton, and H. Finn provided field assistance. Grants and support were provided by National Geographic Expeditions Council, National Geographic Special Projects, Monkey Mia Dolphin Resort, NSERC Canada grant A6869 to LMD, the National Science Foundation (Graduate Research Fellowship to MRH), Columbus Zoo, PADI Foundation, American Museum of Natural History, Society for Marine Mammalogy (Shane Award to MRH), Monkey Mia Wildlife Sailing, Mercury Marine, Shakespeare Electronics, Humminbird, the Burghardt family, Fisheries WA, Green Cape Wildlife Films, Kodak Australia, Singapore Airlines, Eurocom Computers, and public donations. Special thanks go to G. Marshall, B. Buhleier, and the Special Projects team for providing Crittercams and technical assistance throughout the project. The Monkey Mia Dolphin Resort, Shark Bay Fish Factory, and Tradewinds Supermarket all provided storage space for bait. B. Barton, D. Charles, R. Swann, R. Lane, and A. Fraser provided logistical support throughout the project. Thanks also go to R. Holst and J. Heymans for their generosity and hospitality. This research was carried out while MRH was a Ph.D. student at Simon Fraser University and a visiting research associate at the Department of Anatomy and Human Biology (University of Western Australia) and under the authority of Fisheries WA permits 67/97 and 69/97, Department of Conservation and Land Management permits SF002347, NE001808, DI000044, NE001649, and Simon Fraser University Animal Care permits. I thank the Shark Bay dolphin research group for helping identify dolphin age/sex classes, and I. Hamilton for statistical advice. Finally, I would like to thank L. Dill, B. Crespi, B. Roitberg, R. Connor, I. Hamilton, and three anonymous reviewers for helpful comments on this manuscript.

9.7 LITERATURE CITED

Abrahams, M.V. and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999-1007.

Allen, M. C. and A. J. Read. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Marine Mammal Science 16: 815-824.

Au, W. W. L. 1993. Sonar of Dolphins. Springer-Verlag, New York.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 64-96 *in* J. R. Krebs and N. B. Davies, editors. Behavioural Ecology: An Evolutionary Approach, Fourth Edition. Blackwell, Oxford.

Brown, J. S., R. A. Morgan, and B. D. Dow. 1992. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. Annales Zoologici Fennici 29: 311-318

Connor, R. C. and M. R. Heithaus. 1996. Great white shark approach elicits flight response in bottlenose dolphins. Marine Mammal Science 12: 602-606.

Connor, R. C., R. A. Smolker, and A. F. Richards. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). Proceedings of the National Academy of Sciences, USA 89: 987-990.

Connor, R. C., A. F. Richards, R. A. Smolker, and J. Mann. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133: 37-69.

Connor, R. C., M. R. Heithaus, and L. M. Barre. 1999. Superalliance of bottlenose dolphins. Nature 397: 571-572.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour 53: 667-686.

Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? Journal of Animal Ecology 63: 589-600.

Gilliam, J. F. and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856-1862.

Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Animal Ecology 33: 786-792.

Grand, T. C. and L. M. Dill. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. Behavioral Ecology 8: 437-447.

Heithaus, M. R. in press a. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92.

Heithaus, M. R. in press b. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. Marine Mammal Science 17.

Heithaus, M. R. in press c. The biology of tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes.

Heithaus, M. R. in press d. Predator-prey and competitive interactions between sharks (Order Selachii) and dolphins (Suborder Odontoceti): a review. Journal of Zoology (London).

Heithaus, M. R. in review. Seasonal abundance and habitat use of dugongs (*Dugong dugon*) in Shark Bay, Western Australia.

Heithaus, M. R. and I. M. Hamilton. in review. Assessing animal habitat use from tracking data.

Heithaus, M. R., G. Marshall, B. M. Buhleier, and L. M. Dill. in press. Employing Crittercam to study habitat use and behavior of large sharks. Marine Ecology Progress Series 109.

Hill, R. A. and P. C. Lee. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. Journal of Zoology 245: 447-456.

Holland, K. N., B. W. Wetherbee, C. G. Lowe, and C. G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134: 665-673.

