# PREDATION-SENSITIVE FORAGING BEHAVIOUR OF DUGONGS (*DUGONG DUGON*)

by

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# Abstract

Foraging decisions by herbivores are of great interest to ecologists, as spatial and temporal patterns of herbivory may structure plant communities. Yet, in marine systems, the factors governing foraging choices of large herbivores (e.g., sea turtles, sirenians) remain poorly understood. Between 2002 and 2004, I assessed the use of habitat and alternative feeding tactics by dugongs (*Dugong dugon*) foraging under risk of predation by tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Western Australia. Use of two primary foraging habitats (shallow banks, deep channels) by dugongs was monitored systematically using transect passes through 14 survey zones allocated evenly to the habitat types; use of two microhabitats within shallow areas (edge, interior) by foragers was also quantified using transects. The time allocated to each of two alternative feeding tactics (cropping, excavation) by individual dugongs was quantified using focal animal follows. The threat of tiger shark predation was indexed using catch rates on drumlines. Overall, foraging dugongs showed a consistent preference for shallow habitats, which are rich in food (seagrass). However, the degree to which foragers used deep habitats, where seagrass is sparse but safety from sharks is relatively high, changed in a threat-sensitive manner: forager densities in deep habitat were equivalent to those predicted by food supply when sharks were scarce, and greatly exceeded levels predicted by food alone when sharks were common. Within shallow habitats, foragers preferred interior feeding microhabitats when sharks were scarce, and shifted to edge microhabitats, which offer swift escape into deep water, when sharks were common. Finally, foraging dugongs spent the majority of their time cropping seagrass. However, during months when excavation occurred (Feb – May of all years), use of this tactic was inversely related to shark abundance, likely because it constrains vigilance. These results suggest that dugongs adaptively manage their risk of mortality by reducing their use of dangerous habitats, microhabitats, and feeding tactics when the likelihood of encountering predators is elevated. It follows that, by mediating patterns of dugong herbivory, tiger sharks may exert a powerful indirect effect on Shark Bay's seagrass meadows.

*In loving memory of Marie Emilia Wirsing*

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# Chapter 1

# General Introduction

## 1.1 Overview

Factors governing herbivore foraging behaviour are of great interest to ecologists, as patterns of foraging by these species may dramatically affect plant biomass, composition, diversity and, ultimately, community structure (Crawley 1983; Danell and Bergström 2002). The effects of one such factor – consumption by predators – on herbivore foraging have long been appreciated (Errington 1946). Widespread study of the influence of intimidation by predators (i.e., the fear of death) on herbivore feeding decisions has occurred more recently, encouraged primarily by seminal reviews by Lima and Dill (1990) and Lima (1998). These investigations have revealed that the threat of predation frequently leads herbivores to underuse profitable but dangerous patches or foraging tactics (Lima and Dill 1990); such food-safety trade-offs can in turn affect traits of third parties within communities, triggering trophic cascades (Paine 1980; Pace et al. 1999; Preisser et al. 2005). To date, most studies of the relationship between herbivore foraging decisions and predation risk have been undertaken in terrestrial or aquatic environments, leaving the effects of predator intimidation on herbivory in marine systems largely unresolved (Dill et al. 2003).

In heterogeneous environments, individual herbivores can make foraging decisions at multiple scales (Senft et al. 1987; WallisDeVries et al. 1999), and each decision may be subject to the influence of predation danger (Lima and Dill 1990; Lima 1998). Broadly, for example, relative use of patches offering differential amounts of food (or levels of food quality) by herbivores may be influenced by patch-specific levels of predator abundance or prey vulnerability. Once within a foraging patch where food quantity and quality are consistent, herbivores can choose between microhabitats (i.e., feeding sites) offering different levels of safety or allowing for different levels of surveillance. Finally, while engaged in feeding, herbivores can choose between foraging tactics allowing for different levels of energy intake and vigilance.

This thesis addresses the influence of predation danger on the foraging behaviour of dugongs (*Dugong dugon*) in the Eastern Gulf of Shark Bay, Western Australia. In Shark Bay, dugongs are subject to predation by tiger sharks (*Galeocerdo cuvier*) (Heithaus 2001). Chapter 2 describes the temporal pattern of local abundance characterizing these sharks, which I use as an index of the relative threat they pose to dugongs throughout the year, while Chapter 3 explores the relationship between their use of the study area, sea surface temperature, and the availability of several major prey species, including dugongs.

Dugongs have access to two primary feeding habitats in Shark Bay: shallow banks (typically < 4 m in depth) and deep channels (typically > 6 m). Deep channels offer only a fraction of the food (seagrass, Marsh et al. 1984) available in shallower habitats, but are used less heavily by tiger sharks (Heithaus et al. 2002) and likely allow for increased probability of escape following encounters with predators. Thus, if danger from tiger sharks is an important determinant of dugong habitat use, then individual foragers may switch between shallow and deep habitats in a threat-sensitive manner. In Chapter 4, I address the use of these two habitats by foraging dugongs, asking in particular whether individual foragers overuse relatively safe but impoverished deep patches (after adjusting for food supply) during periods when the likelihood of encountering tiger sharks is elevated.

When using shallow bank habitats, which are dominated by expansive seagrass meadows, dugongs can forage in two primary microhabitats: edge and interior. Both offer similar amounts of seagrass but food quality is higher in interior microhabitats. However, edge microhabitats offer more water volume and are closer to deep habitats, suggesting that dugongs attacked by tiger sharks while feeding along the edges of seagrass meadows are more likely to outmanoeuvre and escape their predators (Heithaus et al., *in review*). In Chapter 5, I explore the use of these two microhabitats by foraging dugongs, and test the hypothesis that individual foragers prefer nutritious interior feeding sites when sharks are scarce and relatively safe edge feeding sites when sharks are common.

Once they have selected a feeding site, individual dugongs can harvest seagrass using one of two tactics: cropping and excavation (Anderson 1986). Excavation allows dugongs to harvest seagrass rhizomes, which are high in nutrients (de Iongh et al. 1995), while cropping is used to consume the terminal stems and leaves of seagrass plants, which tend to be less nutritious (Anderson 1986). However, excavation also requires dugongs to bury their rostra in the substrate and results in the creation of large sediment plumes, and therefore likely constrains vigilance, while the act of cropping allows for frequent scans. Hence, it is possible that individual dugongs adjust their use of these two foraging tactics, when and where both are feasible, in a threat-sensitive manner, devoting the least time to excavation when tiger sharks are most abundant. This hypothesis is addressed in Chapter 6.

Grazing by dugongs has the potential to radically alter seagrass meadow biomass and composition (de Iongh et al. 1995). Thus, factors that change patterns of foraging by dugongs may indirectly influence seagrass meadows and, ultimately, the structure of nearshore benthic communities. In Chapter 7, I conclude by discussing the possibility that tiger sharks exert such an indirect influence and, as a result, play an important role within marine communities. Since the future status of tiger sharks and dugongs is uncertain (Preen 1998; Baum et al. 2003), this chapter also seeks to place my results in the context of the conservation of these two species.

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# Chapter 2

# Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from seven years of standardized fishing effort

## 2.1 Abstract

The tiger shark (*Galeocerdo cuvier* Peron and Lesueur 1822) is a widely distributed predator with a broad diet and the potential to affect marine community structure, yet information on local patterns of abundance for this species is lacking. Tiger shark catch data were gathered over seven years of tag and release research fishing (1991 – 2000, 2002 – 2004) in Shark Bay, Western Australia (25° 45' S, 113° 44' E). Sharks were caught using drumlines deployed in six permanent zones (~ 3 $km^2$ in area). Fishing effort was standardized across days and months and, following adjustment for differences in bait efficacy, daily catch rates were expressed as the number of sharks caught per $h^{-1}$. A total of 449 individual tiger sharks was captured; 29 were recaptured. Tiger shark catch rate showed seasonal periodicity, being higher during the warm season (Sep – May) than during the cold season (Jun – Aug), and was marked by inter-annual variability. The most striking feature of the catch data was a consistent pattern of slow, continuous variation within each year from a peak during the height of the warm season (February) to a trough in the cold season (July). Annual growth rates of recaptured individuals were generally consistent with estimates from other regions, but exceeded those for populations elsewhere for sharks > 275 cm fork length (FL), perhaps because mature sharks in the study area rely heavily on large prey. The data suggest that (1) the threat of predation faced by animals consumed by tiger sharks fluctuates dramatically within and between years, and (2) efforts to monitor large shark abundance should be extensive enough to detect inter-annual variation and sufficiently intensive to account for intra-annual trends.

## 2.2 Introduction

The tiger shark, *Galeocerdo cuvier*, is a large carcharhinid that often is an apex predator in marine ecosystems (Randall 1992). Commonly found within tropical and warm-temperate regions of the world's oceans (Randall 1992), tiger sharks have a broad diet that shifts ontogenetically, with small individuals acting primarily as piscivores and larger ones consuming both teleosts and a variety of large-bodied species (e.g., elasmobranchs, marine reptiles, and marine mammals; Simpfendorfer 1992; Lowe et al. 1996; Heithaus 2001; Simpfendorfer et al. 2001). Consequently, the tiger shark has the potential to influence marine communities via trophically- and behaviourally-mediated interactions with a variety of prey species (e.g., Lowe et al. 1996; Heithaus 2001; Simpfendorfer et al. 2001; Heithaus et al. 2002; Dill et al. 2003; Heithaus 2004). The nature and magnitude of this influence may be dynamic if the abundance of tiger sharks fluctuates within a given area (see Holling 1959; Lima 2002); therefore, analyses of temporal variation in the abundance of this top predator would improve understanding of the marine systems of which they are a part.

Tiger sharks have been studied in a variety of locations, including the east coast of North America (e.g., Northwest Atlantic and Gulf of Mexico, Branstetter et al. 1987; western North Atlantic, Natanson et al. 1999; Northwest Atlantic, Baum et al. 2003), the Gulf of Mexico (Branstetter et al. 1987), the Hawaiian Islands (Polovina and Lau 1993; Holland et al. 1999), the east coast of South Africa (e.g., Wintner and Dudley 2000), and the northeastern (Simpfendorfer 1992) and western coastlines of Australia (Simpfendorfer et al. 2001; Heithaus 2001; Heithaus and Dill 2002). These inquiries have revealed that tiger shark populations are comprised at least in part of individuals that maintain defined, though likely very large, home ranges and return to specific areas on a regular basis (Holland et al. 1999; Heithaus 2001), that relative use of particular areas by tiger sharks may be size- and sex-biased (Lowe et al. 1996; Heithaus 2001), that local tiger shark abundance may be characterized by substantial variability as well as seasonal periodicity (e.g., between 1997 and 1999 in Shark Bay, Western Australia, tiger shark numbers consistently peaked during the warm season, September – May; Heithaus 2001; Heithaus and Dill 2002; see also Simpfendorfer 1992), and that many tiger shark populations in areas exploited by commercial fishing apparently are in sharp decline (Baum et al. 2003; Ward and Myers 2005). Studies addressing localized tiger shark population dynamics over an extended duration (> 5 years) have been conducted (e.g., Simpfendorfer 1992; Baum et al. 2003), but no protracted investigation to date has carefully controlled for fishing effort in an area where tiger sharks are neither commercially harvested nor subjected to control measures. Consequently, baseline data allowing for rigorous, inter-annual assessments of regional trends in cohort-specific and overall abundance in this species are lacking.

Here, I present results from a seven-year (1997 – 2000, 2002 – 2004) study of tiger sharks in Shark Bay, Western Australia. Over the course of the investigation, which is an extension of the work presented by Heithaus (2001), sampling location, timing, and effort were held relatively constant. Thus, I was able to (1) determine whether the seasonal pattern of shark abundance documented by Heithaus (2001) remained consistent over a longer time interval, (2) test for variation in shark abundance within both warm and cold seasons, (3) address the magnitude of inter-annual variation in tiger shark abundance within a local area, and (4) compare growth rates of recaptured individuals to those of tiger sharks elsewhere. Because bait used in the study varied over time, I also (5) asked whether tiger shark catch rates were affected by different baits.

## 2.3 Materials and Methods

### 2.3.1 Study site

This study was undertaken in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (25° 45' S, 113° 44' E). Shark Bay is a large (13,000 $km^2$), semi-enclosed basin located roughly 900 km north of Perth, Western Australia (Fig. 2.1a, b). The study site (160 $km^2$; Fig. 2.1b) features a patchwork of open embayment plains (6.5 – 15.0 m deep), swift-current channels (6.5 – 12.0 m), and shallow banks (< 4.0 m). Most of the shallow habitat within the bay is dominated by extensive seagrass meadows (Walker 1989). In 1991, the Shark Bay region was listed as a World Heritage Area. The local tiger shark (*Galeocerdo cuvier* Peron and Lesueur 1822) population has been free from commercial fishing since 1994, and has never been subject to heavy harvest (Heithaus 2001). Thus, the study site has an intact and protected assemblage of tiger sharks and their major prey species (dugongs, *Dugong dugon*; pied cormorants, *Phalacrocorax varius*; sea snakes, primarily *Hydrophis elegans*; and sea turtles, *Caretta caretta*, *Chelonia mydas*; Heithaus 2001).

### 2.3.2 Field methods

Over the course of the investigation (1997 – 2000, 2002 – 2004), I sampled tiger sharks in six deep-water fishing zones (Fig. 1b). Individual sharks were captured using drumlines equipped with a single hook (Mustad Shark Hook; size 13/0 used predominantly, with occasional use of sizes 12/0 and 14/0) fished at a depth of 0.7 – 2.0

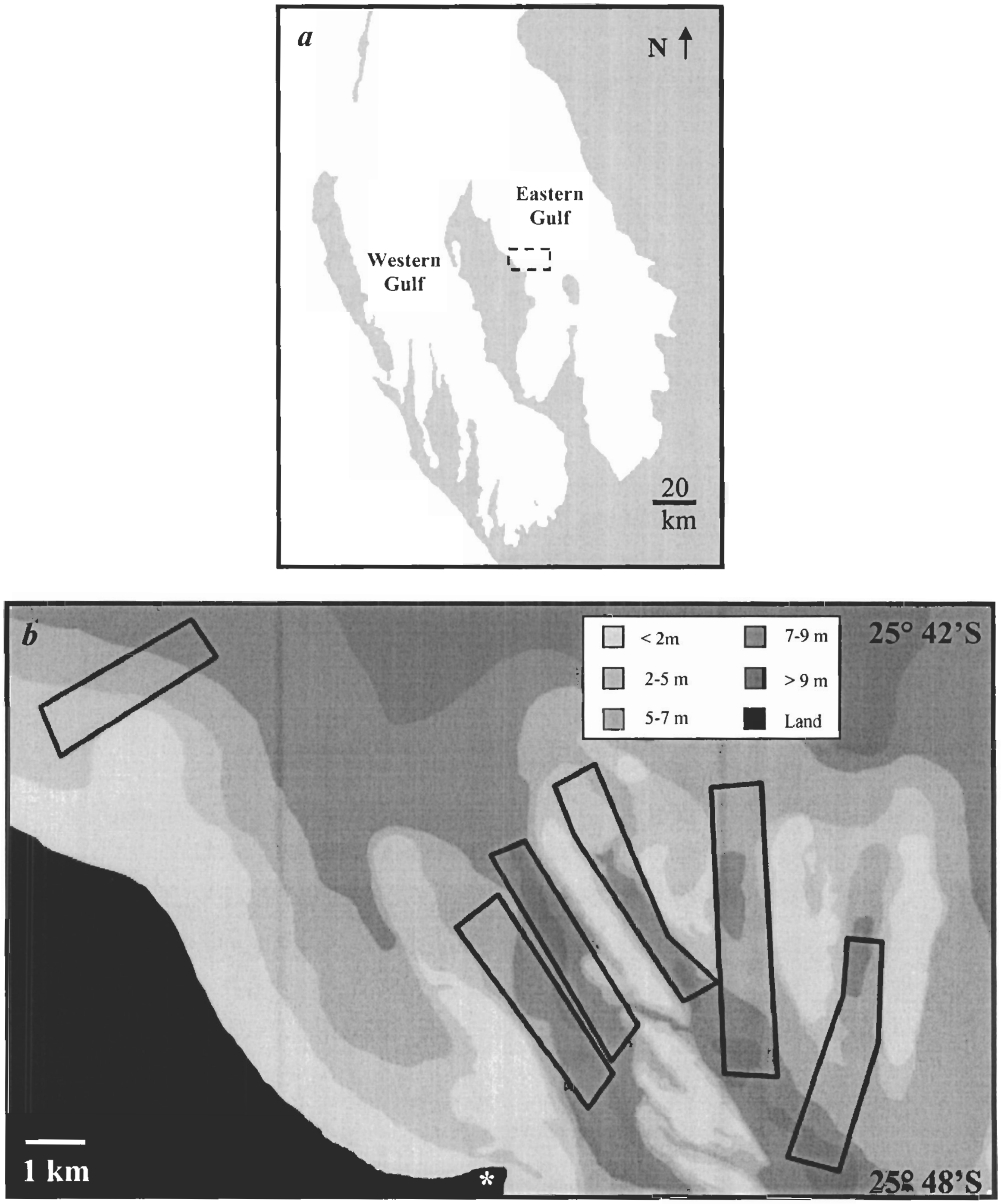

**Figure 2.1 Shark Bay, Western Australia, study site, and tiger shark fishing zones** Tiger sharks were caught in the Eastern Gulf (*a*, hatched box) with drumlines deployed in six sampling zones (*b*; Monkey Mia Dolphin Resort designated with an asterisk).

m. Ten drumlines were deployed concurrently in one or two zones and spaced 300 or 700 m apart (Heithaus 2001). Shark catch rates may in part be a function of sampling design (Heithaus 2001). However, daily catch rates (sharks $h^{-1}$, see below) for the two deployment protocols (one zone with 300-m spacing versus two zones with 700-m spacing) did not differ (paired *t*-test based on catch values for days falling within the same week during which one protocol was used exclusively, $t_6 = -0.542, p = 0.607$), so all catch rate data have been pooled for the purposes of this analysis.

Hooks were baited predominantly with Australian salmon (*Arripis truttaceus*, AS; 9,771 h; 70% of total fishing time). Between 2002 and 2004, four other bait species were used when AS was not available: baldchin groper (*Choerodon rubescens*, G; 189 h), sea mullet (*Mugil cephalus*, M; 256 h), pink snapper (*Pagrus auratus*, PS; 2,451 h), and tailor (*Pomatomus saltatrix*, T; 1,273 h). Sharks may show preferences for certain bait types over others, and rates of bait loss may be influenced by bait type as well (Heithaus 2001). Consequently, use of different baits may bias shark catch results, impeding group-specific and temporal comparisons (Heithaus 2001). I evaluated this possibility by comparing hourly tiger shark catch rates associated with each of the four alternative baits to those for AS using a series of ANCOVAs (Table 2.1). Comparisons between each alternative bait and AS were made using only those days on which both were fished, and incorporated an interaction term (bait type by day-of-year) to address the possibility that differences in bait-specific catch rates varied temporally. I did not consider fishing days falling within months during which catch rates were negligible (June – August). The mean catch rate for hooks baited with tailor (T) was less than half that obtained using the reference species (AS). Thus, all catch rates associated with T were multiplied by 2.1 to

**Table 2.1 Bait comparison**

Comparisons (ANCOVA) between tiger shark catch rates for a reference bait species (Australian Salmon, *Arripis truttaceus*, AS) and four alternative baits (baldchin groper, *Choerodon rubescens*; sea mullet, *Mugil cephalus*; pink snapper, *Pagrus auratus*; tailor, *Pomatomus saltatrix*) fished in Shark Bay, Western Australia. Number of days on which alternative baits were fished concurrently with AS, total hook soak time (h) for alternative baits, soak time for reference species (AS h), and mean catch rate conversion between alternative baits and AS presented. Significant conversion values ($\alpha = 0.05$, highlighted in bold) were applied to achieve bait equivalency. Note, significant interactions between pairwise bait differences and time were not detected (all $P \geq 0.23$).

| Bait | Days | Hours | AS hours | Conversion | *F* | *P* |
|---|---|---|---|---|---|---|
| *C. rubescens* | 4 | 55 | 232 | 0.79 | $5.68e^{-4}$ | 0.98 |
| *M. cephalus* | 7 | 115 | 293 | 1.4 | 0.53 | 0.48 |
| *P. auratus* | 9 | 251 | 252 | 1.1 | 0.06 | 0.81 |
| *P. saltatrix* | 11 | 347 | 300 | **2.11** | **5.12** | **0.03** |

achieve equivalency. In contrast, differences between catch rates associated with the remaining alternative bait species and AS were not significant. Therefore, I used raw catch values for these baits.

Following deployment at dawn, drumlines were checked every 2 to 4 hours. During each check, I noted whether bait was present or absent on all hooks that failed to catch sharks. I defined soak time as the number of hours elapsing between deployment and removal for hooks that retained bait for an entire fishing day. For hooks from which bait was lost or on which a shark had been caught, soak time was considered to have ended half way between the previous point at which bait presence was verified and the time when bait loss or a shark was detected.

I used a shark handling procedure consistent with that of Heithaus (2001). Briefly, hooked sharks were brought alongside a 4.5-m vessel and allowed to swim slowly while the boat idled forward. Each shark was then measured (pre-caudal length [PCL], fork length [FL], and total length [TL]), sexed, tagged (numbered rototag in the dorsal or pectoral fin), and released. Length measurements from recaptured sharks for which time at liberty exceeded 0.5 years were used to generate growth rates (previous year's growth [cm] $y^{-1}$). I used the previous year's change in cm FL as the basis for growth calculations in order to facilitate comparisons with previous studies of tiger shark growth conducted elsewhere (Branstetter et al. 1987; Natanson et al. 1999; Wintner and Dudley 2000).

### 2.3.3 Statistical analyses

I expressed catch rates for tiger sharks as the number of sharks caught $h^{-1}$ of fishing effort (Heithaus 2001; Heithaus and Dill 2002). Catch rates for bait types (e.g., AS versus G) fished on the same day were compared using paired *t*-tests (Zar 1999). Using only data adjusted to account for differences in bait efficacy, catch rates were calculated for each day during which drumlines were deployed ($n = 241$), and then variation in daily catch rates over the course of the entire study in relation to day-of-year (DOY), season (warm [September – May] versus cold [June – August]; Heithaus 2001), and year was analyzed using a generalized linear model. The dependent variable consisted of non-negative integer values with a low mean and large variance, so a negative binomial error distribution served as the basis for statistical inference (White and Bennetts 1996). For the purposes of this temporal analysis, DOY was considered to be a continuous variable, whereas seasons and years were expressed as discrete categories (Sokal and Rohlf 1995). During all years of the study, fishing effort from November –January was minimal. Thus, I censored sampling data collected during these months from the temporal analysis. Many previous attempts to monitor shark demographic trends using catch rates have been plagued by uncertain or variable sampling effort (Xiao and Walker 2000; Kohler and Turner 2001). I believe, however, that the present analysis was robust to the problem of effort variability given that daily fishing times were relatively consistent (mean = 53.50 h of total bait soak time, sd = 21.73), and effort was distributed relatively evenly across the months during which fishing took place ($n = 40$, mean = 331.62 hours of total bait soak time, sd = 215.09). Importantly, daily catch rates in the study area are believed to reliably index tiger shark abundance since the rate at which free-swimming sharks (tagged and untagged) are sighted is directly related to the frequency with which sharks are being hooked, the presence of acoustically tagged sharks ($n = 8$) within the fishing zone has only been detected during periods when catch rates are high (Heithaus 2001), and tiger sharks have been caught even when water temperatures are at their lowest, indicating that feeding is not suspended during cold periods. I evaluated the sex ratio of caught sharks (for all sharks and for large individuals ≥300 cm TL; see Heithaus 2001) against the null expectation of 1:1 using chi square contingency tables. Unless otherwise specified, reported means are accompanied by 95% confidence intervals.

## 2.4 Results

Over the course of the investigation, a total of 492 sharks was caught, of which 449 were *Galeocerdo cuvier* (91.3%). Other species included dusky sharks, *Carcharhinus obscurus* ($n = 5$), gray reef sharks, *Carcharhinus amblyrhynchos* (n = 1), great hammerhead sharks, *Sphyrna mokarran* ($n = 1$), lemon sharks, *Negaprion brevirostris* ($n = 2$), mako sharks, *Isurus oxyrinchus* (n = 3), nervous sharks, *Carcharhinus cautus* (n = 5), sandbar sharks, *Carcharhinus plumbeus* (n = 23), scalloped hammerhead sharks, *Sphyrna lewini* ($n = 1$), and silky sharks, *Carcharhinus faliciformis* (n = 2). Among the tiger sharks for which reliable measurements were taken (excluding recaptures), sizes ranged from 148 to 445 cm TL, with mean TL for males ($n = 115$, mean = 300.6 cm, 290.7 – 310.5 cm) exceeding that for females ($n = 281$, mean = 284.2 cm, 95% CI = 277.4 – 290.9 cm) (two-sample *t*-test, $t_{394} = 2.63$, $P = 0.009$). Among tiger sharks for which sex could be determined ($n = 422$), the overall sex ratio was female biased (ratio = 2.6:1, $\chi^2 = 69.59$, df = 1, $P < 0.001$). For sharks < 300 cm TL ($n = 235$), this skew was particularly strong (ratio = 3.7:1): all seven years included in the study featured a female bias, four to a significant degree (Table 2.2). The overall sexual skew for larger sharks ( $\geq$300 cm TL, $n = 185$) was less pronounced (ratio = 1.8:1). When large shark catch data were analyzed on a yearly basis, a significant bias was detected in only two of seven cases.

### 2.4.1 Abundance

Daily tiger shark catch rates varied sharply over the seven years of the study, with values ranging from 0 to 0.28 sharks $h^{-1}$ (Fig. 2.2). However, the seasonal pattern observed by Heithaus (2001), with relatively high shark catch rates typifying the warm months of September – May and relatively low catch rates prevailing during the cold months of June – August, is clearly manifest in this extended dataset as well (Table 2.3, Fig. 2.2). The lack of a significant interaction between the season and year variables in the generalized linear model ($P = 0.98$) indicates that this seasonal pattern was present in all years of the investigation. Day-of-year (DOY) was retained as a significant factor in the model, implying that much of the observed heterogeneity in daily capture rates could not be explained by seasonal fluctuations alone. Rather, strong covariation existed between mean daily catch rate and DOY, and the lack of a significant season by DOY interaction ($P = 0.20$) indicates that this pattern of covariation was a feature of both warm and cold periods. Finally, I detected significant yearly variation in tiger shark catch rates. Inter-annual catch rate variation was evident during both warm and cold periods (i.e., an interaction between year and season variables was not detected). However, the absence of a significant interaction between the year and DOY terms in the model ($P = 0.41$) suggests that tight covariation between mean daily tiger shark catch rate and DOY was manifest in all years of the study.

**Table 2.2 Sex ratios for tiger sharks caught over seven years in Shark Bay, Western Australia**

For each year, observed ratios were evaluated against the null expectation of 1:1 using chi square tests. Ratios deviating significantly from 1:1 in bold.

| | | Small sharks (< 300 cm TL) | | | |
|---|---|---|---|---|---|
| Year | Females | Males | Ratio | $\chi^2$ | *p* |
| 1997 | 26 | 13 | 2.0 | 4.3 | **0.037** |
| 1998 | 16 | 10 | 1.6 | 1.4 | 0.24 |
| 1999 | 38 | 9 | 4.2 | 17.9 | < **0.001** |
| 2000 | 10 | 4 | 2.5 | 2.6 | 0.11 |
| 2002 | 10 | 5 | 2.0 | 1.7 | 0.20 |
| 2003 | 55 | 7 | 7.9 | 37.2 | < **0.001** |
| 2004 | 33 | 3 | 11.0 | 25.0 | < **0.001** |
| | | Large sharks ( ≥300 cm TL) | | | |
| 1997 | 16 | 16 | 1.0 | 0.0 | 1 |
| 1998 | 16 | 5 | 3.2 | 5.8 | **0.016** |
| 1999 | 27 | 19 | 1.4 | 1.4 | 0.24 |
| 2000 | 8 | 3 | 2.7 | 2.3 | 0.13 |
| 2002 | 11 | 6 | 1.8 | 1.5 | 0.23 |
| 2003 | 13 | 8 | 1.6 | 1.2 | 0.28 |
| 2004 | 26 | 9 | 2.9 | 8.3 | **0.004** |

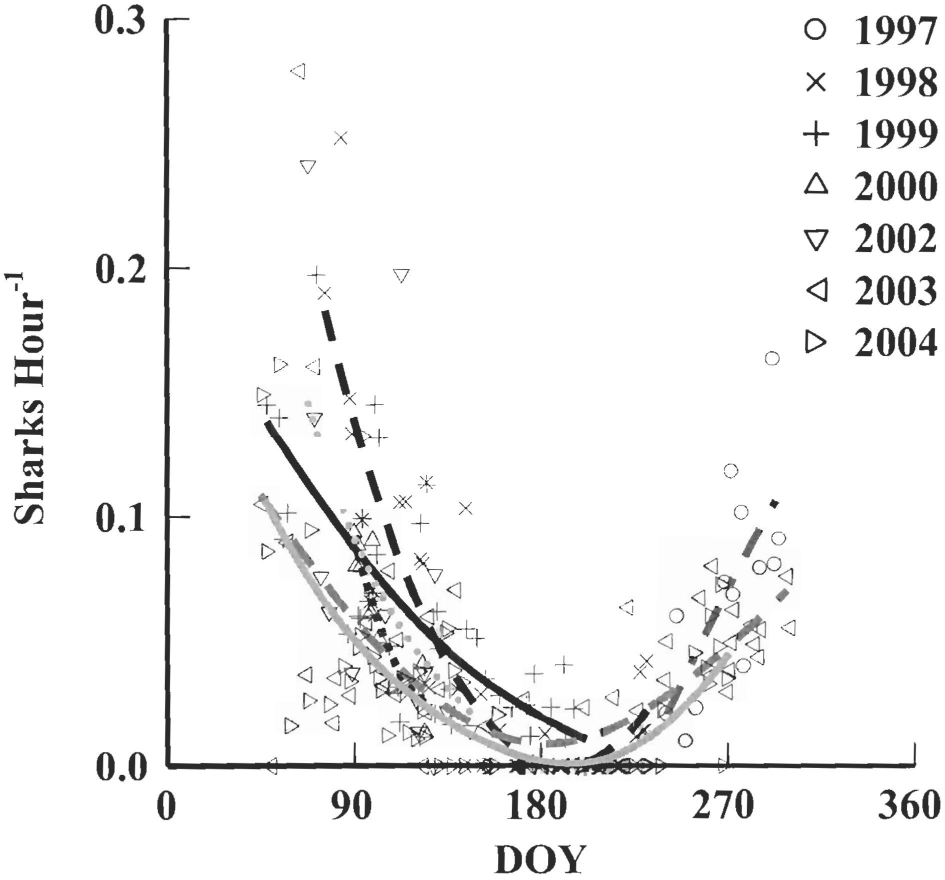

**Figure 2.2 Daily tiger shark catch rates from seven years versus day-of-year (DOY)** Estimates generated in the Eastern Gulf of Shark Bay over seven years (1997 – 2004, 2001 excluded) using relatively consistent fishing effort (mean total bait soak time = 53.50 h d$^{-1}$, s = 21.73). Distance-weighted least squares (DWLS, tension 1.0) trend lines are designated as follows: 1997 (▪▪▪▪▪▪▪); 1998 (▬ ▪ ▬); 1999 (▬ ▬); 2000 (——); 2002 (·······); 2003 (▬ ▬); 2004 (——).

**Table 2.3 Generalized linear model of variation in tiger shark catch rates in relation to three temporal variables**

Tiger shark catch rates (*n* = 241 d) as a function of three temporal variables: day-of-year (DOY), season (warm versus cold), and year. For all independent variables, coefficient estimates ($\theta$) are accompanied by standard errors and 95% confidence intervals (C.I.). All interactions were excluded from the final model ($P = 0.413$ for DOY*year interaction, 0.975 for season*year interaction, 0.204 for DOY*season interaction, and 0.207 for DOY*season*year interaction).

| Factor | df | $\theta$ | SE ($\theta$) | 95% C.I. | *P* |
|---|---|---|---|---|---|
| DOY | 1 | -0.002 | 0.001 | -0.003, -0.001 | **0.036** |
| Season | 1 | 1.719 | 0.159 | 1.407, 2.031 | **< 0.001** |
| Year | 6 | -0.086 | 0.020 | -0.125, -0.046 | **0.012** |

### 2.4.2 Recapture and growth rate

Twenty-nine tiger sharks were recaptured, yielding a minimum recapture rate of 0.06. However, 12 additional tiger sharks bore clear evidence of tag loss (e.g., scars or loss of tissue along the leading edge of the dorsal fin near the point of tag insertion), implying a higher recapture rate (0.09). Recaptured sharks ranged in size between 219 and 394 cm TL (mean = 302.17, 284.28 – 320.06), and, like sharks caught for the first time, tended to be female (ratio = 2.2:1, $\chi^2 = 4.17$, df = 1, $P = 0.04$). Among those sharks for which reliable growth estimates could be generated ($n = 19$, mean time at liberty = 0.78 y, range = 0.5 – 1.37 y), annual growth rates ranged from 7.9 to 49.8 cm FL (mean = 21.41 cm, 16.18 – 26.64). Growth rate declined significantly with size ($r^2 = 0.40$, $p < 0.01$; Fig. 2.3). A comparison of corrected Akaike's Information Criteria ($AIC_c$, Burnham and Anderson 1998) for linear and non-linear configurations of the independent variable revealed that an exponential decay function best fit the growth data (i.e., the $AIC_c$ for the linear model exceeded that for non-linear [exponential decay] model by > 2; Fig. 2.3). This model yielded growth estimates for the study population ranging from approximately 35 cm FL year$^{-1}$ for sharks 175 cm in length (FL) to roughly 12 cm FL y$^{-1}$ for sharks 300 cm in length (FL) (Fig. 2.3). The estimated growth rate for sexually mature tiger sharks (~ 250 cm FL; Heithaus 2001) was ~ 20 cm FL y$^{-1}$.

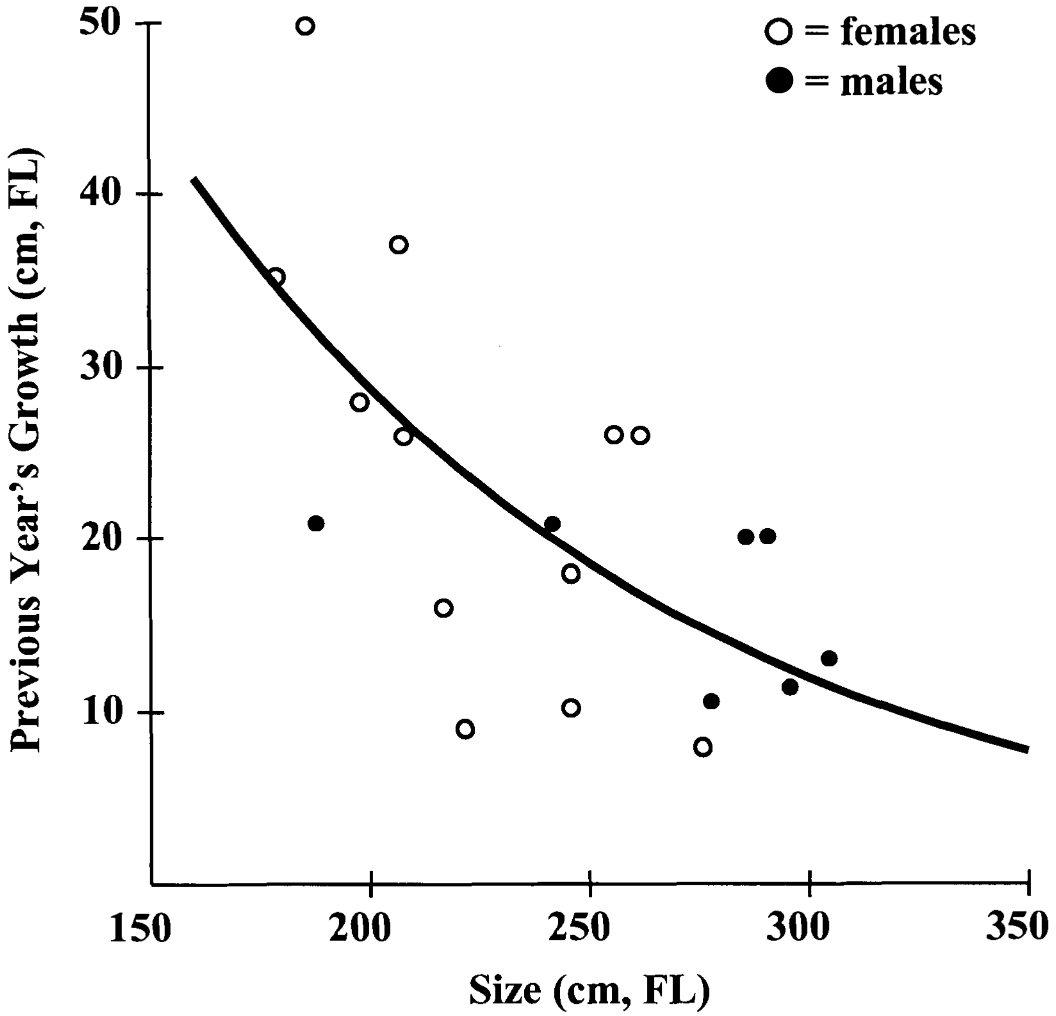

**Figure 2.3 Relationship between size and growth of tiger sharks caught in the Eastern Gulf of Shark Bay**

Size (cm FL) and growth ($y^{-1}$) in tiger sharks (n = 19) caught in the Eastern Gulf of Shark Bay was best explained by an exponential decay equation (previous year's growth = 162.795 × $e^{(-0.00866 \times FL)}$; $r^2 = 0.43$, $p < 0.005$). Growth estimates used to generate equation based upon length measurements from recaptured individuals (mean time at liberty = 0.78 y).

## 2.5 Discussion

Large sharks are assumed to play important roles within marine ecosystems (Baum et al. 2003; Baum and Myers 2004; Heithaus 2004). Yet, trophic and behavioural interactions between sharks and their prey with the potential to produce community effects rarely have been documented (Heithaus 2004). This paradox could be due to a lack of area-specific information on the patterns of abundance of these apex predators. In the absence of localized numerical data required to estimate the likelihood of shark attack, for example, trends in the behaviour of prey species consumed by large sharks have been difficult to analyze in an antipredator context (Heithaus 2004). Similarly, the scarcity of numerical information concerning large sharks has hampered attempts to quantify large shark predation rates on particular prey species. Thus, systematic efforts to quantify the presence of large sharks in particular areas are needed to facilitate rigorous assessments of the influence of these predators on marine community dynamics.

Here, I present catch data from a *Galeocerdo cuvier* population study employing a standardized and long-term sampling protocol in the Eastern Gulf of Shark Bay. My results show that seasonal periodicity in catch rates is a consistent feature of the study population: over seven years, shark catch rates were always higher during the warm season (September – May, days 45 – 151 and 244 – 300; Figure 2.2), when surface water temperatures (measured daily from a constant location; Heithaus 2001) tend to be above $20^{\circ}$ C, than during the cold season (June – August, days 152 – 243). Furthermore, within both seasons, significant yearly variation was detected. However, even after accounting for the effects of season and year, I found a strong and remarkably consistent pattern of covariation between day-of-year (DOY) and mean daily catch rate. During all years of the study and within the range of months sampled, both daily catch values and catch variance tended to (1) be greatest at or near the peak of the warm season (February through early March, ~ days 40 – 75), (2) decline continuously thereafter, reaching a minimum in July (the mid-point of the cold season), and (3) increase steadily again beginning in late August (near the end of the cold season, generally between days 230 and 245). The consistent temporal trend in shark catch rates reported here has two important implications for studies of both tiger shark-prey interactions and shark-mediated community effects in the Eastern Gulf of Shark Bay: (1) those potential prey individuals remaining in the study area during the cold season can be assumed to experience a temporal refuge from predation, or at least reduced predation risk; and (2) in so far as relative predator abundance serves as a metric of predation danger (i.e., the likelihood of predator encounter and, by extension, mortality; Holling 1959; Gilliam and Fraser 1987), we should expect the magnitude of antipredator behavioural responses by prey to vary with shark catch rate throughout the year, given that within-season catch rates are not constant. Such responses have been observed in bottlenose dolphins (*Tursiops aduncus*) and pied cormorants (*Phalacrocorax varius*) in Shark Bay (Heithaus and Dill 2002; Heithaus 2005).

Recaptured sharks from which reliable measures of fork length (FL) were taken were all at least three years old, based upon the aging criteria of Natanson et al. (1999) and Wintner and Dudley (2000). For Shark Bay tiger sharks just beyond this lower age limit (175 cm FL), the growth equation suggests a growth rate of approximately 35 cm FL $y^{-1}$, which is generally consistent with growth estimates for similarly aged tiger sharks in populations in the Gulf of Mexico (31 cm FL $y^{-1}$), along the east coast of North

America (32 cm FL $y^{-1}$) and the east coast of South Africa (32 cm FL $y^{-1}$ [note: estimated from PCL measurements, which are closely correlated with FL, $r^2 = 0.999$, see Compagno 1984], Wintner and Dudley 2000). However, the estimated growth rate for the study population declines less rapidly as a function of size than in populations elsewhere. Although initially small, the magnitude of this disparity in growth rate is notable for sharks $\geq$275 cm in FL, with the estimated value for the Shark Bay population (~15 cm FL $y^{-1}$) exceeding those calculated for populations in the Gulf of Mexico, Northwestern Atlantic (Branstetter et al. 1987), waters along North America's eastern seaboard, and South Africa by factors of 1.5- to 2.2 (Table 2.4). Similarly, among the largest size class available for comparison (300 cm FL), the growth estimate of the study population (~12 cm FL $y^{-1}$) was 1.7- to 2.8-fold higher than those for other populations.