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Biology 12: 197-229.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45 (Suppl. A): 151-169.

Janson, C. H. and M. L. Goldsmith. 1995. Predicting group size in primates: foraging costs and predation risks. Behavioral Ecology 6: 326-336.

Lessels, C. M. 1995. Putting resource dynamics into continuous input ideal free distribution models. Animal Behavior 49: 487-494.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Mann, J., R. C. Connor, L. M. Barre, and M. R. Heithaus. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group size effects. Behavioral Ecology 11: 210-219.

Marshall, G.J. 1998. Crittercam: an animal-borne imaging and data logging system. Marine Technology Society Journal 32: 11-17.

McNamara, J. M. and A. I. Houston. 1990. State-dependent ideal free distributions. Evolutionary Ecology 4: 298-311.

Mills, M. G. L. and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11: 1397-1406.

Norris, K. S. and T. P. Dohl. 1980a. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin US 77: 821-849.

Norris, K. S. and T. P. Dohl. 1980b. The structure and function of cetacean schools. Pages 211-261 *in* L. M. Herman, editor. Cetacean Behavior: Mechanisms and Functions. Wiley, New York.

Oksanen, T., M. E. Power, and L. Oksanen. 1995. Ideal free habitat selection and consumer-resource dynamics. American Naturalist 146: 565-585.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades in diverse ecosystems. Trends in Ecology and Evolution 14: 483-488.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138: 123-155.

Polis, G. A. and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147: 813-846.

Sheaves, M. J. 1992. Patterns of distribution and abundance of fishes in different habitats of a mangrove-lined tropical estuary, as determined by fish trapping. Australian Journal of Marine and Freshwater Research 43: 1461-1479.

Sheaves, M. J. 1995. Effect of design modifications and soak time variations on Antillean-Z fish trap performance in a tropical estuary. Bulletin of Marine Science 56: 475-489.

Simpfendorfer, C. A., A. B. Goodreid, and R. B. McAuley. in press . Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123: 38-69.

Terborgh, J. W. 1983. Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton.

Turchin, P. 1998. Quantitative Analysis of Movement. Sinauer Associates, Sunderland, MA.

Wells, R. S., A. B. Irvine, and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pages 263-317 *in* L. M. Herman, editor. Cetacean Behavior: Mechanisms and Functions. Wiley, New York.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 *in* H. H. Genoways, editor. Current Mammalogy, Volume 1. Plenum Press, New York.

Werner, E. E. and D. J. Hall. 1988. Ontogenetic shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Williams, T. M., A. W. Friedl, M. L. Fong, R. M. Yamada, P. Sedivy, and J. E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355: 821-823.

Würsig, B., R. S. Wells, K. S. Norris, and M. Würsig. 1994. A spinner dolphin's day. Pages 65-102 *in* K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, editors. The Hawaiian Spinner Dolphin. University of California Press, Berkeley.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall Inc, Englewood Cliffs, NJ.

CHAPTER 10

General Conclusions

There have been few field tests in relatively complex natural communities with the goal of determining the influences of predation risk and prey availability on animal habitat use in a community context. I used a behavioral ecological framework to test the prediction that bottlenose dolphins would modify their patterns of habitat use during foraging in response to variation in food availability and predation risk. Because manipulative experimentation was not possible, the use of this framework in conjunction with natural variation in predation risk regimes was the only method for gaining insight into the factors influencing dolphin habitat use.

My review of competitive and predator-prey interactions between dolphins and sharks showed that they may engage in asymmetrical intraguild predation (IGP, Chapter 2). Because there were no models of habitat use under such conditions, I created a game theoretic model of asymmetrical IGP (Chapter 3). I found that the level of dietary overlap between intraguild (IG) predators (e.g. sharks) and IG prey (e.g. dolphins) and the presence of alternative resources for IG predators (e.g. dugongs, sea snakes, sea turtles) greatly influence the predicted spatial distributions of IG predators and prey. Therefore, community context is an important consideration, and it is important to understand the basic ecology of both predators and prey.