These growth comparisons must be interpreted cautiously, as the studies on which they are based used different means to estimate yearly growth (vertebral banding patterns were used by Branstetter et al. [1987] and Wintner and Dudley [2000] to estimate age). Moreover, the growth estimate for the Shark Bay population may have been biased by sampling error and/or a lack of large individuals (> 300 cm FL). Finally, comparisons of populations from different regions may be confounded by variation in population-specific aging patterns. Nevertheless, it appears that large Shark Bay tiger sharks (and in particular those $\geq$275 cm FL) grow more swiftly than large tiger sharks in other regions. This putative regional disparity may stem from differences in local temperature regimes, with sharks inhabiting warm waters achieving relatively high growth rates. However, tiger sharks in the coldest region (South Africa) manifested growth rates second only to those of Shark Bay (Table 2.4). Alternatively, it may derive from differences in diet.

Reliance on large-bodied prey (e.g., sea turtles and marine mammals) by sexually mature tiger sharks ingest is generally low (De Crosta 1984; Simpfendorfer 1992; Lowe et al. 1996). For example, the occurrence of sea turtle remains in the stomachs of large tiger sharks off New Caledonia (Rancurel and Intes 1982), eastern Australia (Simpfendorfer 1992), and the main Hawaiian Islands (Lowe et al. 1996) was always < 15% (Lowe et al. 1996), though ~ 50% of large tiger sharks caught off the Northwestern Hawaiian Islands had ingested sea turtle tissue (De Crosta et al. 1984; Lowe et al. 1996). Marine mammal occurrence in large tiger shark stomachs ranged from 0 to 20% in the same four areas (Lowe et al. 1996). In contrast, large tiger sharks in Shark Bay appear to rely heavily on large-bodied prey: 60% of large sharks ($n = 5$) caught just outside Shark Bay contained sea turtle remains, and 20% contained marine mammal (dugong) remains (Simpfendorfer et al. 2001); similarly, 80% of large sharks ($n = 5$ individuals for which stomach contents could be fully catalogued) caught in the Bay's Eastern Gulf (the study area) had recently ingested sea turtles, and 100% of these sharks contained dugong tissue (Heithaus 2001). Large prey items, and in particular marine mammals, represent a relatively energy-rich food source (Robbins 1993), so regular consumption of these prey types by sexually mature sharks may lead to heightened net energy intake rates and elevated growth.

I recorded a female bias for both tagged and recaptured sharks. This trend is consistent with most previous studies based on tiger shark catch data (e.g., Clark and von Schmidt 1965; Stevens and McLoughlin 1991; Simpfendorfer 1992; Krogh 1994; Wintner and Dudley 2000; Simpfendorfer et al. 2001). However, in contrast to these studies and in accord with the more limited results presented by Heithaus (2001), I also found that the degree of this bias was strongly size dependent. The tendency for small

**Table 2.4 Growth estimates for tiger sharks caught in four different regions**
Growth estimates (cm FL $y^{-1}$) for tiger sharks in the present study[1], Branstetter et al. (1987)[2], Natanson et al. (1999)[3], and Wintner and Dudley (2000)[4]. Note that estimates for Eastern Gulf of Shark Bay were derived from a growth equation based upon length measurements from recaptures (n = 19, mean time at liberty = 0.78 y), while remaining estimates were back-calculated using population-specific von Bertalanffy growth parameters. Growth estimates given for six sizes ranging from 175 cm to 300 cm FL.

| | Growth (cm FL) $\text{Year}^{-1}$ | | | | | |
|---|---|---|---|---|---|---|
| Location | 175 cm | 200 cm | 225 cm | 250 cm | 275 cm | 300 cm |
| **Shark Bay[1]** | **36** | **29** | **23** | **19** | **15** | **12** |
| Gulf of Mexico[2] | 31 | 25 | 20 | 15 | 10 | 5 |
| Northwestern Atlantic[2] | 18 | 15 | 12 | 10 | 8 | 4 |
| East coast of North America[3] | 32 | 27 | 22 | 17 | 12 | 7 |
| South Africa[4] | 32 | 28 | 22 | 17 | 11 | 6 |

sharks (< 300 cm TL) to be female was approximately twice that for larger sharks, and when years were analyzed individually, a female bias was detected more frequently for small sharks than for large ones. Moreover, for both small and large sharks, the degree to which catches were female biased varied considerably from year to year. The reasons for this size-dependent trend, and its marked variability, remain to be determined.

Among the bait species used in this investigation, only tailor, *P. saltatrix* (T), was characterized by a significantly different mean shark catch rate than the reference species, Australian salmon (*A. truttaceus*, AS). Individual sharks in our study area may avoid hooks baited with this species, or the difference in efficacy between T and AS may have stemmed from a disparity in bait-specific hook retention times. An ANOVA incorporating only those hours for hooks that were soaked during the warm season (Sep – Oct and Feb – Apr, when catch rates were appreciable) and did not catch sharks revealed significant differences among the retention times for the five baits ($F_{4,778} = 9.62$, $P < 0.01$). However, in support of the latter explanation, only the pairwise contrast between the mean retention times for AS ($n = 323$ hooks, mean = 5.24 h, 4.94 – 5.54) and T ($n = 126$ hooks, mean = 3.75 h, 3.37 – 4.13) was significant after Bonferroni correction ($P < 0.01$; $P \geq 0.24$ for all remaining contrasts). Thus, while bait species of similar size may often be interchangeable, tiger shark catch rates furnished by studies that use multiple baits without checking for variation in bait efficacy may be subject to bias.

Populations of macropredatory fishes, including the tiger shark, are undergoing a global decline, due in large part to the effects of commercial harvest (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005). Given the putatively important role played by these species in marine ecosystems, there is much interest in their conservation

(Baum et al. 2003), but reliable baseline numerical data upon which effective conservation protocols might be based are lacking (Xiao and Walker 2000; Kohler and Turner 2001; Baum and Myers 2004). My data provide a baseline for the dynamics of a protected tiger shark population in a highly productive area (Shark Bay), which might be used to assess the status of tiger shark populations in less pristine regions. My results suggest that catch rates for large sharks may vary markedly both within and between years. Consequently, I argue that monitoring programs designed to assess shark population status and promote recovery must not only be long-term and standardized across years, but also intensive enough to account for within-year numerical patterns.

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# Chapter 3

# Numerical responses by tiger sharks to local changes in prey availability vary according to predator size and prey type

## 3.1 Abstract

Apex marine predators can structure marine communities, so factors underlying their distribution and abundance are of great interest to ecologists. Using data collected over five years in Shark Bay, Western Australia, I assessed the relationship between tiger shark (*Galeocerdo cuvier*) abundance, water temperature, and the availability of known prey (dugongs, cormorants, sea snakes, and sea turtles). Abundance of sharks in five size categories ( $\leq$240 cm total length, TL; 241 – 270 cm; 271 – 300 cm; 301 – 330 cm; $\geq$331 cm) was indexed using daily catch rates ($h^{-1}$); prey density was measured using transects. For all size categories, thermal conditions were a strong determinant of shark abundance, with numerical peaks coinciding with periods of high water temperature. However, for sharks exceeding 300 cm TL, the inclusion of dugong density significantly improved abundance models based on temperature, indicating that use of particular areas by large tiger sharks is in part determined by the availability of this sirenian. I conclude that large shark population models may benefit from the inclusion of measures of prey availability, and that reductions in the density of important prey species may affect the behavior of alternative prey and, ultimately, community structure by precipitating shark population declines.

## 3.2 Introduction

Top predators can exert a powerful influence on the structure of communities (Werner 1998; Berger et al. 2001; Schmitz and Suttle 2001; Schmitz 2003; Fortin et al. 2005). Therefore, factors determining the abundance and distribution of these species are of great interest to ecologists (Clark et al. 1996; Noss et al. 1996). Studies of apex predator population dynamics and space use are complicated by the tendency of large carnivores to exist at low densities, disperse widely, use broad home ranges, and so elude detection (Noss et al. 1996; Williams et al. 2004). These complications are exacerbated in marine settings, where counts and continuous behavioural observation are often impossible, and effective tracking and monitoring methods (e.g., acoustic and satellite telemetry, mark-recapture) are difficult to employ (Williams et al. 2004). Consequently, even basic elements of the relationship between most apex marine predators and their environment remain poorly understood.

Large sharks, which likely play an important structural role in marine ecosystems (Baum and Myers 2004; Heithaus 2004a), are undergoing a global decline (Baum et al. 2003; Baum and Myers 2004). To date, little is known about the determinants of their abundance and distribution (Xiao and Walker 2000; Kohler and Turner 2001; Baum and Myers 2004), hindering both predictions concerning population viability and the establishment of effective conservation measures. Here, we explore the relationship between the abundance of tiger sharks (*Galeocerdo cuvier*), prey availability, and the thermal environment in Shark Bay, Western Australia.

In Shark Bay, tiger shark numbers show strong annual periodicity, with peak levels of abundance coinciding with the height of the Austral summer (Jan – Feb) and troughs occurring during the cold season (July) (Chapter 2). When assessed on a monthly basis, this trend in shark abundance showed strong, positive correlation with sea surface temperature (Heithaus 2001a). However, a substantial amount of variation in shark abundance was left unexplained (25%), leading to speculation that changes in tiger shark numbers within and between years may be driven in part by the availability of their major prey species (dugongs, *Dugong dugon*; pied cormorants, *Phalacrocorax varius*; sea snakes, *Aipysurus pooleorum*, *Disteria major*, *Hydrophis elegans*; and sea turtles, *Caretta caretta*, *Chelonia mydas*; Heithaus 2001a). Using data collected systematically over a period of five years (1998 – 2004, 2000 – 2001 excluded), I sought to address this possibility by comparing the efficacy of shark abundance models based solely on temperature to those including prey availability. Given that tiger sharks undergo ontogenetic dietary shifts (Lowe et al. 1996; Simpfendorfer et al. 2001), I also asked whether any predictive improvements stemming from the inclusion of large-bodied prey (i.e., dugongs and sea turtles) availability were restricted to models of large ( ≥300 cm total length, TL) shark abundance.

## 3.3 Materials and Methods

### 3.3.1 Study site

This study was undertaken in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (Red Cliff Bay; ~ 25° 45' S, 113° 44' E). Shark Bay has been listed as a World Heritage Area since 1991, and the local tiger shark population is virtually undisturbed (Heithaus 2001a). Thus, I was able to assess the numerical relationship between tiger sharks and their prey under relatively pristine conditions.

### 3.3.2 Tiger shark abundance

Tiger sharks were caught on drumlines ($n$ = 10) equipped with a single hook, baited primarily with Australian salmon (*Arripis truttaceus*), and deployed at dawn in six permanent fishing zones throughout the study area (160 $\text{km}^2$); all sharks caught throughout the day were measured (total length, cm TL), tagged, and released (for methodological detail, see Heithaus 2001a and Chapter 2). Daily catch rates ($n$ = 204 days spanning 32 mo; all mo represented save November and December) were expressed as the number of sharks hooked per baited hook hour. A measure of sea surface temperature (°C) was recorded at a constant location (see Heithaus 2001a) on each day shark fishing took place.

### 3.3.3 Prey availability

I assessed patterns of prey abundance using transect passes through 14 survey zones (SZ), which were allocated evenly to deep ( $\geq 6$ m in depth) and shallow ( $\leq 4$ m) habitats within the study area. Each zone consisted of a 200 m sighting belt bisected by a central transect line, yielding an average sampling area of 0.71 $km^2$ (sd = 12.75). Transect effort was distributed evenly across days ($n$ = 189; mean = 7.63 passes $d^{-1}$, sd = 2.45), months (mean = 45.61 ± 18.01 passes $month^{-1}$), and between shallow and deep SZ (shallow: mean = 3.96 ± 1.64 passes; deep: 3.71 ± 1.68 passes). Survey zones within shallow and deep categories were selected haphazardly to ensure that all portions of the study area were monitored evenly, and each SZ was not visited more than once per day. To reduce the effects of tidal and diel variation, the order and direction in which transects were driven each day also were haphazard. Transects were conducted in Beaufort wind conditions $\leq 2$ to minimize sighting bias caused by poor weather.

Transect passes were conducted using a small (4.5 m) vessel driven at a speed of 6 – 9 km $h^{-1}$. All pied cormorants, dugongs, sea snakes (species combined), and sea turtles (species combined) sighted at the surface within the survey area before being passed by the boat were recorded. These prey species were chosen because they represent the majority of the biomass consumed by tiger sharks in our study area (Heithaus 2001a). Any bias stemming from the exclusion of large teleost fishes, which constitute a substantial proportion of the tiger shark's diet elsewhere (e.g., the Hawaiian Islands, Lowe et al. 1996), from my estimates of prey availability were minimal given that their availability in the study area shows broad spatial and temporal consistency (Heithaus 2004b). Indian Ocean bottlenose dolphins also are attacked periodically by tiger sharks in Shark Bay (Heithaus 2001b). However, they are rarely consumed (Heithaus 2001a; Simpfendorfer et al. 2001), and so were not included in this investigation.

Prey densities for individual SZ were calculated by dividing the number of animals sighted by the area searched (km$^2$). Dugongs are large and difficult to miss from close range (i.e., within 100 m), so all dugongs recorded during each pass through a SZ were used to generate density estimates. In contrast, cormorants and sea turtles were difficult to spot reliably beyond 30 m from the boat, and sea snake sightings were confined to the immediate vicinity of our vessel. Thus, to minimize sighting bias, I generated density estimates for cormorants and sea turtles using a 60 m sighting belt, and estimated sea snake density using a 10 m sighting belt. Species-specific prey densities for all SZ visited on a given day were pooled into shallow and deep categories; daily densities for the study area were derived by summing the densities for shallow and deep habitats, weighted by the proportional coverage of each habitat class. Assessment of prey and shark numbers was rarely concurrent. Thus, prior to analysis, daily estimates of shark abundance were coupled with a weekly density average for each of the four prey types; these weekly averages were derived from daily prey density measures calculated during the four days before and four days after the date on which shark fishing took place.

For air breathing vertebrates, time spent at the surface may differ according to water depth. To account for this potential source of sighting bias, I multiplied my estimates of dugong and sea turtle density in deep SZ by the ratio of their surface times in the two habitats (Heithaus et al. 2001; Wirsing et al. *unpublished data*). Cormorant and sea snake counts in deep SZ were not converted because habitat-specific surface times were not available. To test for bias stemming from the use of raw deep-habitat density estimates for these two prey types, I conducted sensitivity analyses involving cormorant and sea snake count data from deep SZ multiplied by factors of two and one-half (i.e., factors of greater magnitude than those characterizing the conversions for dugongs and sea turtles). These analyses produced results matching those reported below.

### 3.3.4 Data analysis

Daily catch rates were generated for tiger sharks belonging to five size categories: (1) ≤240 cm TL (minimum = 148 cm); (2) 241 – 270 cm; (3) 271 – 300 cm; (4) 301 – 330 cm; and (5) ≥331 cm (maximum = 445 cm). I assumed that sharks belonging to each successive category would be increasingly likely to kill and consume large-bodied prey (see Heithaus 2001a, b), and that sharks within particular categories would target similar prey. The categories contained large and approximately even proportions (0.20, 0.19, 0.18, 0.17, and 0.25, respectively) of the overall number of sharks caught (*n* = 379).

I used information theoretic methodology (Burnham and Anderson 1998) to evaluate the relationship between tiger shark density, prey availability, and the thermal environment. This approach ranks models of the relationship between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore allows for more rigorous comparison of competing hypotheses than traditional statistical techniques (e.g., stepwise regression; Johnson and Omland 2004). Models of tiger shark abundance within each size category were generated using all possible linear combinations of the independent variables (cormorant, dugong, sea snake, and sea turtle density, and sea surface temperature; $n = 32$). Importantly, correlation between the independent variables was low enough (all Pearson correlation coefficients $\leq$ 0.48, mean = 0.25) to allow for independent assessment (Burnham & Anderson 1998). The dependent variable for the models, daily shark catch rate, consisted of non-negative integer values (i.e., counts), divided by the number of hours fished. Moreover, within each shark size category, the modal catch count was zero. Thus, models were fit using maximum-likelihood under the assumption of a Poisson error distribution (Selvin 1995).

I evaluated the strength of each model using Akaike's Information Criterion, corrected for small sample size ($AIC_c$; Burnham and Anderson 1998; Anderson et al. 2000). Akaike weights ($w$, ranging from 0 – 1), which index the likelihood that a particular model is best among a set of competitors, were used to assess model uncertainty (Burnham and Anderson 1998). The predictive strengths of individual explanatory variables were evaluated using both the sum of the $w$ for all models in which particular variables appeared (i.e., parameter Akaike weights [$w_p$]), and model-averaged coefficient estimates with unconditional standard errors and 95% confidence intervals (Burnham and Anderson 1998; Anderson et al. 2000). Explanatory variables associated with high $w_p$ (approaching one) and model-averaged coefficient estimates with 95% confidence intervals not encompassing zero were considered to be statistically significant and biologically meaningful (Burnham and Anderson 1998).

## 3.4 Results

### 3.4.1 Tiger sharks ≤240 cm TL

The model best explaining the abundance of tiger sharks ≤240 cm TL incorporated cormorant density and sea surface temperature (Table 3.1). This model was highly significant ($P = 0.006$), but explained only 6% of the observed daily variation in the abundance of these sharks (maximum-likelihood based $r^2$ analog [$r^2_L$]; see Hosmer & Lemeshow 1989]). The Akaike weight ($w$) for this model suggested that its probability of being superior to all others under investigation was relatively low, but its closest competitor was less than half as likely to be best (Table 3.1). Both variables were likely to be included in the best model among those considered (high $w_p$; Table 3.2). The model-averaged coefficient estimate for the temperature variable was positive and featured an unconditional 95% confidence interval that did not include zero (Table 3.3), meaning that the abundance of sharks within this size category increased as ambient temperature rose. The 95% confidence interval for the cormorant density variable was negative (Table 3.3), meaning that sharks ≤240 cm TL became more abundant as cormorant density dropped. Thus, the statistical relationship between cormorant density and shark abundance

**Table 3.1 Top five models of tiger shark abundance**

Top five models of tiger shark abundance for each of five size categories (size divisions based on total length [TL, cm]) in Shark Bay, Western Australia. Independent variables included sea surface temperature (°C, T), pied cormorant density (C), dugong density (D), sea snake density (S), and sea turtle density (Tu). Models were generated using maximum likelihood under the assumption of a Poisson error distribution, and were ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$). For each model, *w* is the Akaike weight, or the likelihood that a particular model is best among those under consideration (*n* = 32).

| Tiger Shark Size Class (cm TL) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| ≤240 | | 241 - 270 | | 271-300 | | 301-330 | | ≥331 | |
| Model | *w* | Model | *w* | Model | *w* | Model | *w* | Model | *w* |
| **T+C** | **0.32** | **T** | **0.16** | **T+Tu** | **0.26** | **T+D** | **0.27** | **T+D** | **0.30** |
| T+C+D | 0.13 | T+S | 0.09 | T | 0.14 | T+D+S | 0.13 | T+D+S | 0.16 |
| T+C+Tu | 0.12 | T+C+D+S | 0.09 | T+D+Tu | 0.09 | T+C+D+S+Tu | 0.12 | T+D+Tu | 0.13 |
| T+C+S | 0.11 | T+D+S | 0.08 | T+S+Tu | 0.09 | T+C+D+S | 0.10 | T+C+D+S+Tu | 0.12 |
| T+C+D+Tu | 0.05 | T+C+D | 0.07 | T+C+Tu | 0.09 | T+D+Tu | 0.10 | T+C+D+Tu | 0.08 |

**Table 3.2 Parameter Akaike weights (wp) for five independent variables potentially influencing the abundance of five size categories of tiger sharks**

Parameter Akaike weights ($w_p$) for five independent variables (sea surface temperature, T; cormorant density, C; dugong density, D; sea snake density, S; sea turtle density, Tu) potentially influencing the abundance of five size categories of tiger sharks. Calculated as the sum of the Akaike weights ($w$) for all models in which a given variable appears, $w_p$ values provide a measure of the likelihood that the variable in question is a constituent of the best predictive model.

| | Tiger Shark Size Class (cm TL) | | | | |
|---|---|---|---|---|---|
| | ≤240 | 241-270 | 271-300 | 301-330 | ≥331 |
| Variable | $w_p$ | $w_p$ | $w_p$ | $w_p$ | $w_p$ |
| T | **0.8676** | **0.9999** | **0.9999** | **0.9447** | **0.9999** |
| C | **0.9655** | 0.3782 | 0.2609 | 0.4424 | 0.3485 |
| D | 0.3003 | 0.4820 | 0.2584 | **0.9999** | **0.9993** |
| S | 0.2816 | 0.4769 | 0.2582 | 0.4343 | 0.4160 |
| Tu | 0.2747 | 0.3266 | **0.6435** | 0.3459 | 0.3953 |

**Table 3.3 Estimates of effect for variables in models of abundance of five size categories of tiger shark**

Estimates of effect for variables (var; sea surface temperature, T; cormorant density, C; dugong density, D; sea snake density, S; sea turtle density, Tu) made available for inclusion in models for abundance of five size categories of tiger shark. Within each size category, variables are accompanied by a model-averaged coefficient estimate (θ), which is the mean coefficient estimate characterizing all models containing that variable, adjusted by each model's Akaike weight (*w*), and an unconditional 95% confidence interval (in parentheses), which is a weighted measure incorporating both uncertainty in the coefficient estimate and uncertainty in the chosen model.

| | Tiger Shark Size Class (cm, TL) | | | | |
|---|---|---|---|---|---|
| Var. | ≤240 | 241-270 | 271-300 | 301-330 | ≥331 |
| T | **0.09 (0.02, 0.16)** | **0.2 (0.12, 0.29)** | **0.21 (0.13, 0.30)** | **0.14 (0.05, 0.23)** | **0.25 (0.17, 0.33)** |
| C | **-17.29 (-3.06, -31.52)** | 4.51 (-9.49, 18.51) | 1.2 (-11.71, 14.11) | -12.82 (-29.35, 3.72) | 8.98 (-2.01, 19.98) |
| D | 46.84 (-329.71, 423.40) | 128.54 (-18.07, 575.16) | 13.24 (-11.91, 238.39) | **438.99 (60.45, 817.52)** | **278.53 (5.03, 552.03)** |
| S | 3.11 (-108.14,114.36) | -26.11 (-81.63, 29.41) | -0.71 (-41.97, 40.54) | 16.78 (-59.07, 92.64) | -13.19 (-45.74, 19.36) |
| Tu | 1.98 (-118.50,122.47) | 3.01 (-40.79, 46.82) | **24.98 (-0.48, 50.44)** | -8.19 (-127.78, 111.40) | -12.64 (-53.77, 28.49) |

described here lacks biological meaning [note, in a companion analysis excluding cormorant density as an independent variable, the best model of shark density within this size category included only temperature, $w = 0.31$]. The remaining explanatory variables were poor predictors of the abundance of sharks $\leq$240 cm TL (Tables 3.2 and 3.3).