In Chapter 4, I showed that tiger sharks are the major threat to bottlenose dolphins in Shark Bay, Western Australia, and more than 10% of dolphins are attacked each year. However, dolphins are a minor component of tiger shark diets in Shark Bay (Chapter 5, Simpfendorfer et al. in press). Instead, the tiger sharks in the Eastern Gulf of Shark Bay feed predominantly on sea snakes, dugongs, and sea turtles, and occasionally on rays and teleost fish. This indicates that IGP probably occurs between tiger sharks and bottlenose dolphins in the study area, but dietary overlap is low and there are alternative resources for the IG predator (tiger sharks).

Tiger sharks were not present in the study area throughout the year and there was a strong correlation between water temperature and catch rate. However, changes in tiger shark abundance also appeared to be linked to changes in the availability of dugongs and sea snakes (Chapter 5). Prey availability was also important in determining tiger shark habitat use (Chapter 6, 7). When tiger sharks were present in the study area, they showed a significant preference for shallow seagrass habitats where the density of all primary prey species was greater. A similar spatial distribution was found for dolphin food resources with the biomass of fish being greater in shallow habitats (Chapter 8).

Chapter 9 showed that bottlenose dolphins trade-off food availability and predation risk when making habitat use decisions. I used temporal and spatial variation in predation risk and data on food availability to test the prediction that dolphins would reduce their use of dangerous but productive habitats when faced with high tiger shark densities. I found that dolphins matched the distribution of their food when tiger sharks were absent. However, when predation risk was high, foraging dolphins largely avoided the food-rich but dangerous shallow habitats. These results are consistent with the predictions made by a variety of behavioral ecological models of animals foraging under the risk of predation.

Perhaps the most intriguing finding of this study was that habitat use by dolphins may be influenced indirectly by species that are not competitors, predators, or prey. Chapter 3 suggested that the presence of alternative resources for predators can have a substantial influence on the habitat use of their prey, and tiger sharks consume a number of alternative prey species (Simpfendorfer et al. in press, Chapter 5), so behaviorally mediated indirect interactions are possible. The seasonal abundance of dugongs appears to be influenced by changes in water temperature while habitat use decisions are based largely on the distribution of seagrass (Heithaus in review). The decisions made by dugongs in turn influence tiger shark seasonal abundance and habitat use (Chapters 5, 7). Therefore, since the presence and spatial distribution of tiger sharks influence dolphin habitat use, dolphin habitat use is at least partially influenced by seasonal movements and habitat use decisions of species with which they do not interact directly (e.g. dugongs and sea snakes, Figure 10.1). If behaviorally mediated indirect interactions are important in the Shark Bay community, it is possible that changes in the abundance or behavior of one species in the community may have predictable effects on others. For example, if dugongs and sea snakes abundance dropped substantially, tiger sharks might have to modify their habitat use to take advantage of potential prey in deep habitats and cause dolphins to switch to preferentially using shallow habitats when tiger sharks are present. Also, the removal of tiger sharks may allow dolphins and loggerhead turtles to increase

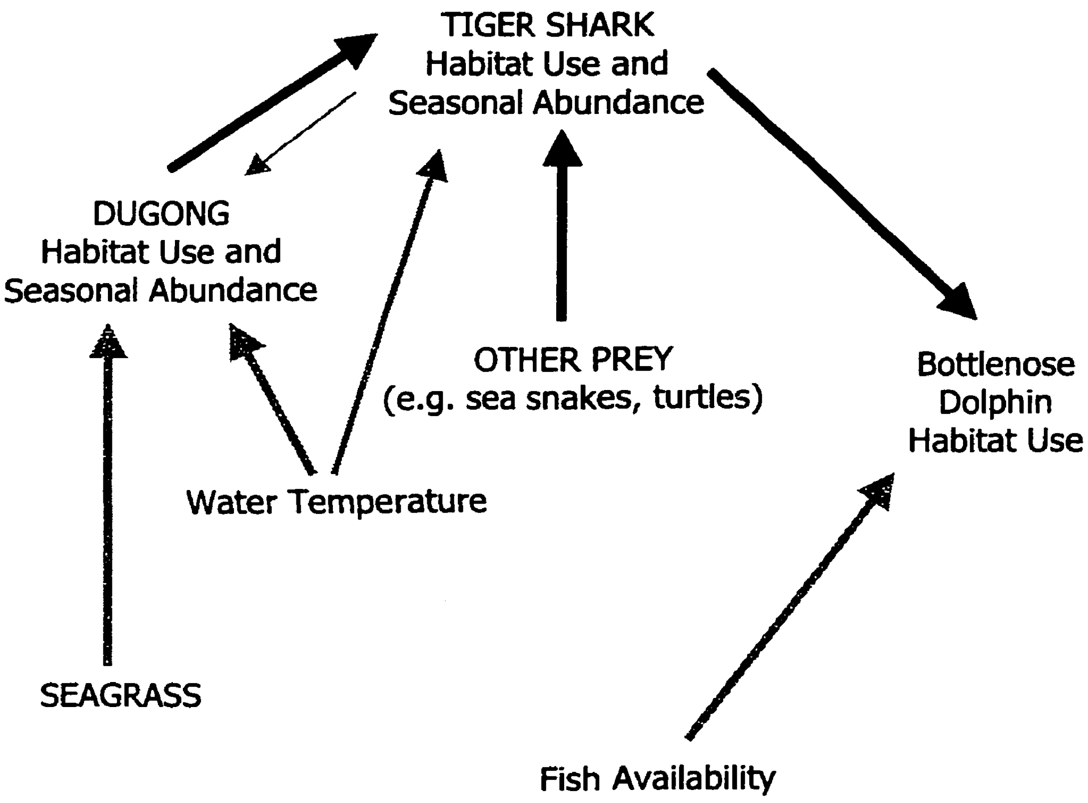


Figure 10.1. Possible behaviorally mediated indirect interactions in the Shark Bay community. Behavioral decisions made by dugongs and other prey of tiger sharks may indirectly affect the habitat use of dolphins because of their effect on habitat use and seasonal abundance of tiger sharks. Black arrows indicate the pathway for an behaviorally mediated indirect interaction between dugongs and dolphins. Gray arrows indicate other factors identified as important in habitat use decisions.

their relative use of shallow habitats resulting in changes in communities of both fish and benthic invertebrates.

Despite the apparent importance of the community context of habitat use decisions, most theoretical and empirical studies have been conducted in very simple systems. Few natural communities are so simple that they contain only one predator, its prey, and the food resources of the prey (e.g. Polis 1991, Polis and Strong 1996). When communities are more complex, habitat use decisions of one species are likely to be influenced indirectly by species with which they share a common predator, even if they do not interact directly. Investigations of behavioral decisions within a community context and attempts to understand the links between behavioral decisions and community dynamics, a current topic of interest in behavioral ecology (e.g. Fryxell and Lundberg 1997), are likely to be fruitful avenues of research, both theoretical and empirical. Only with a full understanding of how animals make habitat use decisions within their natural communities can we hope to make predictions about how animal populations, and perhaps communities, will respond to changes in their environment. With the rate of human-induced changes to environments rapidly accelerating, behavior-based predictive models may form a cornerstone of future conservation efforts (Gill and Sutherland 2000).

10.1 LITERATURE CITED

Fryxell, J. M. and P. Lundberg. 1997. Individual Behavior and Community Dynamics. Chapman & Hall, New York.

Gill, J. A. and W. J. Sutherland. 2000. Predicting the consequences of human disturbance from behavioral decisions. Pages 51-64 *in* L. M. Gosling and W. J. Sutherland, editors. Behavior and Conservation Cambridge University Press, Cambridge.

Heithaus, M. R. in review. Seasonal abundance and habitat use of dugongs (*Dugong dugon*) in Shark Bay, Western Australia.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138: 123-155.

Polis, G. A. and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147: 813-846.

Simpfendorfer, C. A., A. B. Goodreid, and R. B. McAuley. in press. Size, sex, and geographic variation in the diet of the tiger shark (*Galeocerdo cuvier*) in Western Australian waters. Environmental Biology of Fishes.