### 3.4.2 Tiger sharks 241 - 270 cm TL

The abundance of tiger sharks between 241 and 270 cm TL was best explained by a model incorporating sea surface temperature (Table 3.1). This model was highly significant ($P = 0.002$), but explained only 9% of the observed daily variation in the abundance of these sharks. The probability that this model was superior to the others under consideration was low, though nearly twice that of its closest competitor (Table 3.1). The temperature variable had a high $w_p$ (Table 3.2) and a positive model-averaged coefficient estimate with a 95% confidence interval not encompassing zero (Table 3.3), meaning that the abundance of sharks within this size category increased as ambient temperature rose. Relationships between the remaining explanatory variables and the abundance of sharks within this size category were relatively weak (Tables 3.2 and 3.3).

### 3.4.3 Tiger sharks 271 - 300 cm TL

The model best explaining the abundance of tiger sharks between 271 and 300 cm TL included sea turtle density and temperature (Table 3.1). This model was highly significant ($P < 0.001$) and explained 11% of the daily variation in the abundance of these sharks, though its probability of being superior to all others was relatively low (Table 3.1). The temperature variable was highly likely to be included in the best model, while the overall probability of inclusion of the turtle variable was intermediate (Table 3.2).

The model-averaged coefficient estimates for the sea turtle and temperature variables (Table 3.3) indicate that increases in the abundance of sharks within this size category coincided with elevated turtle density and water temperature. However, the 95% confidence interval for the sea turtle variable (Table 3.3) casts some doubt on the biological significance of the relationship between turtle density and shark abundance. The remaining variables were not important predictors of the abundance of sharks within this size category (Tables 3.2 and 3.3).

### 3.4.4 Tiger sharks 301 - 330 cm TL

The model best explaining the abundance of tiger sharks between 301 and 330 cm TL included both dugong density and sea surface temperature (Table 3.1). This model was highly significant ($P < 0.001$) and explained 21% of the observed daily variation in the abundance of these sharks, though its $w$ suggests a modest probability of being superior to all others (Table 3.1). Both variables were highly likely to be included in the best model, unlike the remaining variables (Table 3.2). Positive model-averaged coefficient estimates and unconditional 95% confidence intervals (Table 3.3) suggest increases in the abundance of sharks within this size category corresponded with elevated dugong density and water temperature.

### 3.4.5 Tiger sharks ≥331 cm TL

The best model of the abundance of tiger sharks larger than 330 cm TL included dugong density and sea surface temperature (Table 3.1). This model was highly significant ($P < 0.001$) and explained 19% of the observed daily variation in the abundance of these sharks, though its probability of being superior to all others was only moderate (Table 3.1). Both variables were highly likely to be included in the best model (Table 3.2). Their positive model-averaged coefficient estimates and unconditional 95% confidence intervals (Table 3.3) imply that increases in the abundance of these large sharks coincided with increased dugong density and water temperature. The remaining variables were poor predictors of the abundance of sharks within this largest size category (Tables 3.2 and 3.3).

## 3.5 Discussion

The possibility that large, predatory shark abundance is linked to that of their prey has been a matter of much speculation (e.g., Klimey 1994; Heithaus 2001a; Simpfendorfer et al. 2001; Boustany et al. 2002; and see review by Heithaus 2004a), but non-anecdotal evidence in support of this hypothesis is lacking. Here, I present the first empirical demonstration of a temporally-consistent link between large shark abundance and local prey availability. Using census data collected systematically over five years in a pristine subtropical embayment (Shark Bay), I show that (i) numerical changes in the abundance of tiger sharks can be predicted from measures of sea surface temperature and prey density, and (ii) the degree to which tiger shark abundance tracks prey availability depends on both the shark size class and the prey species considered. My findings have important implications for tiger shark conservation and for the structure of marine communities.

The inclusion of prey density failed to improve upon temperature-based models of shark abundance within the two smallest size categories (ignoring the biologically meaningless relationship between cormorant density and the abundance of sharks $\leq$240 cm TL). This result may indicate that use of particular areas by tiger sharks below 271 cm TL (termed small sharks hereafter) is driven exclusively by changes in their thermal environment. That is, cold temperatures may slow the metabolism of small sharks to a level precluding efficient prey capture, and thereby force habitat shifts. Alternatively, small sharks may respond numerically to changes in the availability of prey species we failed to monitor. For example, while overall teleost biomass is temporally consistent in our study area (Heithaus 2004b), fluctuations in the abundance of particular fish species may influence the abundance of these sharks.

For tiger sharks between 271 and 300 cm TL (termed intermediate sharks hereafter), the inclusion of sea turtle density improved the predictive ability of abundance models based solely on sea surface temperature. By implication, dietary reliance on green and loggerhead sea turtles by intermediate sharks may be sufficient for individuals to adjust their use of particular areas in response to changes in turtle density; this possibility is supported by tiger shark dietary analyses in Shark Bay (Heithaus 2001a; Simpfendorfer et al. 2001). However, the $w_p$ for the sea turtle variable was only 0.63, and the unconditional 95% confidence interval for the model-averaged turtle density coefficient estimate encompassed zero, albeit barely, meaning that the significance of the relationship between the abundance of intermediate sharks and sea turtle density is questionable. Consequently, the possibility that intermediate sharks use areas based in part on turtle availability must remain speculative. Intermediate sharks may rely differentially on the two species used to generate sea turtle densities, and therefore future analyses focusing on green and loggerhead turtles separately may clarify the relationship between sea turtle availability and shark abundance.

The presence of large tiger sharks near dugong aggregations in Shark Bay has been noted (Anderson 1982), and these sharks incorporate dugongs in their diet, leading to speculation that large tiger shark abundance within particular regions of the bay may be linked to the availability of this sirenian (Heithaus 2001a). Accordingly, I found that the abundance of tiger sharks greater than 300 cm TL (termed large sharks hereafter) was best predicted by the combination of sea surface temperature and dugong density. While dugong numbers were characterized by marked temporal variability over the course of this investigation, an overall decline was not observed (Chapter 4), indicating that large sharks varied their use of our study area in response to both inter- and intra-annual variation in dugong abundance. The fact that sea turtle density was not retained in the best predictive model implies that large sharks use areas in relation to the availability of dugongs in particular, rather than large-bodied prey in general, perhaps because dugongs represent an especially energy-rich food source (Robbins 1993). My finding that large tiger shark abundance is influenced strongly by the local availability of dugongs runs counter to the widely-held notion that tiger sharks are opportunistic feeders (Randall 1992), and suggests instead that the habitat use patterns and movements of large individuals of this species may track spatial and temporal patterns of the abundance of favoured prey.

Tiger shark numbers appear to be in global decline (Baum et al. 2003), yet information required to preserve this species is lacking, in large part because of the logistical obstacles facing regional monitoring efforts. By taking advantage of an unprecedented opportunity to simultaneously evaluate trends in tiger shark abundance and the availability of known prey over five years, I have shown that, after accounting for the effects of the thermal environment, use of particular areas by large tiger sharks is influenced by the density of an energy-rich prey species (dugongs). Thus, I surmise that the abundance of dugongs is a determinant of habitat quality for these sharks and, more generally, that the abundance and distribution of tiger sharks throughout the species' range are likely influenced by the availability of locally important prey. Consequently, models assessing the viability of tiger shark populations will undoubtedly benefit from the inclusion of measures of the availability of major prey species, in particular if sharks within given size classes are matched to appropriate prey. The link between dugong and large shark abundance illuminated here also suggests that declines in dugong density could lead to dramatic reductions in the presence of large tiger sharks. Such reductions, which are occurring throughout much of the dugong's distribution (Preen 1998), could threaten the persistence of tiger shark populations where these two species coexist. Given that the danger of tiger shark predation is known to affect the behaviour of a variety of prey species (e.g., dugongs, Chapters 4, 5, 6; Indian Ocean bottlenose dolphins, Heithaus and Dill 2002; pied cormorants, Heithaus 2005), local declines in dugong abundance, and perhaps other heavily consumed species, might also lead indirectly to profound changes in the structure and function of marine communities.

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# Chapter 4

# Fear factor: dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)

## 4.1 Abstract

Predators can influence plants indirectly by altering spatial patterns of herbivory. Thus, studies assessing the relationship between predation risk and habitat use by herbivores may facilitate an improved understanding of community organization. In marine systems, the effects of predation danger on large herbivore space use have not been investigated, despite the possibility that predator-mediated alterations in patterns of grazing by these animals influence the structure of benthic communities. I evaluated the relationship between habitat use by foraging dugongs (*Dugong dugon*) and the threat of tiger shark predation in a subtropical Australian embayment (Shark Bay). Between 1997 and 2004, dugong densities were quantified in inherently dangerous (shallow) and safe (deep) habitats (14 survey zones replicated evenly across two major habitat types), and predation hazard was indexed using catch rates of tiger shark (*Galeocerdo cuvier*) over 3.0 m total length. Food biomass within each zone was indexed in terms of seagrass volume. Overall, dugongs preferentially used shallow habitats, where their food is concentrated. However, foragers used shallow and deep habitats in proportion to food availability (input matching) when large tiger sharks were scarce and overused deep habitats relative to food abundance when sharks were common. In addition, I observed strong synchrony between daily levels of shark abundance and the extent to which deep habitats were overused. Thus, individual dugongs appear to adaptively manage their risk of death by allocating time to inherently safe but impoverished foraging patches in proportion to the likelihood of encountering predators in profitable but more dangerous feeding areas. This food-safety trade-off has important implications for seagrass

community structure in Shark Bay, as it likely results in marked temporal variability in grazing pressure.

## 4.2 Introduction

Foraging by herbivores can lead to dramatic changes in plant biomass, distribution, and diversity (Crawley 1983). Thus, predators may exert powerful indirect effects on plants by altering spatial patterns of herbivory (Abrams 1995; Schmitz 2003; and see review by Schmitz et al. 2004). Predation can influence the distribution of herbivores lethally if individuals are removed differentially across space, or sublethally if a positive correlation between resource and danger levels prompts individuals to trade access to profitable foraging patches for safety (Sih 1980; McNamara and Houston 1987; Peacor and Werner 2000). An increasing amount of evidence suggests that changes in herbivore space use driven by sublethal effects of predators (i.e., intimidation) are especially likely to trigger behavioural cascades within communities (e.g., Peacor and Werner 2001; Preisser et al. 2005); consequently, studies focused on these changes should facilitate an improved understanding of ecosystem organization (Werner 1998). While the link between predator intimidation and space use by terrestrial herbivores is firmly established (Lima and Dill 1990; Lima 1998), the extent to which large, marine herbivores (e.g., sea turtles, sirenians) trade food for safety has not been addressed (Dill et al. 2003), even though their foraging adjustments are likely to have profound consequences for benthic communities.

Here, I explore the influence of food availability and the risk of tiger shark (*Galeocerdo cuvier*) predation on the habitat use decisions of dugongs (*Dugong dugon*) in Shark Bay, Western Australia. Dugongs are seagrass specialists, and forage for much of the day to fuel their metabolism (Marsh et al. 1984). Thus, the habitat use decisions of this sirenian traditionally have been assessed in relation to food supply (e.g., Anderson 1986; Preen 1995); the influence of predation hazard on dugong habitat use has not been addressed.

In Shark Bay, seagrass grows primarily in shallow habitats (generally ≤4 m in depth; Walker et al. 1988; Travers and Potter 2002; Heithaus 2004), so the rate of energetic gain attainable by individual dugongs is likely to be highest in such areas. However, shallow habitats within the Bay also are used preferentially by tiger sharks (Heithaus et al. 2002), the dugong's major local predator (Simpfendorfer et al. 2001; Heithaus 2001). Furthermore, shallow areas are inherently more risky (*sensu* Hugie and Dill 1994) than deep habitats, where manoeuvrability and escape options available to animals under attack from sharks are less constrained (Heithaus et al. 2002). Consequently, dugongs foraging in the shallows are more likely to encounter, and less likely to elude, tiger sharks than are individuals feeding in safer, but relatively impoverished, deep habitats. However, tiger shark densities show marked seasonal periodicity in Shark Bay, peaking at the height of the Austral warm season (January – February) and reaching a nadir during the cold season (July) (Heithaus 2001, Chapter 2). Thus, the extent to which dugongs face increased predation danger while foraging in shallow (versus deep) patches varies dramatically throughout the year.

I tested the hypothesis that dugongs manage their risk of mortality by using inherently safe, but energy poor, foraging habitats in proportion to the abundance of predators in more hazardous feeding areas. This hypothesis predicts that, after adjustment for differences in food supply (seagrass biomass), the degree of equality between foraging dugong densities in safe (deep) and hazardous (shallow) habitats should be influenced by predator (tiger shark) numbers, with foragers showing no preference for safe habitats when sharks are scarce and the strongest preference for safe habitats during periods of peak shark abundance (i.e., when the likelihood of encountering sharks in dangerous foraging patches is greatest). If predation danger does not influence habitat use by foraging dugongs, then, after dividing by food supply, then proportional forager densities should be observed in the two habitat types throughout the year (i.e., input matching; van Baalen and Sabelis 1993). While seasonal changes in the biomass and nutrient content (i.e., quality) of the seagrass species comprising the bulk of the dugong's diet in my study area (*Amphibolis antarctica*; see below) are modest (Walker and McComb 1988), small quantities of tropical species favoured by dugongs elsewhere (e.g., *Halophila ovalis*, *Halodule uninervis*) are available in shallow areas during the warm season (Walker et al. 1988). Thus, shallow habitats may offer higher quality food than deep areas when water temperatures are warmest. This scenario makes my test of the danger-management hypothesis more conservative, however, as it predicts that preference for deep habitats should be weakest when tiger sharks are most abundant. I also tested whether dugongs select safe habitats while resting, when vulnerability to predation presumably is elevated (Lima and Dill 1990).

## 4.3 Materials and Methods

### 4.3.1 Study site

This study was undertaken in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (~ 25° 45' S, 113° 44' E; Figure 4.1). Shark Bay features a mosaic of embayment plains (6.0 – 15 m deep), swift-current channels (6.0 – 12 m), and

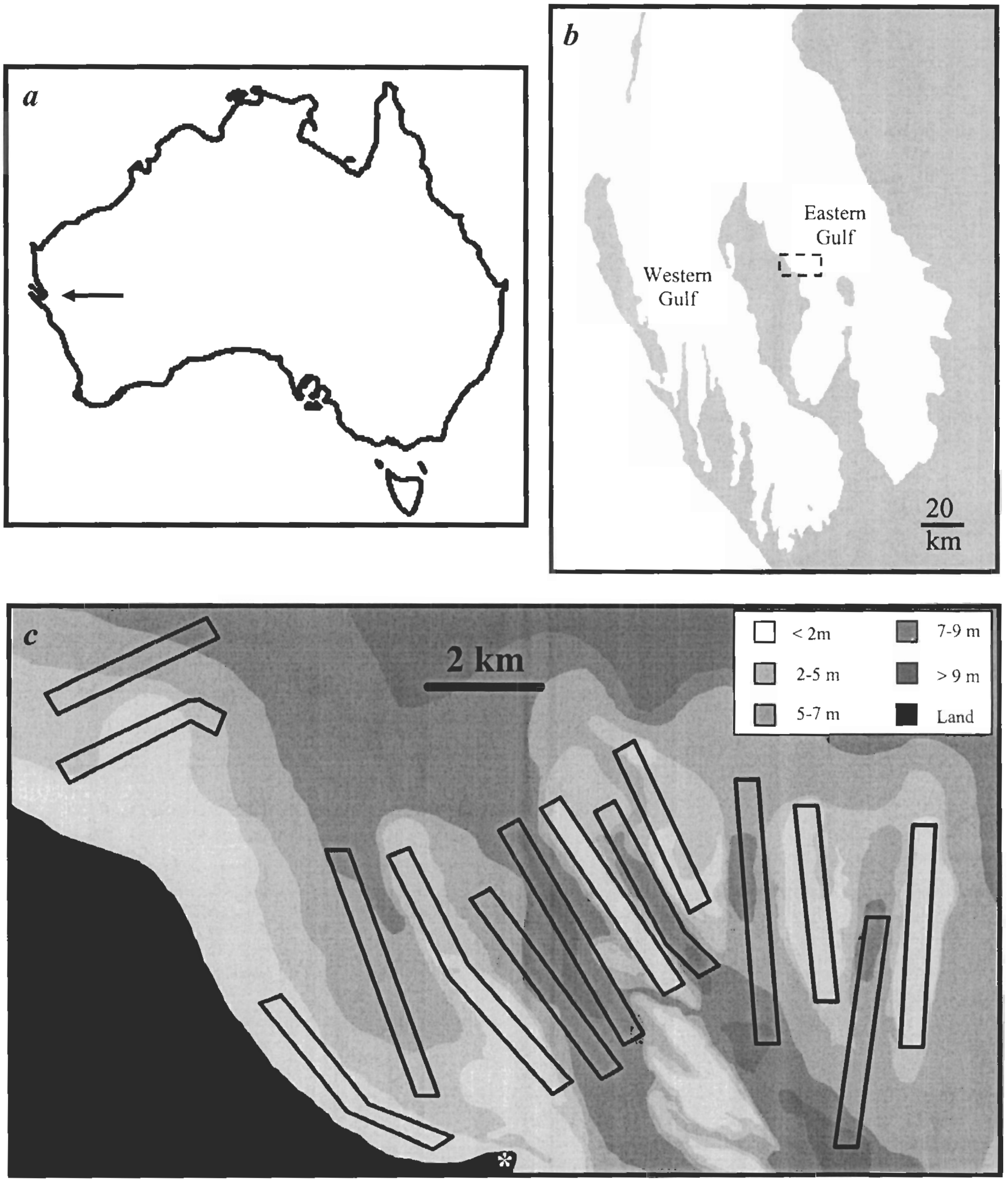

**Figure 4.1** Shark Bay, Western Australia (a)
This study was conducted offshore of the Monkey Mia Dolphin Resort (b). Survey zones (i.e., 400 m sighting belts; n = 14) were stratified across shallow and deep habitats throughout the 160 $km^2$ study area (c; Monkey Mia denoted with an asterisk).

shallow banks (< 4.5 m). Approximately one-third of its area (~ 4,000 $km^2$) is covered by seagrass meadows (Walker et al. 1988), which support 10,000 – 14,000 dugongs (Anderson 1982; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004). In 1991, the Shark Bay region was listed as a World Heritage Area. Thus, I was able to evaluate the habitat use behaviour of dugongs in a system that is heterogeneous with respect to food availability and predation risk and relatively pristine.

### 4.3.2 Food availability

I quantified food availability (biomass) in 14 survey zones (SZ), allocated evenly to deep ($\geq$6 m in depth) and shallow ($\leq$4.5 m) habitats (Figure 1c). Each zone consisted of a central transect line surrounded by a 200 m buffer, yielding an average sampling area of 141.27 ha (sd = 26.17 ha). Sampling stations were positioned systematically at 200 m intervals along the transect line, as well as along parallel lines 100 and 200 m to either side (75 – 120 stations per SZ). At each station, seagrass species coverage and composition were estimated visually within a 1 $m^2$ quadrat by a diver. Seagrass height (cm) was also measured within the quadrat; though within-quadrat height variability was relatively consistent, the point of measurement was selected randomly to minimize bias. Sampling occurred during the late austral winter of 2003 (August – September), when herbivore densities were relatively low, in order to minimize the confounding influence of herbivory, and to minimize shark hazard to divers.

Food biomass was expressed as above-ground seagrass volume (area covered × height; $m^3$); measures from sampling points were pooled to generate overall values for each SZ. Volume measures for all SZ consisted of two seagrass species: *A. antarctica* (mean = 82.7% of total volume) and *Posidonia australis* (mean = 17.3% of total volume).

The value of *P. australis* as a dietary item for dugongs is not known, so its inclusion in estimates of food supply may have introduced bias, but the removal of this species from consideration does not affect the results. I may also have incurred bias by failing to measure rhizomal (i.e., subsurface) biomass (de Iongh et al. 1995). However, rhizomes of the main species in the area (*A. antarctica*) are not available to dugongs as food (Anderson 1986), so bias stemming from their exclusion was likely modest. Finally, my biomass samples did not include tropical seagrass species because sampling occurred during the cold season when quantities of these species are negligible (Anderson 1986). Nevertheless, I believe my measure of food availability to be robust as tropical species are scarce in the study area throughout the year (Walker et al. 1988).

### 4.3.3 Dugong density and habitat use

I assessed patterns of dugong abundance using transect passes through the 14 SZ from 1997 to 2004 (2000 – 2001 excluded). To maintain sampling consistency, transect effort was allocated evenly across days ($n = 218$; mean = 7.52 passes $d^{-1}$, sd = 2.42), months (mean = 44.17 ± 18.24 passes $month^{-1}$), and habitats (shallow SZ: mean = 3.79 ± 1.64 passes $d^{-1}$; deep SZ: 3.86 ± 1.65 passes $d^{-1}$). Survey zones within shallow and deep habitats were selected to ensure that all portions of the study area were monitored evenly, and no SZ was visited more than once per day. Similarly, to reduce the effects of tidal and diel variation, the order and direction in which transects were driven each day were haphazard. Transects were conducted only in Beaufort wind conditions $\leq 2$ to minimize sighting bias caused by poor visibility in bad weather.

Transect passes were conducted using a small (4.5 m) vessel driven at a speed of 6 – 9 km $h^{-1}$. When dugongs were sighted at the surface within a SZ (i.e., a 400 m sighting belt) before being passed by the boat, I recorded their exact GPS position and the water depth and substrate for their sighting location. Between 2002 and 2004 ($n = 114$ days), I also determined the behavioural state (foraging, resting, travelling) of all dugongs sighted based on direct observation and diagnostic surface behaviour (Anderson 1986; Chilvers et al. 2004). Individual dugongs were distinguished using scarring patterns (Anderson 1995) and counted only once per day; individuals were rarely sampled more than once during each year of the investigation.

### 4.3.4 Predator abundance

Catch rates provide a reliable index of tiger shark abundance in Shark Bay (Heithaus 2001). Sharks were caught on drumlines equipped with a single hook, baited primarily with Australian salmon (*Arripis truttaceus*), and deployed at dawn in six fishing zones throughout the study area; all sharks caught throughout the day were measured (total length, TL), tagged, and released (for detailed methods, see Heithaus 2001). Because of substantial ontogenetic shifts in tiger shark diets (Lowe et al. 1996), tiger sharks under 3.0 m total length (TL) are unlikely to pose a threat to dugongs. Thus, only sharks > 3.0 m TL were used to generate daily catch rates.

Although daily fishing effort varied little, fishing frequency (~ 6 fishing d $mo^{-1}$) was too low to allow for an evaluation of the relationship between daily dugong habitat use and predator numbers. Given the strong seasonal pattern in shark abundance in my study area (Heithaus 2001), I used a sinusoidal function with a period of one year to predict the annual trend in daily catch rates (sharks $h^{-1}$). The catch data used in the model were combined for the years 2002 – 2004 because inter-annual variation was not detected after accounting for seasonal effects ($F_{2,117} = 0.97, p = 0.38$). The model was fit using maximum-likelihood under the assumption of a Poisson error distribution since my data consisted of integer values for the number of sharks caught per day (I rarely caught more than one large shark per fishing day).

### 4.3.5 Statistical analyses

Dugong densities for individual SZ were calculated by dividing the number of animals sighted by the area searched (ha). Densities for all SZ visited on a given day were pooled into shallow and deep categories; daily densities for the study area were derived by summing the densities for shallow and deep habitats, weighted by the proportional coverage of each habitat category. Between 1997 and 1999, only dugongs sighted within 100 m of the central transect line (a 200 m sighting belt) were recorded. Thus, densities over the six years of the investigation were calculated using this sighting area to facilitate annual comparison. Factors potentially affecting dugong density were assessed using a generalized linear model with a negative binomial error distribution because the dependent variable consisted of non-negative integer values with a mode of zero, a low mean, and large variance (White and Bennetts 1996); day-of-year (DOY), year, habitat (shallow versus deep), and sea surface temperature (°C) (a putative driver of dugong movements in Shark Bay; Anderson 1986, Marsh et al. 1994) were included as independent variables. A concurrent study involving hour-long focal animal follows ($n$ = 120) revealed that surfacing rates of dugongs differ in shallow (0.96 surface trips min$^{-1}$) and deep (0.84 trips min$^{-1}$) habitats ($t_{118} = 2.19, p = 0.03$) (Wirsing et al., *unpublished data*). Thus, to ensure that dugong density estimates reflected actual patterns of habitat use, I multiplied deep habitat densities by the ratio between these two rates (1.14).

Foraging dugong densities for individual SZ were expressed as the number of feeding animals sighted (i.e., counts within the sighting belt; here, the entire 400 m belt was used to maximize sample size) divided by the volume of seagrass surveyed ($m^3$). This measure assumes that foraging animals driven solely by the need to acquire food should be distributed across habitats in proportion to food availability (i.e., patch-specific densities relative to food should be equal; van Baalen and Sabelis 1993). Thus, after division by food supply, asymmetry between forager densities in two patch types can be used as a proxy for the degree to which habitat choice is influenced by other factors, including predation danger. Densities for SZ visited on a given day were pooled into shallow and deep categories, and deep habitat densities were adjusted using the conversion (1.17) between the surfacing rates of foraging dugongs ($n = 74$) in the two habitats. I sighted ten mother-calf pairs engaged in foraging while conducting transects. The behaviour of dugong calves mirrors that of their mother, so I treated these pairs as one individual for purposes of analysis; removing them from consideration had no measurable effect.

I used information theoretic methodology (Burnham and Anderson 1998) to evaluate the relationship between daily use of shallow and deep habitats by foraging dugongs and predator abundance (predicted large tiger shark catch rate, sharks $day^{-1}$). This approach ranks models of the relationship between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore facilitates rigorous evaluation of competing hypotheses (Burnham and Anderson 1998; Anderson et al. 2000). Independent covariates included habitat (shallow versus deep) and the interaction between habitat and shark abundance, so I could test whether (i) the two habitats were used unequally, after accounting for food biomass, and (ii) predation danger could predict the degree of inequality. Changes in sea surface temperature correlate positively with the nutrient content of *A. amphibolis* and tropical seagrass biomass (Walker and McComb 1988), and may affect thermoregulatory costs of dugongs (Anderson 1986). Therefore, I also included a water temperature variable, and its interaction with habitat, in the analysis to determine if changes in a plant quality proxy and/or the thermal environment could predict the degree of skew in the use of shallow and deep areas. Covariation between water temperature and large tiger shark abundance in Shark Bay (Pearson correlation = 0.43) was insufficient to preclude their independent assessment (Burnham and Anderson 1998). Models of foraging dugong density were generated using all possible linear combinations of the independent variables ($n = 32$). Given that the dependent variable, daily forager counts divided by the volume of seagrass surveyed, consisted of non-negative integer values with a mode of zero, a low mean, and large variance, models were fit using maximum-likelihood under the assumption of a negative binomial error distribution (White and Bennetts 1996). I evaluated the strength of each model using Akaike's Information Criterion, corrected for small sample size ($AIC_c$; Burnham and Anderson 1998; Anderson et al. 2000). Akaike weights ($w$), which index the likelihood that a particular model is best among a set of competitors, and the change in $AIC_c$ between models ($\Delta\ AIC_c$) were used to assess model uncertainty (Burnham and Anderson 1998). The predictive strengths of individual explanatory variables were evaluated using the sum of the $w$ for all models in which particular variables appeared (parameter Akaike weights, $w_p$), and model-averaged coefficient estimates with unconditional standard errors (Burnham and Anderson 1998).

## 4.4 Results

### 4.4.1 Dugong density

Over the course of the investigation, I sighted 528 dugongs while conducting transects. Most sightings were of solitary animals (320/398), and group size averaged 1.33 (± 0.09, 95% CI) individuals, facilitating robust estimation of SZ (and overall) densities. The density of dugongs in the study area showed marked temporal variation, with warm season estimates (September – May) exceeding those for the cold season (June – August) (Figure 4.2a). The retention of the DOY variable in the generalized linear model, coupled with the exclusion of all interaction terms (all $p \geq 0.15$; Table 4.1), indicates that the observed annual trend in dugong abundance was both continuous and conserved across years. However, the magnitude of numerical change showed considerable annual variation (Table 4.1; Figure 4.2b). After blocking for spatial (i.e., SZ) effects, average seagrass biomass estimates for quadrat samples from shallow habitats (0.17 $m^3$ ± 0.01, 95% CI) greatly exceeded those for deep areas (0.01 $m^3$ ± 0.003) ($F_{1,1809} = 1042.58$, $p < 0.001$). Not surprisingly, therefore, dugong densities were consistently higher in shallow than in deep habitats (Table 4.1; Figure 4.2c). Finally, after accounting for temporal and habitat effects, sea surface temperature was a significant predictor of dugong density (Table 4.1). Although the relationship between water temperature and dugong abundance was positive, the highest density estimates coincided with intermediate temperatures (19 – 20°C) (Figure 4.2d).

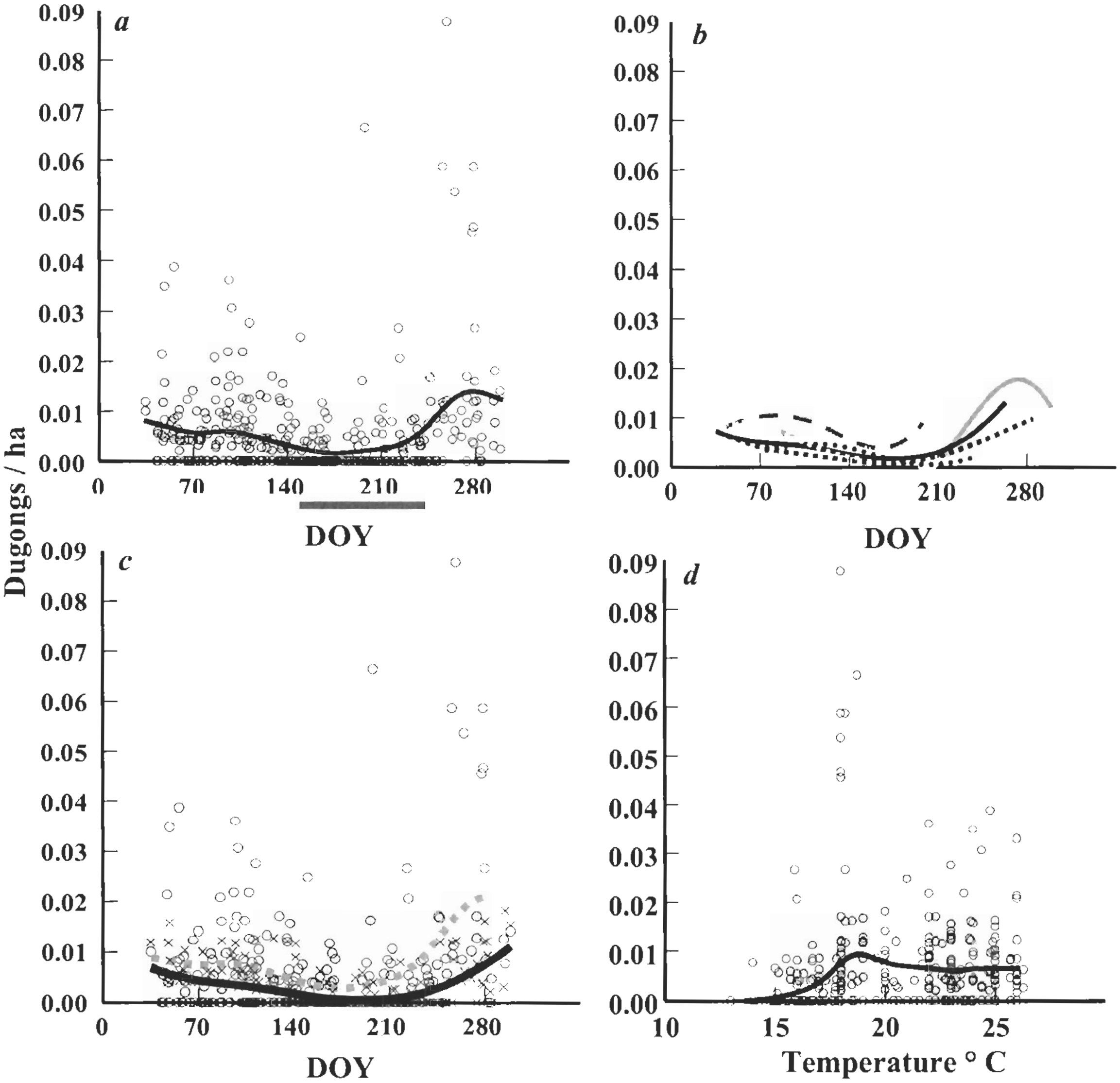

**Figure 4.2 Dugong density.**
Estimates of overall dugong density (*a*, per ha) in relation to day-of-year (DOY; years pooled); cold season (June – August) marked with a grey line. (*b*) Annual trends in dugong density: 1997 (grey line); 1998 (black dotted line); 1999 (dark-grey dashed line); 2002 (light-grey dashed line); 2003 (black dashed line); 2004 (black line). (*c*) Daily estimates of dugong density in shallow (o, dashed grey line) and deep (×, solid line) habitat. (d) Estimates of dugong density in relation to sea surface temperature (°C). Trend lines generated with distance-weighted least squares smoothing (tension 1.0).

**Table 4.1 Generalized linear model of dugong density**

Generalized linear model of dugong density ($d^{-1}$) in Shark Bay, Western Australia, as a function of day-of-year (DOY, expressed continuously), year, habitat (shallow versus deep), and sea surface temperature (°C). For all independent variables, coefficient estimates ($\theta$) are accompanied by standard errors and 95% confidence intervals (C.I.). All interactions were excluded from the final model (all $p \geq 0.15$).

| Factor | df | $\theta$ | SE ($\theta$) | 95% C.I. | $p$ |
|---|---|---|---|---|---|
| DOY | 1 | 0.009 | 0.002 | 0.006 – 0.012 | **< 0.001** |
| Year | 5 | -0.062 | 0.027 | -0.115 – -0.009 | **0.001** |
| Habitat | 1 | -0.859 | 0.143 | -1.139 – -0.578 | **< 0.001** |
| Temperature | 1 | 0.270 | 0.036 | 0.199 – 0.340 | **< 0.001** |

### 4.4.2 Foraging dugong habitat use

Between 2002 and 2004, I sighted 151 foraging dugongs while conducting transects. Most encounters involved solitary animals (83/113), and group size averaged 1.34 (± 0.33) individuals, facilitating reliable estimation of forager densities for SZ and across habitat categories. The best model of foraging dugong density incorporated large tiger shark abundance (S) and the interaction between shark abundance and habitat (H*S; Table 2). Although the Akaike weight ($w$) for this model (0.47) suggested that its probability of being superior to all others under investigation was moderate, its nearest competitor was six-fold less likely to be preeminent (Table 4.2). Furthermore, the parameter Akaike weights ($w_p$) for S and H*S both approached one (Table 4.3), implying that each variable had a high probability of being included in any model that was truly best. Finally, the unconditional 95% confidence intervals for the model-averaged estimates of S and H*S did not encompass zero (Table 4.3), suggesting that the relationships between these parameters and forager density were statistically and biologically significant. The model-averaged coefficient estimate for S was positive (Table 4.3), indicating that foraging dugong density increased with shark numbers. However, the inclusion of H*S in the best model means that the degree to which food-adjusted forager densities and predator abundance were associated differed as a function of habitat: increases in shark abundance corresponded with dramatic elevation in the use of only the deep habitat by foraging dugongs (Figure 4.3). On days when foragers were sighted ($n = 69$), the extent to which use of deep SZ exceeded that of shallow SZ following food adjustment (i.e., preference by foragers for deep foraging patches) correlated positively with tiger shark abundance (linear regression, $r^2 = 0.17$, $t_{67} = 3.73$, $\beta$

**Table 4.2 Top ten models of foraging dugong density**

Top ten models explaining the density of foraging dugongs across two habitat types (shallow and deep). Forager densities within each habitat were expressed as counts within survey zones (*n* = 14, replicated seven times per habitat category) and then divided by food supply (seagrass volume, $m^3$). Models were generated using all possible linear combinations (*n* = 32) of habitat category (H), an estimate of large (> 3 m) tiger shark abundance (S), sea surface temperature (°C) (T), the interaction between habitat category and shark abundance (H*S), and the interaction between habitat and water temperature (H*T), and then ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$). For each model, *K* is the number of parameters in the model + 1, Δ is the change in $AIC_c$ between the model and the "best" model (i.e., the model with the lowest $AIC_c$; highlighted in bold), *w* is the Akaike weight (i.e., the likelihood of preeminence), and $R^2_L$ is the $R^2$ analogue for models analyzed using maximum-likelihood.

| Model | *K* | Δ | *w* | $R^2_L$ |
|---|---|---|---|---|
| **S+(H*S)** | **3** | **0.000** | **0.471** | **0.207** |
| (H*S) | 2 | 3.855 | 0.069 | 0.198 |
| S+T+(H*S) | 4 | 3.958 | 0.065 | 0.205 |
| S+H+(H*S) | 4 | 4.124 | 0.060 | 0.204 |
| S+(H*S)+(H*T) | 4 | 4.848 | 0.042 | 0.203 |
| T+(H*S) | 3 | 5.538 | 0.030 | 0.199 |
| (H*S)+(H*T) | 3 | 5.646 | 0.028 | 0.199 |
| S+T+(H*S)+(H*T) | 5 | 5.912 | 0.025 | 0.205 |
| H+(H*S) | 3 | 6.014 | 0.023 | 0.198 |
| S+H+(H*S)+(H*T) | 5 | 6.014 | 0.023 | 0.204 |

**Table 4.3 Estimates of effect for variables incorporated in models of foraging dugong density**

Explanatory variables are habitat category (Habitat), an estimate of large (> 3 m) tiger shark abundance (Shark Pred), sea surface temperature (Temperature, °C), the interaction between habitat category and shark abundance, and the interaction between habitat category and water temperature. Each variable is accompanied by a parameter Akaiki weight ($w_p$), which is the sum of the Akaiki weight ($w$) for all models containing the variable in question. The model-averaged coefficient estimate ($\theta$) for each variable is the mean coefficient estimate characterizing all models containing that variable, weighted according to each model's $w$. The unconditional standard error of $\theta$ is a weighted measure incorporating uncertainty in the coefficient estimate and uncertainty in the chosen model. Confidence intervals were calculated using the unconditional SE ($\theta$). Variables exerting a significant influence on forager density are highlighted in bold.

| Variable | $w_p$ | Model Averaged $\theta$ | SE($\theta$) | 95% C.I. |
|---|---|---|---|---|
| Habitat | 0.22 | 0.86 | 0.99 | -1.07 – 2.80 |
| **Shark Pred** | **0.77** | **15.63** | **4.20** | **7.40 – 23.86** |
| Temperature | 0.22 | 0.07 | 0.07 | -0.06 – 0.21 |
| **Habitat*Shark Pred** | **0.93** | **64.26** | **23.48** | **18.25 – 110.27** |
| Habitat*Temperature | 0.29 | 0.05 | 0.04 | -0.02 – 0.12 |

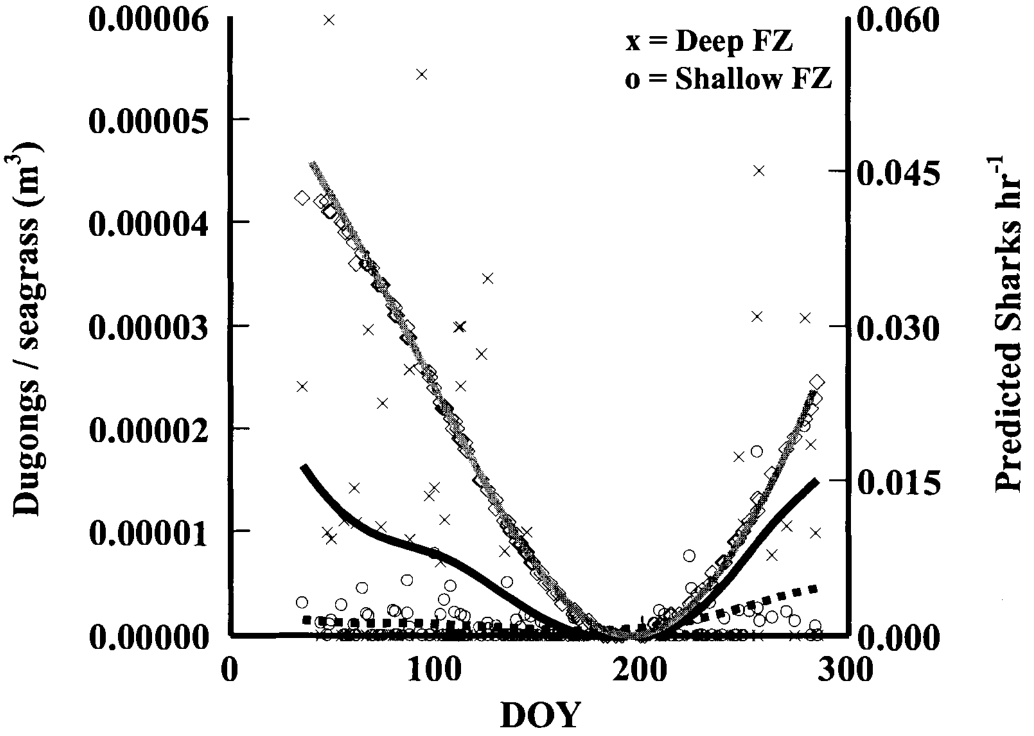

**Figure 4.3 Relationships between foraging dugong density in shallow and deep habitats and large tiger shark catch rate**

Relationships between daily estimates of foraging dugong counts divided by seagrass biomass (volume, m$^3$) in shallow (dashed black line) and deep (solid black line) habitats, predicted large (> 3 m) tiger shark catch rate (d$^{-1}$) (solid gray line, diamonds), and day-of-year (DOY). Trend lines created using DWLS smoothing (tension 1.0).

$= 6.41, p < 0.001$; Figure 4.4). Habitat category (H) alone was not a good predictor of forager density (low $w_p$, unconditional 95% confidence interval encompassing zero; Table 4.3): after adjustment for food, proportional use of the two habitats (input matching) was observed only when sharks were scarce (Figure 4.3). Sea surface temperature (T) and its interaction with habitat class (H*T) also featured low $w_p$ and unconditional 95% confidence intervals including zero (Table 4.3). By inference, (i) the relationship between predator abundance and foraging dugong habitat use is real rather than a spurious result of correlation between shark numbers and temperature, and (ii) elevated water temperatures were not accompanied by increased preference for shallow (i.e., high-quality) foraging patches among dugongs.

### 4.4.3 Resting dugong habitat use

I sighted 31 resting dugongs while conducting transects, all of which were solitary. Only 4 (12.9 %) individuals were observed in shallow habitat, precluding an evaluation of the possibility that resting animals switch between shallow and deep habitats in accord with shark abundance. Overall, however, the tendency for resting individuals to use deep habitat was highly significant (logistic regression, $t_{229} = 3.67, p < 0.001$).

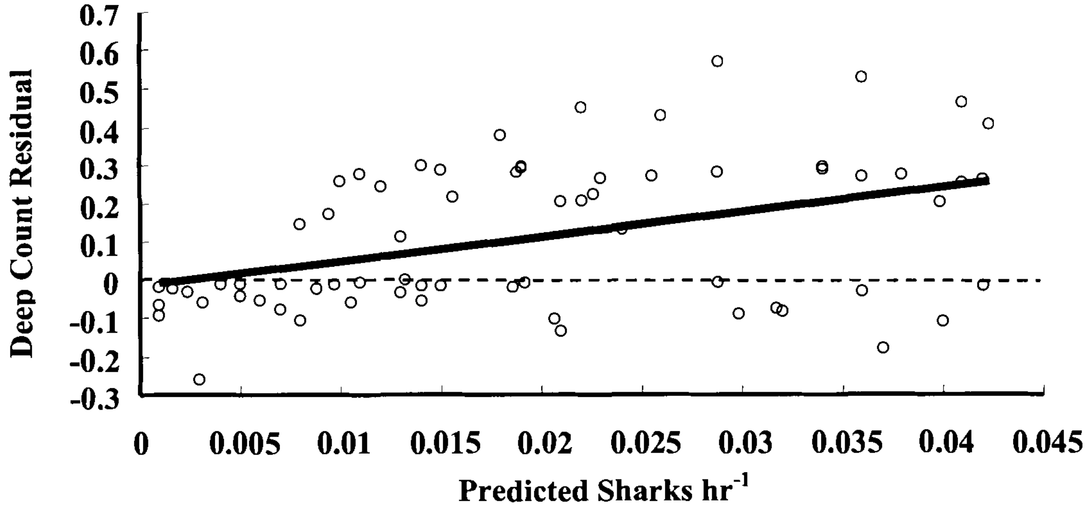

**Figure 4.4** **Residual counts of foragers in deep habitat versus large tiger shark catch rate.**

Residual counts of foragers in deep habitat (observed counts - expected counts based on food supply) versus large tiger shark catch rate (d$^{-1}$). Residuals were log (x+1) transformed to homogenize variances. Equality between observed and expected deep counts (i.e., residual values equaling zero; dashed line) signifies proportional habitat use by foragers, after adjustment for food biomass (input matching); large, positive residual values signify overuse of deep habitat.

## 4.5 Discussion

My results support the hypothesis that habitat use by foraging dugongs is influenced by predator intimidation. After adjustment for food supply, foraging dugong densities were not proportional in shallow and deep habitats throughout the year (food availability hypothesis), and relative use of shallow habitat did not increase with water temperature (food quality hypothesis). Rather, the degree of similarity between forager densities relative to food in shallow and deep habitats was a function of large tiger shark abundance: I observed input matching when sharks were scarce, overuse of deep (safe) habitats when sharks were common, and strong association between daily levels of shark abundance and the extent to which deep habitats were overused. Thus, I surmise that dugongs are sensitive to variation in predation risk across habitats, and that individuals manage their probability of death by allocating time to inherently safe but impoverished foraging patches in proportion to the likelihood of encountering predators in profitable but more dangerous feeding areas.

My conclusion that dugongs perceive deep foraging areas as havens from predation is corroborated by the tendency of animals at rest, a high-risk activity, to use deep habitat almost exclusively, and the facts that individuals surprised in the shallows by boats (a predator proxy; Frid and Dill 2002) usually flee to deeper water while those approached in deep areas rarely respond (A. Wirsing, *unpublished data*). I recognize, however, that the existence of a trade-off between food and safety also requires that excess foragers in deep habitat, following correction for food biomass, are unable to compensate nutritionally. For dugongs in the study area, deep water foraging likely entails a substantial nutritional cost. In regions where seagrass rhizomes are largely unavailable to dugongs, intake rates are believed to correlate positively with above-ground biomass (André et al. 2005). Given that the rhizomes of *A. antarctica* (the primary food source for herbivores in our study area) are inaccessible to dugongs (Anderson 1986), and that above-ground seagrass biomass was extremely low in deep SZ, it is very likely that individuals feeding in the deep habitats we surveyed experience depressed intakes. Furthermore, deep substrates in my study area comprise primarily sand and silt (Travers and Potter 2002; Heithaus 2004), and are largely devoid of tropical seagrass species (Walker et al. 1988; *personal observation*). Thus, dugongs foraging in these habitats presumably are also faced with higher search times and a lower quality food supply than those feeding in the shallows. Finally, dugongs in deep habitats undoubtedly expend more energy per unit time diving to the ocean floor to acquire food than do individuals in shallow patches.

The predator-mediated habitat shifts reported here could have been the product of territoriality if individuals were excluded from desirable (i.e., shallow) feeding areas during periods of peak dugong abundance (when sharks also happen to be most common). I consider this scenario to be unlikely since territorial behaviour has not been observed in the study area and foraging dugongs often congregate in preferred feeding areas (Marsh et al. 1984; Preen 1995). Furthermore, foraging dugongs adjusted their use of shallow and deep habitats on a continuous basis, responding to changes in predator abundance even during periods of low dugong density when the influence of any territoriality would have been minimal.

The periodic pattern of overall dugong abundance for my study site corresponded with sea surface temperature, a trend consistent with previous studies of dugong distribution in Shark Bay (e.g., Anderson 1982; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004). Yet, the highest densities we observed coincided with water temperatures between 19 and 20°C, which approach the value proposed as the lower physiological threshold for dugongs (19°C; Anderson 1986), rather than peak temperatures (26°C), and I sighted dugongs with some regularity even when water temperatures were as low as 16°C. Thus, while dugong densities are influenced by water temperature, individuals apparently can tolerate ambient temperatures below 19°C.

Previous work in Shark Bay has revealed that increases in the threat of tiger shark predation elicit reductions in the use of shallow habitats by piscivores (Indian Ocean bottlenose dolphins, *Tursiops* sp.; pied cormorants, *Phalacrocorax varius*), which may in turn provide a temporary reprieve for seagrass fishes (Heithaus and Dill 2002; Heithaus 2005). Dugongs, which represent an attractive prey resource for tiger sharks, use shallow areas preferentially. Thus, it is possible that their presence leads sharks to hunt predominantly in the shallows and, consequently, that dugongs initiate this indirect relationship between sharks and teleosts (Dill et al. 2003). Here, I show that increases in the danger of encountering and being attacked by sharks in profitable feeding patches induce dugongs to increase their use of safer, but relatively impoverished, foraging areas. Because grazing by dugongs can dramatically affect the composition and structure of seagrass meadows and upset detrital cycles (de Iongh et al. 1995; Preen 1995; Nakaoka and Aioi 1999; Masini et al. 2001), these behavioural changes may in turn help to determine the distribution and abundance of other species (e.g., invertebrates, teleosts) that rely on seagrass for shelter and subsistence. It follows that adjustments in dugong foraging location elicited by tiger sharks may not only exert a powerful indirect influence on seagrass meadows (e.g., by sheltering preferred but dangerous areas from herbivory and/or preventing seagrass species requiring disturbance from gaining a foothold among more persistent types) but also cascade through multiple trophic levels within seagrass communities. Collectively, these results underscore the important role played by large herbivores in marine communities, and suggest that apex predators such as tiger sharks can help to structure marine ecosystems from the top down by intimidating their vertebrate prey, in addition to eating them. In Shark Bay, the scope of the tiger shark's top-down role will of course remain hypothetical until studies quantifying the effects of predator-mediated changes in foraging by its prey on fish and seagrass biomass and community structure are conducted.

In summary, foraging dugongs appear to make predator-mediated habitat use decisions with potentially profound community consequences. This discovery has several important implications for the conservation and management of dugongs and the seagrass ecosystems of which they are a part. Though plentiful in Shark Bay, dugongs are threatened with extinction throughout much of their range (Preen 1998). Consequently, factors affecting the viability of dugong populations are of great interest. Given that the individual fitness costs of predator intimidation can heavily impact population demography (Preisser et al. 2005), my results suggest that future population viability analyses should incorporate measures of predation danger. Insofar as tiger shark abundance and water temperature are linked (Heithaus 2001), my results also suggest that changes in thermal regimes where dugongs and sharks coexist (e.g., as a result of global warming) may alter the foraging patterns of individual dugongs and, ultimately, seagrass community structure. Finally, given that marine vessels are often perceived as general predation risk stimuli (Frid and Dill 2002), approaches by boats may elicit crucial habitat use adjustments by dugongs. Thus, efforts to protect areas where these imperilled sirenians remain should seek to control the volume and distribution of boat traffic.

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# Chapter 5

# Living on the edge: dugongs prefer foraging microhabitats allowing for escape when predators are abundant

## 5.1 Abstract

When under threat of predation, prey animals engaged in foraging can either cease feeding and seek refuge or shift to feeding sites (microhabitats) that offer increased safety. Predator-induced microhabitat shifts by large herbivores are of particular interest to ecologists, as spatial patterns of foraging by these animals can shape plant communities. To date, the influence of predation risk on the microhabitat use behaviour of large herbivores in marine systems remains poorly understood. I explored the relationship between microhabitat use by dugongs (*Dugong dugon*) and the threat of tiger shark (*Galeocerdo cuvier*) predation in a subtropical Australian embayment (Shark Bay) over a period of three years. Use by foraging dugongs of two microhabitats within seagrass patches – edge (offering low-quality seagrass but swift escape from sharks) and interior (offering high-quality seagrass but fewer escape options) – was monitored in seven survey zones. The danger of shark predation was indexed using catch rates. After correction for food supply (biomass), the degree of dissimilarity between forager densities in edge and interior microhabitats was a function of large tiger shark abundance: foragers underused edge (safe) microhabitat when sharks were scarce, overused it when sharks were common, and responded to daily changes in shark abundance in threat-sensitive fashion, showing the greatest preference for edge microhabitat when shark abundance was highest. Thus, I conclude that dugongs manage their probability of death by allocating more time to safe but low-quality feeding microhabitats when the likelihood of encountering sharks is elevated. Intensive grazing by dugongs can influence seagrass biomass and patch composition, so tiger sharks likely affect the microhabitat structure of

seagrass meadows, and ultimately their benthic communities, indirectly by altering the way these sirenians use feeding patches.

## 5.2 Introduction

When confronted with the danger of predation, prey animals often make the costly decision to abandon foraging habitats in search of refuge (Sih 1987; Lima and Dill 1990; Lima 1998). Such costs can be reduced, however, if microhabitat variation within feeding patches enables prey to adjust their mortality risk while continuing to acquire resources (Lima and Dill 1990). For example, selection of feeding microhabitats facilitating crypsis, predator detection, escape, or access to refuges may allow prey under threat of predation to continue foraging without paying heavy fitness penalties (see reviews by Lima and Dill 1990; Lima 1998). Predator-induced microhabitat shifts by large herbivores are of particular interest to ecologists (Schmitz et al. 2004), as spatial patterns of foraging by these animals may influence plant community organization (Crawley 1983; Danell and Bergström 2002). In marine systems, the influence of predation danger on the microhabitat use behaviour of large herbivores remains poorly understood (Dill et al. 2003).

Here, I explore the microhabitat selection of dugongs (*Dugong dugon*) foraging on seagrass under risk of tiger shark (*Galeocerdo cuvier*) predation in Shark Bay, Western Australia. In Shark Bay, seagrass grows in expansive meadows found primarily in shallow habitat (< 4.5 m in depth; Walker et al., 1988) that can be divided into edge and interior microhabitats (Heithaus et al., *in review* a). Located along the periphery of seagrass patches, edge microhabitats offer increased water volume (depths generally between 2.5 and 4.5 m) and swift access to deep habitat (> 6.5 m). Consequently, dugongs encountering predators in these microhabitats are presumably better able to manoeuvre and escape to deeper water, where tiger sharks are more easily evaded (Heithaus et al., 2002), than are those in interior microhabitats (Heithaus et al., *in review* a). However, in edge microhabitat, concentrations of organic carbon, a plant constituent of alleged importance to dugongs (de Iongh et al. 1995; Preen 1995), in the seagrass species forming the bulk of the dugong's diet in our study area (*Amphibolus antarctica*) are reduced (Heithaus et al., *in review* b). Thus, although dugongs are likely less vulnerable to shark predation in edge microhabitats, food quality apparently is higher in seagrass patch interiors.

I sought to test the hypothesis that dugongs manage their risk of mortality by using safe, but relatively energy poor, foraging microhabitats in proportion to the threat of predatory attack. This hypothesis predicts that, after adjustment for differences in food supply (seagrass biomass), the degree of dissimilarity between foraging dugong densities in safe (edge) and hazardous (interior) microhabitats will be linked tightly to predator (tiger shark) abundance, with foragers showing no preference for safe microhabitats when sharks are scarce and the strongest preference for safe microhabitats during periods of peak shark abundance (i.e., when the likelihood of encountering and being attacked by sharks is greatest). Alternatively, predation danger may not influence microhabitat use by foraging dugongs, in which case foragers should either (i) distribute themselves proportionally across the two microhabitat types relative to food supply (i.e., input matching; van Baalen and Sabelis, 1993) throughout the year, or (ii) consistently overuse interior microhabitats if the seagrass available along meadow edges is indeed of inferior nutritional quality.

## 5.3 Materials and Methods

### 5.3.1 Study site

This study was undertaken in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (~ 25° 45' S, 113° 44' E; Figure 5.1). Shark Bay is home to a large population of dugongs (between 10,000 and 14,000 individuals; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004), many of which use our study area (Chapter 3). In 1991, the Shark Bay region was listed as a World Heritage Area, and anthropogenic activities in the region have always been minimal. Thus, I was able to evaluate the microhabitat use of individual dugongs belonging to a healthy population under relatively pristine conditions.

### 5.3.2 Sampling zones

For the purposes of this study, I defined edge microhabitats as portions of shallow banks characterized by water depths between 2.5 and 4.5 m as well as areas with depths < 2.5 m but within 75 m of deep water (> 4.5 m); interior microhabitats were defined as areas featuring water depths < 2.5 m and > 75 m from deep water. These microhabitat designations were selected because (i) they are each well represented in our study site, and (ii) we assumed that dugongs occupying them are differentially able to manoeuvre and escape to deep (safe) patches while under attack from tiger sharks (Heithaus et al., 2002; Heithaus et al., *in review* a). Edge and interior microhabitats were quantified in seven survey zones (SZ; average sampling area = 141.27 ha ± 26.17, sd), each allocated to a discrete seagrass patch in shallow habitat ($\leq$4.5 m in depth; Figure 5.1b), using a georeferenced bathymetric map and GIS software (MapInfo Professional version 4.5,

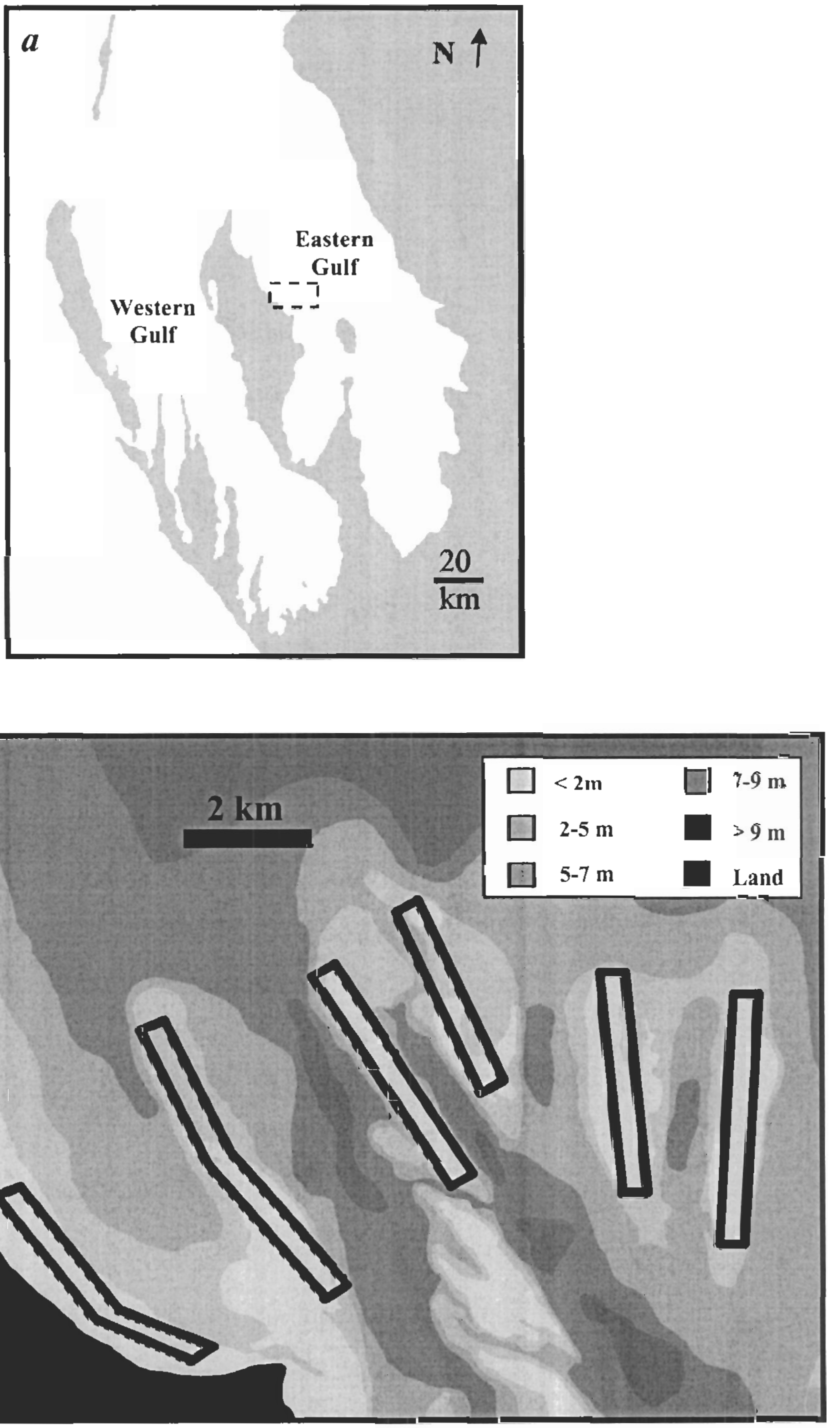

**Figure 5.1 Shark Bay, Western Australia**
This study was undertaken in the Eastern Gulf of Shark Bay (*a*). Survey zones ($n = 7$) were stratified evenly across shallow seagrass habitats throughout the study area (hatched box, 160 km$^2$, *b*).

MapInfo Corporation). Edge microhabitat comprised between 16.7% and 83.7% of the total sampling area for each SZ, averaging 52.4% (± 24.8%, sd).

### 5.3.3 Food availability

I quantified food availability (an index of biomass) within each SZ using sampling stations positioned at 200 m intervals along a central transect line, as well as along parallel lines 100 and 200 m to either side (75 – 120 stations per SZ). At each station, seagrass species coverage and composition were estimated within a 1-$m^2$ quadrat by a diver. Seagrass height (cm) was also measured within the quadrat; the point of measurement was selected randomly to minimize bias stemming from height variability. Sampling occurred during the late winter of 2003 (August – September), when herbivore densities were low, to minimize the confounding influence of herbivory and shark hazard to divers.

Food biomass was expressed as above-ground seagrass volume (area covered × height; $m^3$); measures from sampling points within edge and interior microhabitats were pooled to generate overall values for each SZ. Microhabitat volume measures for all SZ consisted of two seagrass species: *A. antarctica* (mean = 82.71% of total volume) and *Posidonia australis* (mean = 17.29% of total volume). The value of *P. australis* as a dietary item for dugongs is unknown, so its inclusion in estimates of food supply may have introduced bias. The removal of this species from consideration, however, did not affect the results reported later. Although I may also have incurred bias by failing to measure rhizomal (i.e., subsurface) biomass (de Iongh et al. 1995), such bias likely was modest given that rhizomes of the main species in our area (*A. antarctica*) are unavailable to dugongs as food (Anderson 1986). Finally, my biomass samples did not include tropical seagrass species (e.g., *Halodule uninervis*), likely because sampling occurred during the cold season when biomass of these species is low (Anderson 1986). Nevertheless, I consider our measure of food availability within the two microhabitats to be robust given that tropical species are always scarce in our study area (Walker et al. 1988).

### 5.3.4 Dugong density and microhabitat use

I assessed patterns of dugong abundance in edge and interior microhabitats using transect passes through the seven SZ from 2002 to 2004. To ensure sampling consistency, transect effort was distributed evenly across days ($n = 114$; mean = 3.79 passes $d^{-1}$, sd = 1.64), and months (mean = 22.85 ± 9.36 passes $month^{-1}$); the area of each microhabitat surveyed per day was roughly equivalent (edge mean = 249.23 ha, sd = 104.91; interior mean = 239.65 ha, sd = 105.07). Survey zones were not visited more than once per day, and the order and direction in which transects were driven each day were haphazard to reduce the effects of tidal and diel variation. Transects were only conducted in Beaufort wind conditions $\leq 2$ to minimize sighting bias caused by poor visibility in bad weather.

Transect passes were performed using a small (4.5 m) vessel driven at 6 – 9 km $h^{-1}$. When dugongs were sighted at the surface within 200 m of the transect line (i.e., within a 400 m sighting belt) before being passed by the boat, I determined their exact position using a GPS, the water depth and substrate characterizing their sighting location, and their behavioural state (foraging, resting, travelling) based on direct observation and diagnostic surface behaviour (Anderson 1986; Chilvers et al. 2004; and see Chapter 3).

Individual dugongs were distinguished using scarring patterns (Anderson 1995) and only counted once per day; intra-annual resampling was rare.

### 5.3.5 Predator abundance

Catch rates are assumed to provide a reliable index of tiger shark abundance in Shark Bay (Heithaus 2001). Sharks were caught on drumlines equipped with a single hook, baited primarily with Australian salmon (*Arripis truttaceus*), and deployed at dawn in six fishing zones within the study area; all sharks caught throughout the day were measured (total length, TL), tagged, and released (for methodological detail, see Heithaus 2001). Because of notable ontogenetic shifts in tiger shark diets (e.g., Lowe et al. 1996), tiger sharks under 3.0 m total length (TL) are unlikely to pose a threat to dugongs. Consequently, only sharks > 3.0 m TL were used to calculate daily catch rates.

Although variability in daily fishing effort was minimal, fishing frequency was insufficient (~ 6 fishing days month$^{-1}$) to allow for an evaluation of the relationship between daily microhabitat use by foraging dugongs and predator numbers. In light of the strong seasonal pattern in shark abundance in our study area (Heithaus 2001), I used a sinusoidal function with a period of one year to predict the annual trend in daily catch rates (sharks h$^{-1}$). Catch data used in the model were combined for the years 2002 through 2004 because interannual variation was not detected after accounting for seasonal effects ($F_{2,117} = 0.97, p = 0.38$). The model was fit using maximum-likelihood under the assumption of a Poisson error distribution because the data consisted of integer values for the number of sharks caught per day (I rarely caught more than one large tiger shark per fishing day).

### 5.3.6 Statistical analysis

Foraging dugong densities for individual SZ were calculated by dividing the number of animals sighted by the area searched (ha). After blocking for spatial (SZ) effects, seagrass biomass did not differ between edge and interior microhabitats ($F_{1,599}$ = 0.20, $P = 0.65$). Thus, for any given SZ, I assumed that proportional use of the two microhabitats after adjusting for their relative areas signified input matching (i.e., distributions driven solely by food supply), and that the degree to which forager densities in edge microhabitats exceeded those in interior microhabitats could be used as a proxy for the extent to which microhabitat choice is influenced by predation danger (van Baalen and Sabelis 1993; Heithaus and Dill 2002). Seagrass quality and the vulnerability of dugongs to tiger shark predation in the two microhabitats examined in this study are inversely related, so my use of this framework was not confounded by microhabitat differences in food quality, rather than quantity (i.e., dugongs seeking high-quality food would be expected to forage predominantly in interior microhabitats throughout the year). Calculated densities for edge and interior microhabitats within all SZ visited on a given day were averaged prior to analysis. I sighted six mother-calf pairs engaged in foraging while conducting transects. Given that the behaviour of dugong calves is constrained by that of their mother, these pairs were treated as one individual for purposes of analysis; removing them from consideration did not alter the results.

I used information theoretic methodology (Burnham and Anderson 1998) to evaluate the relationship between predator abundance (predicted large tiger shark catch rate, sharks $d^{-1}$) and daily use of edge and interior microhabitats by foraging dugongs. This approach ranks models of the relationship between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore facilitates rigorous evaluation of competing hypotheses (Burnham and Anderson 1998; Anderson et al. 2000; Johnson and Omland 2004). Independent covariates included microhabitat (edge versus interior) and the interaction between microhabitat category and shark abundance, so we could test whether (i) the two microhabitats were used unequally, and (ii) predation danger could predict the degree of inequality. Sea surface temperatures correlate positively with the nutrient content of *A. amphibolis* as well as tropical seagrass biomass (Walker et al. 1988), and may influence thermoregulatory costs of dugongs (Anderson 1986). Therefore, I also included a water temperature variable, and its interaction with microhabitat, in the analysis to determine if changes in a proxy for plant quality and/or the thermal environment could predict the degree of skew in the use of edge and interior microhabitats. Covariation between water temperature and large tiger shark abundance in Shark Bay (Pearson correlation = 0.43) was not sufficient to preclude their independent assessment (Burnham and Anderson 1998). Models of foraging dugong density were generated using all possible combinations of the independent variables ($n = 32$). The dependent variable for the models, daily forager counts divided by the relative area of edge and interior microhabitat surveyed, consisted of non-negative integer values with a mode of zero, a low mean, and large variance. Thus, I fit the models using maximum-likelihood under the assumption of a negative binomial error distribution (White and Bennetts 1996). The strength of each model was evaluated using Akaike's Information Criterion, corrected for small sample size ($AIC_c$; Burnham and Anderson 1998; Anderson et al. 2000). Akaike weights ($w$), which index the likelihood that a particular model is best among a set of competitors, and the change in $AIC_c$ between models ($\Delta$ $AIC_c$) were used to assess model uncertainty (Burnham and Anderson

1998). The predictive strengths of individual explanatory variables were evaluated using the sum of the *w* for all models in which particular variables appeared (parameter Akaike weights, $w_p$), and model-averaged coefficient estimates with unconditional standard errors (Burnham and Anderson 1998).

## 5.4 Results

I sighted a total of 105 foraging dugongs while conducting transects through the seven shallow SZ; 64 individuals were found in edge microhabitat, while 41 were located in interior microhabitat. Most encounters involved solitary animals (53/75), and group size averaged 1.40 (± 0.81, sd), facilitating robust estimation of daily densities for SZ and across microhabitat categories. The best model of foraging dugong density incorporated large tiger shark abundance (S) and the interaction between shark abundance and microhabitat (M*S; Table 5.1). While the Akaike weight (*w*) for this model (0.29) suggested that its probability of being superior to all others under investigation was relatively low, its nearest competitor was nearly three-fold less likely to be best (Table 5.1). Moreover, the parameter Akaike weights ($w_p$) for S and M*S approached one (Table 5.2), and both variables were contained in nine of the top ten models, implying that each variable had a high probability of being included in any model that was truly best. Finally, the unconditional 95% confidence intervals for the model-averaged estimates of S and M*S did not encompass zero (Table 5.2), suggesting that the relationships between these parameters and forager density were statistically significant and biologically meaningful. The model-averaged coefficient estimate for S was positive (Table 5.2), indicating that, overall, foraging dugong density increased in accord with shark numbers.

**Table 5.1 Top ten models explaining density of foraging dugongs in edge and interior microhabitats**

Top ten models explaining the density of foraging dugongs ($ha^{-1}$) across two microhabitats (edge and interior) within shallow seagrass patches. Forager densities for microhabitats were expressed as counts within survey zones ($n$ = 7), divided by the respective area covered by each microhabitat. Models were generated using all possible linear combinations ($n$ = 32) of microhabitat (M), an estimate of large (> 3 m) tiger shark abundance (S), sea surface temperature (°C) (T), the interaction between microhabitat and shark abundance (M*S), and the interaction between microhabitat and water temperature (M*T), and then ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$). For each model, $K$ is the number of parameters in the model + 1, $\Delta$ is the change in $AIC_c$ between the model and the "best" model (i.e., the model with the lowest $AIC_c$; highlighted in bold), $w$ is the Akaike weight (i.e., the likelihood of preeminence), and $R^2_L$ is the $R^2$ analogue for models analyzed using maximum-likelihood.

| Model | $K$ | $\Delta$ | $w$ | $R^2_L$ |
|---|---|---|---|---|
| **S+M*S** | **3** | **0.000** | **0.289** | **0.094** |
| S+T+M*S | 4 | 2.039 | 0.105 | 0.094 |
| S+T+M*S+M*T | 5 | 2.311 | 0.091 | 0.098 |
| M+S+T+M*S | 5 | 2.345 | 0.090 | 0.098 |
| S+M*S+M*T | 4 | 3.025 | 0.064 | 0.092 |
| M+S+T+M*S+M*T | 6 | 3.071 | 0.062 | 0.100 |
| M+S+M*S+M*T | 5 | 3.089 | 0.062 | 0.096 |
| M+S+M*S | 4 | 3.137 | 0.060 | 0.091 |
| M*S | 2 | 3.449 | 0.052 | 0.082 |
| S+T+M | 4 | 5.225 | 0.021 | 0.087 |

**Table 5.2 Estimates of effect for variables in models of foraging dugong density for edge and interior microhabitats**

Estimates of effect for variables incorporated in models of foraging dugong density for two microhabitats (edge and interior) within shallow seagrass patches. Explanatory variables are microhabitat (Microhabitat), an estimate of large (> 3 m) tiger shark abundance (Shark prediction [Pred]; see text), sea surface temperature (Temperature, °C), the interaction between microhabitat category and shark abundance, and the interaction between microhabitat category and water temperature. Each variable is accompanied by a parameter Akaiki weight ($w_p$), which is the sum of the Akaiki weight ($w$) for all models containing the variable in question. The model-averaged coefficient estimate ($\theta$) for each variable is the mean coefficient estimate characterizing all models containing that variable, weighted according to each model's $w$. The unconditional standard error of $\theta$ is a weighted measure incorporating uncertainty in the coefficient estimate and uncertainty in the chosen model. Confidence intervals were calculated using the unconditional SE ($\theta$). Variables exerting a significant influence on forager density are highlighted in bold.

| Variable | $w_p$ | Model Averaged $\theta$ | SE($\theta$) | 95% C.I. |
|---|---|---|---|---|
| Microhabitat | 0.35 | 0.23 | 0.71 | -1.15 – 1.61 |
| **Shark Pred** | **0.92** | **24.53** | **7.90** | **9.03 – 40.02** |
| Temperature | 0.42 | 0.13 | 0.07 | -0.02 – 0.26 |
| **Microhabitat*Shark Pred** | **0.89** | **32.25** | **9.19** | **14.24 – 50.26** |
| Microhabitat*Temperature | 0.36 | 0.04 | 0.04 | -0.04 – 0.13 |

However, the inclusion of M*S in the best model means that, following adjustment for food supply (i.e., area searched for each microhabitat), the degree to which forager densities and predator abundance were associated differed as a function of microhabitat: increases in shark abundance corresponded with dramatic elevation in the use of edge microhabitat by foraging dugongs, whereas forager densities in interior microhabitats actually reached minimal levels during periods of peak shark abundance (Figure 5.2). On days when foragers were sighted ($n$ = 53), the extent to which use of edge microhabitat exceeded that predicted by food supply alone (i.e., preference for edge microhabitats) correlated positively with tiger shark abundance (linear regression, $r^2 = 0.15$, $t_{52} = 3.01$, $\beta = 0.42$, $p = 0.004$; Figure 5.3). Furthermore, when shark abundance was at its lowest, foragers overused (i.e., preferred) interior microhabitats (Figure 5.3).

Microhabitat category (M) alone was not a good predictor of forager density (low $w_p$, unconditional 95% confidence interval encompassing zero; Table 5.2), meaning that, after adjustment for food, densities were not consistently higher in either microhabitat, and that proportional use of the two habitats (i.e., input matching) did not occur (Figure 5.2). Sea surface temperature (T) and its interaction with microhabitat (M*T) also featured low $w_p$ and unconditional 95% confidence intervals including zero (Table 5.2). By implication, the relationship between predator abundance and foraging dugong microhabitat use is real rather than a spurious result of correlation between shark numbers and temperature.

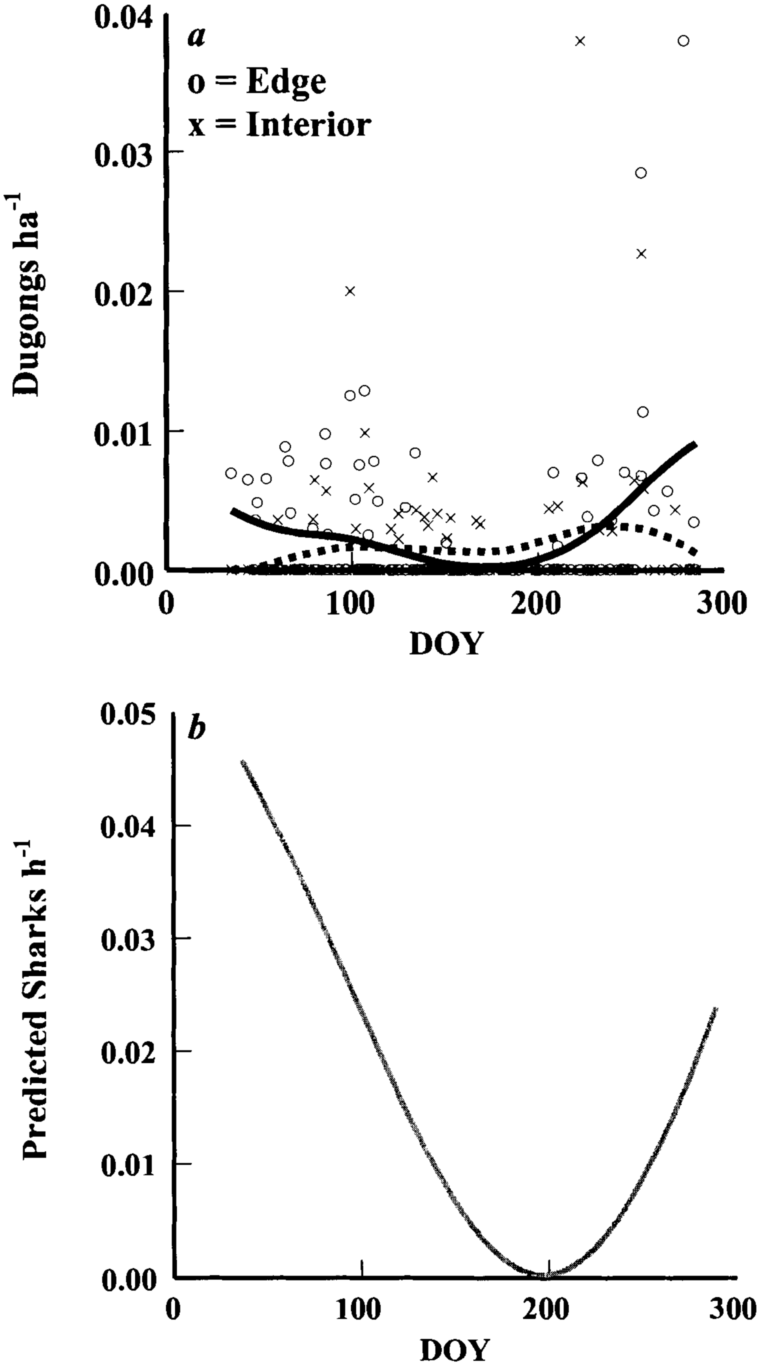

**Figure 5.2 Relationships between day-of-year (DOY), foraging dugong density in edge and interior microhabitat, and large tiger shark abundance**
Relationships between day-of-year (DOY) and (a) daily estimates of foraging dugong density (ha$^{-1}$) in edge (solid line) and interior (dashed line) microhabitats, and (b) large (> 3 m) tiger shark catch rate (d$^{-1}$) (grey line).

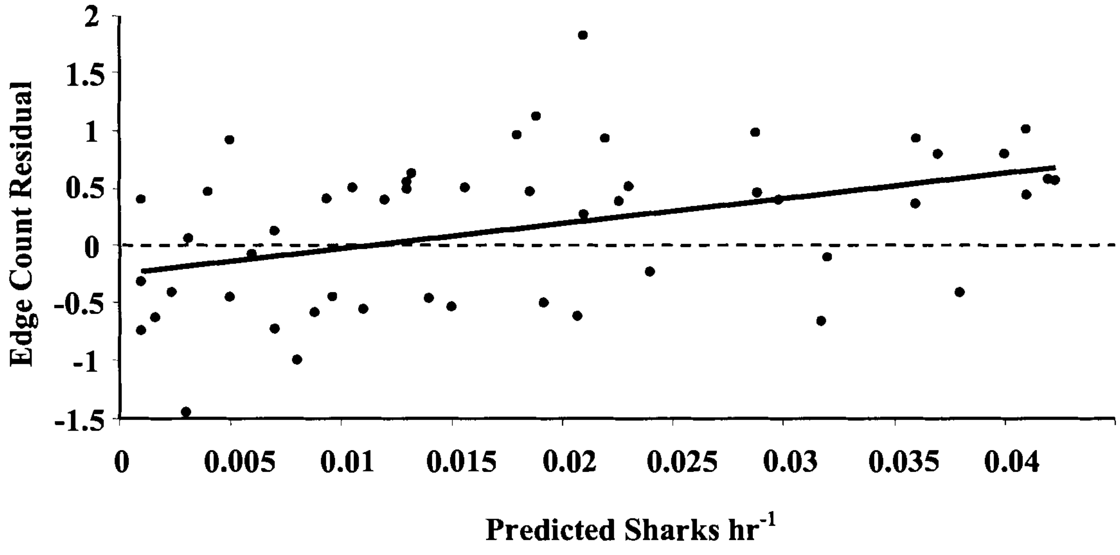

**Figure 5.3 Residual counts of foraging dugongs in edge microhabitat versus large tiger shark abundance**

Residual counts of foragers in edge microhabitat (observed counts - expected counts based on food supply [i.e., the proportion of total area within a SZ defined as edge]) versus large tiger shark catch rate (d$^{-1}$). Equality between observed and expected edge counts (i.e., residual values equalling zero; dashed line) signifies proportional microhabitat use by foragers relative to food (input matching), positive residual values signify overuse of edge microhabitat, and negative residual values signify overuse of interior microhabitat.

## 5.5 Discussion

The results of this investigation are consistent with the hypothesis that microhabitat use by dugongs foraging over seagrass meadows is influenced by the danger of predation. After adjustment for food supply, foraging dugong densities were not equivalent in edge and interior microhabitats throughout the year, nor did foragers consistently overuse meadow interiors. Instead, the degree of dissimilarity between forager densities relative to food in edge and interior microhabitats was a function of large tiger shark abundance: foraging dugongs underused edge (safe) microhabitat when sharks were scarce and overused edge microhabitat when sharks were common. Moreover, individual foragers responded to daily changes in shark abundance in a threat-sensitive manner (e.g., Helfman 1989), showing the greatest preference for edge microhabitat when shark abundance was highest. Thus, I surmise that dugongs are sensitive to variation in predation risk across microhabitats within feeding patches, and that individuals manage their probability of death by allocating time to safe but low-quality feeding microhabitats in proportion to the likelihood of encountering predators.

Large tiger sharks were most abundant when dugong numbers in our study area were highest. Thus, the predator-induced pattern of microhabitat use reported here may have instead been the result of territorial behaviour if individuals were excluded from preferred interior feeding sites during periods of high dugong density. I consider this scenario to be unlikely, however, given that territorial behaviour has not been observed in our study area, and that dugongs aggregate freely at feeding sites within seagrass patches (Marsh et al. 1984; Preen 1995). Moreover, foraging dugongs adjusted their use of edge and interior microhabitats on a continuous basis, responding to changes in predator abundance even during periods of low dugong density when the potential influence of territoriality would have been negligible. I also dismiss the possibility that the observed microhabitat shifts were driven by thermoregulatory requirements (i.e., the need to forage in high-quality microhabitats during the cold season, when shark abundance happens to be low, to meet increased metabolic costs). The addition of daily temperature information failed to improve upon predictive models of dugong density in the two microhabitats based solely on shark abundance, and relative use of the microhabitats was extremely sensitive to changes in shark abundance even during warm months when the cost of thermoregulation presumably was low (i.e., between February and April, when sea surface temperatures consistently exceed 22 °C).

When foraging over shallow seagrass meadows, tiger sharks show a consistent preference for edge microhabitats (Heithaus et al., *in review* a). Consequently, dugongs foraging in edge microhabitats are more likely to encounter sharks than those feeding in meadow interiors. Yet, individual dugongs increased their use of edge, instead of interior, microhabitats in response to elevated shark abundance. Thus, under the assumption that attack probabilities were equal across the two microhabitat categories, I conclude that dugongs assess the danger associated with particular microhabitats based on their likelihood of escape rather than predator encounter rates. This may be because the likelihood of future encounters with predators in particular areas is difficult to predict based upon prior sampling (Sih 1992). Indian Ocean bottlenose dolphins (*Tursiops* sp.) in my study area also select foraging microhabitats facilitating escape, rather than those with the lowest predator encounter rates, during periods of heightened danger (Heithaus and Dill, *in review*). That is, preference for feeding sites offering escape options, rather than low predator abundance, may be common among animals under threat of predation (e.g., Grubb and Greenwald 1982; Kotler et al. 1991). The preference for edge microhabitat by dugongs under elevated threat of predation also suggests that deep habitats are perceived as refugia by these sirenians (and see Chapter 3), since meadow edges offer swift access to this habitat type.

The tendency of foraging dugongs to select interior microhabitats during periods of low predation danger, rather than to input-match, can be explained by the depressed nutrient (organic carbon) content of *A. antarctica* plants growing along the edges of the seagrass patches used in this study (Heithaus et al., *in review* b). However, it is also possible that dugongs foraged preferentially in interior microhabitats during safe periods in part to (i) avoid paying energetic costs associated with diving more deeply to access seagrass growing in edge microhabitats, and/or (ii) because tropical seagrass species not included in our food biomass estimates are less available in edge microhabitats. The latter alternative is unlikely, given that a disparity in tropical seagrass biomass between edge and interior microhabitats is not known to exist, and that the overall availability of these species in our study area tends to be extremely low when tiger sharks are scarce (i.e., June – August) (Walker and McComb 1988; Walker et al. 1988).

In a companion study, I showed that the danger of tiger shark attack affects the use of shallow and deep habitats by foraging dugongs, with individuals overusing deep but impoverished refugia when large shark abundance was elevated (Chapter 3). The present investigation reveals that dugongs also adjust their use of safe but energy-poor microhabitats while feeding in accord with changes in predation danger. Collectively, these results indicate that the threat of tiger shark predation can influence not only use of profitable but dangerous feeding patches by large marine herbivores (i.e., broad-scale habitat selection, in this case on the order of 100s of m to km), but also choice of feeding sites within these foraging patches (i.e., fine-scale habitat selection, in this case on the order of 10s of m). Grazing by dugongs can dramatically alter seagrass biomass and patch composition, especially where foraging pressure is heavy (i.e., at high-quality feeding sites within patches; de Iongh et al. 1995, Preen 1995, Nakaoka and Aioi 1999, Masini et al. 2001). Therefore, by altering the use of foraging microhabitats by dugongs, tiger sharks may exert powerful indirect effects on seagrass, alleviating pressure experienced by plants growing at preferred but dangerous feeding sites (e.g., interiors) and augmenting pressure experienced by nutritionally inferior plants growing at relatively safe feeding sites (e.g., edges). By implication, changes in patterns of large shark abundance and space use where dugongs, as well as other large marine herbivores (e.g., sea turtles; Heithaus at al., *in review* b), occur may have profound consequences for the microhabitat structure of seagrass patches and, ultimately, benthic communities.

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# Chapter 6

# Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger

## 6.1 Abstract

Foraging and vigilance may be mutually exclusive for some foraging tactics but not others. Thus, in response to changes in the danger of predation, prey species with multiple foraging tactics may switch facultatively between them, allowing for differential levels of vigilance. Using data from standardized focal observations collected over a period of three years (2002 – 2004) in Shark Bay, Western Australia, I explored the use of two tactics, cropping and excavation, by dugongs (*Dugong dugon*) foraging under risk of predation by tiger sharks (*Galeocerdo cuvier*). Overall, dugongs predominantly used the cropping tactic, which allows for regular visual scans, to harvest temperate seagrass species. The extent to which dugongs used the excavation tactic, which precludes regular visual scans but allows individuals to access the nutritious rhizomes of preferred tropical seagrass species, was a function of both water temperature and tiger shark abundance. Dugongs only excavated seagrass during warm periods (i.e., February – May) when tropical species were most available; during these warm periods, the time allocated to excavation was inversely related to shark abundance. I conclude that use of foraging tactics by dugongs is sensitive to predation danger, and that individuals manage their risk of mortality via reduced use of a profitable but potentially hazardous tactic when the likelihood of encountering a predator is high. Excavating dugongs are more likely to disrupt seagrass meadow structure and promote succession than are those engaged in cropping. Thus, by altering the time dugongs devote to these alternative tactics, tiger sharks may exert a strong indirect effect on seagrass patch composition and structure and, ultimately, benthic communities.

## 6.2 Introduction

The act of foraging can limit the ability of prey animals to be vigilant (Stephens and Krebs 1986; Krause and Godin 1996; Bednekoff and Lima 1998; Lima and Bednekoff 1999). Consequently, prey individuals under threat of predation often lose opportunities to acquire energy while scanning their environment (Lima and Bednekoff 1999). However, not all feeding modes constrain antipredator vigilance to the same degree (Bednekoff and Lima 1998; Kaby and Lind 2003). For example, foraging tactics that are complex (Kaby and Lind 2003) or involve body postures restricting vision (Krause and Godin 1996) are much more likely to impede predator detection and escape than those allowing simultaneous surveillance. It follows that prey animals may switch between foraging tactics in a threat-sensitive manner, avoiding tactics that preclude vigilance when danger is heightened (e.g., Helfman 1989). Predator-induced changes in the foraging tactics employed by herbivores are of particular interest to ecologists, for they may alter the pressure these species exert on plants and, ultimately, community structure (Crawley 1983; Schmitz et al. 2004). In marine systems, the influence of predation risk on the choice of foraging tactics by large herbivores has not been addressed.

Here, I explore the use of alternative foraging tactics by dugongs (*Dugong dugon*) under risk of predation by tiger sharks (*Galeocerdo cuvier*) in a Western Australian embayment (Shark Bay). Dugongs employ two primary tactics to harvest seagrass: cropping, whereby clusters of leaves are stripped from the branching stems of seagrass plants (Anderson 1982), and excavation, whereby individuals root into the substrate with their rostra to consume both above- and below-ground (i.e., rhizomal) portions of seagrass plants (Anderson and Birtles 1978). In Shark Bay, dugongs crop the temperate seagrass species *Amphibolis antarctica* (Anderson 1986), which is widely available as food (~ 90% of total seagrass cover; Walker et al. 1988), while apparently using excavation foraging to consume tropical seagrass species (e.g., *Halodule uninervis*, *Halophila ovalis*) that are more sparsely distributed (Walker et al. 1988). Tropical seagrass species are generally preferred over temperate ones (Anderson 1986; Preen 1995; Masini et al. 2001), likely because their rhizomes are energy-rich and contain relatively high concentrations of important nutrients (e.g., organic carbon; de Iongh et al. 1995). Thus, dugongs engaged in excavation may achieve higher energy intake rates than those using the cropping tactic. However, while the act of cropping allows for frequent scans between bites (*personal observation*), the process of excavation involves lengthy periods of digging that undoubtedly preclude vigilance. Moreover, excavating dugongs usually produce large sediment plumes that likely impede surveillance and may even attract predators. Consequently, dugongs electing to excavate in areas where, and during time periods when, both tactics are feasible may pay the cost of increased mortality risk (see Godin and Smith 1988 for an example of such a cost in foraging guppies, *Poecilia reticulata*). The magnitude of this cost is not constant, however, as tiger shark abundance in Shark Bay shows strong seasonal variation (Heithaus 2001; Chapter 2).

I tested the hypothesis that dugongs manage their risk of mortality by using the dangerous but profitable foraging tactic (excavation) in inverse proportion to the likelihood of encountering predators. The biomass of tropical seagrass species in Shark Bay is linked to water temperature, being greatest at the peak of the warm season (January – February) and declining sharply during months when water temperatures are below 20°C (June – October; Anderson 1986; Walker and McComb 1988). Consequently, dugongs generally do not excavate tropical species during these cold months, cropping *A. antarctica* instead (Anderson 1986). Accordingly, this hypothesis predicts that, when excavation is feasible (i.e., November – May), the time dugongs allocate to excavation while foraging should be inversely related to tiger shark abundance. Conversely, if the time dugongs devote to excavation is driven solely by the availability of tropical seagrass species, then the frequency with which this tactic is employed should be greatest during months when water temperatures are highest (i.e., January – March). Given that tiger shark abundance and temperature are positively correlated (Heithaus 2001), an inverse relationship between shark abundance and excavation time during these months should not exist under this latter scenario (i.e., time allocated to excavation should be maximal when both shark abundance and temperature are highest). In addition to looking at foraging tactics, I also asked whether the overall time dugongs spent foraging, and the time spent foraging in the two primary feeding habitats in our study area (deep channels, > 6.5 m in depth; shallow banks, < 4.5 m), corresponded with changes in shark abundance and/or water temperature.

## 6.3 Materials and Methods

### 6.3.1 Study site

This study was conducted in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (Red Cliff Bay; ~ 25° 45' S, 113° 44' E). Shark Bay has been listed as a World Heritage Area since 1991, and is home to a large dugong population (between 10,000 and 14,000 individuals; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004), many of which use our study area (Chapter 4). Thus, I was able to evaluate the foraging decisions of dugongs belonging to a healthy population under relatively pristine conditions.

### 6.3.2 Dugong foraging behaviour

Between 2002 and 2004, I assessed the foraging behaviour of individual dugongs using focal animal follows (*n* = 128; Altmann 1974). Individual adults sighted randomly during transect passes through shallow and deep habitat (see Chapter 4) for methodological detail) were targeted for focal observation, minimizing the likelihood that starting positions were spatially biased (Heithaus et al., *in review*), and focal follows were only conducted in Beaufort wind conditions $\leq 1$ to facilitate reliable observation. Dugongs selected for behavioural observation were approached at slow speed (~ 1 km $h^{-1}$) and then allowed to acclimate to my vessel (a 4.5 m runabout) for 5 minutes from a distance of roughly 50 m; subsequently, behavioural observations were made from a distance of 10-20 m. I am confident that this method of observation was minimally invasive: focal animals rarely changed their behaviour or moved in response to my approach, moved freely about the vessel without investigating, and often rested in close proximity to the boat, implying that I was perceived neither as a distraction nor as a threat. Dugongs that did respond to my approach by moving off or changing their behaviour (i.e., by terminating foraging or resting bouts; *n* = 5) were not followed. Focal observation periods averaged 52.77 min (± 22.3 min, sd); follows lasting less than 30 minutes were not included in this analysis. During each follow, I recorded water depth (m) and the position (with a GPS) and predominant behaviour (foraging, travelling, resting, unknown) of the focal individual every two minutes. When animals could not be observed while submerged, activity states were distinguished using diagnostic behaviour and characteristics at the surface (Anderson 1986; Chilvers et al. 2004): foraging (slow, meandering search with irregular surface intervals, often associated with sediment plumes and deep dives); resting (little displacement, regular surface intervals, shallow and relaxed breaths); travelling (directional movement with few/no stops, regular surface intervals). In shallow habitat ( ≤4.5 m in depth), I also noted whether foraging animals cropped or excavated seagrass during each two-minute observation interval. These two tactics proved easy to distinguish when used in the shallows: dugongs engaged in cropping tended to meander and take haphazard bites of seagrass, while excavating animals tended to confine their foraging effort to particular areas and usually created large sediment plumes. When possible, unique marking and scarring patterns (Anderson 1995) were recorded during each follow to ensure that individuals were not sampled repeatedly.

Data collected using focal follows are often autocorrelated, as all behavioural observations are constrained by the behaviour of the focal animal when the follow is initiated unless observations are separated by long intervals (Manly et al. 1993). I believe that my assessment of dugong foraging behaviour is robust to this potential problem, however, given that (i) follows were initiated randomly with respect to location and behavioural state, and (ii) the focal data we collected were subject to a consistent level of bias (i.e., there is no reason to assume that levels of autocorrelation characterizing our follow data changed over time), allowing reliable comparison of foraging budgets associated with varying levels of predation danger and water temperature.

### 6.3.3 Predator abundance

Catch rates are assumed to provide a reliable index of tiger shark abundance in Shark Bay (Heithaus 2001). Sharks were caught on drumlines equipped with a single hook, baited primarily with Australian salmon (*Arripis truttaceus*), and deployed at dawn in six fishing zones within the study area (160 $km^2$); all sharks caught throughout the day were measured (total length, TL), tagged, and released (for methodological detail, see Heithaus 2001). Because of notable ontogenetic shifts in tiger shark diets (e.g., Lowe et al. 1996), tiger sharks under 3.0 m total length (TL) are not likely to pose a threat to dugongs. Thus, only sharks > 3.0 m TL were used to calculate daily catch rates.

Daily variability in fishing effort was minimal. However, fishing frequency was insufficient (~ 6 fishing days $mo^{-1}$) to allow for an evaluation of the relationship between the daily foraging budgets of focal individuals and predator numbers. Thus, in light of the strong seasonal pattern in shark abundance in our study area (Heithaus 2001), I employed a sinusoidal function with a period of one year to predict the annual trend in daily catch rates (sharks $h^{-1}$). Catch data used in the model were combined for the years 2002 through 2004 as inter-annual variation was not detected after accounting for seasonal effects (ANCOVA: $F_{2,117} = 0.97$, $P = 0.38$). The model was fit using maximum-likelihood under the assumption of a Poisson error distribution because my data consisted of integer values for the number of sharks caught per day (Chapter 4). Each focal follow was assigned a shark catch rate (i.e., a predation risk level) generated by the model, which has been shown to have explanatory value in this system (Chapters 4, 5).

### 6.3.4 Statistical analysis

The dependent variables in this study were expressed as (i) the number of two-minute observation intervals during which focal animals engaged in foraging, divided by the total number of observation intervals for the follow, (ii) the number of observation intervals during which animals engaged in deep water foraging, divided by the total number of intervals for which foraging was the dominant behaviour, and (iii) the number of intervals during which animals engaged in excavation foraging, divided by the total number of intervals during which foraging occurred in the shallows. For the latter two dependent variables, follows during which the focal individual engaged in foraging or shallow water foraging, respectively, for fewer than five observation intervals were deleted from the data to avoid bias stemming from low sampling time. For all three variables, data from the three years of the investigation were analyzed collectively as annual differences between times devoted to foraging (ANOVA: $F_{2,125} = 0.09$, $P = 0.92$), foraging in deep water ($F_{2,95} = 0.33$, $P = 0.72$), and excavation ($F_{2,89} = 2.37$, $P = 0.10$) were not detected.

I examined the extent to which models based solely on predator (tiger shark) abundance, solely on sea surface temperature (°C; measured daily from a constant location), and on the combination of these two factors could predict each of the three dependent variables using information theoretic methodology (Burnham and Anderson 1998; Anderson et al. 2000). This approach ranks models of the relationship between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore allows for rigorous comparisons of competing hypotheses (Anderson et al. 2000; Johnson and Omland 2004). Linear models of the three dependent variables were fit using maximum-likelihood; since all dependent variables were proportions with a modal value of zero, a low mean, and large variance, a binomial error distribution served as the basis for statistical inference (Lloyd 1999). Though correlated, the two independent variables were sufficiently divergent to allow for independent assessment in the models (Chapter 4). Support for each model was quantified using Akaike's Information Criterion, corrected for small sample size ($AIC_c$; Burnham and Anderson 1998; Anderson et al. 2000); non-linear transformations of the independent variables were used if they substantially improved the support for a given model (i.e., lowered its $AIC_c$ by $\geq 2$; Burnham and Anderson 1998). Akaike weights (*w*), which measure the likelihood that a particular model is best among a set of competitors, and the change in $AIC_c$ between models ($\Delta$ $AIC_c$), were used to assess model uncertainty (Burnham and Anderson 1998).

## 6.4 Results

### 6.4.1 Foraging

The 128 dugongs that were subject to focal observation ($\geq$30 min) devoted an average of 48.74% (± 36.34%, sd; min = 0, max = 100%) of their time to foraging. The best model of time allocated to foraging by dugongs included only sea surface temperature (T; Table 1). The Akaike weight (*w*) for this model (0.51) suggested that it was likely to be superior to its competitors (Table 6.1). However, it was not significant ($P = 0.107$) and explained only 0.12% of the observed variation in the time individual dugongs devoted to foraging (Table 6.1), meaning that correspondence between trends in temperature and large tiger shark abundance and the pattern of foraging we observed was relatively weak (i.e., individual foraging times were governed primarily by factors not included in the model). Indeed, while water temperature and shark abundance varied

**Table 6.1 Models of time devoted to foraging by dugongs in Shark Bay, Western Australia**

Foraging data were collected using focal animal follows (*n* = 128) exceeding 30 min. Models were generated using all linear combinations (*n* = 3) of two independent variables: large (> 3 m TL) tiger shark abundance (S) and sea surface temperature (°C) (T). The dependent variable, the proportion of two-minute observation intervals during which foraging was the dominant behaviour, featured a constrained maximum and a modal value of zero. Thus, models were fit with binomial regression, and then ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$). For each model, $K$ is the number of parameters in the model, $\Delta$ is the change in $AIC_c$ between the model and the "best" model (i.e., the model with the lowest $AIC_c$; highlighted in bold), $w$ is the Akaike weight (i.e., the likelihood of preeminence), and $R^2_L$ is the $R^2$ analogue for models analyzed using maximum-likelihood.

| Model | $K$ | $\Delta$ | $w$ | $R^2_L$ |
|---|---|---|---|---|
| **T** | **1** | **-** | **0.512** | **0.001** |
| S+T | 2 | 1.275 | 0.271 | 0.001 |
| S | 1 | 3.020 | 0.113 | 0.000 |

Note: *w* for the constant-only model was 0.104.

dramatically over the course of the investigation (Chapter 4), the time dugongs budgeted to foraging remained fairly consistent (Fig. 1).

### 6.4.2 Deep habitat foraging

Among the 98 dugongs that engaged in foraging for a minimum of five observation intervals during focal follows, individuals allocated an average of 9.85% (± 26.77%, sd; min = 0, max = 100%) of their foraging time to deep habitat (> 6.5 m in depth). The model best explaining deep habitat foraging by dugongs included large tiger shark abundance (S; Table 6.2). Although this model explained a relatively small proportion of the observed variation in deep habitat foraging (5%), it was highly significant ($P = 0.001$) and likely to be superior to its competitors ($w = 0.58$). The coefficient estimate for S was positive (42.70), implying that the amount of time dugongs spent foraging in deep habitat increased in conjunction with large shark abundance (Fig. 6.2).

### 6.4.3 Excavation

A total of 92 dugongs foraged in shallow habitat (< 4.5 m in depth) for a minimum of five observation intervals. These individuals allocated an average of 11.96% (± 28.00%, sd; min = 0, max = 100%) of their shallow habitat foraging time to excavation. The best model of excavation in the shallows included both sea surface temperature (T) and large shark abundance (S) (Table 6.3). This model was significant ($P < 0.001$), explained a substantial amount of the observed variation in excavation time (52%), and was clearly superior to the other models under consideration (i.e., $w$ approaching one, Table 6.3). The relationship between these two variables and excavation time was non-linear (i.e.,

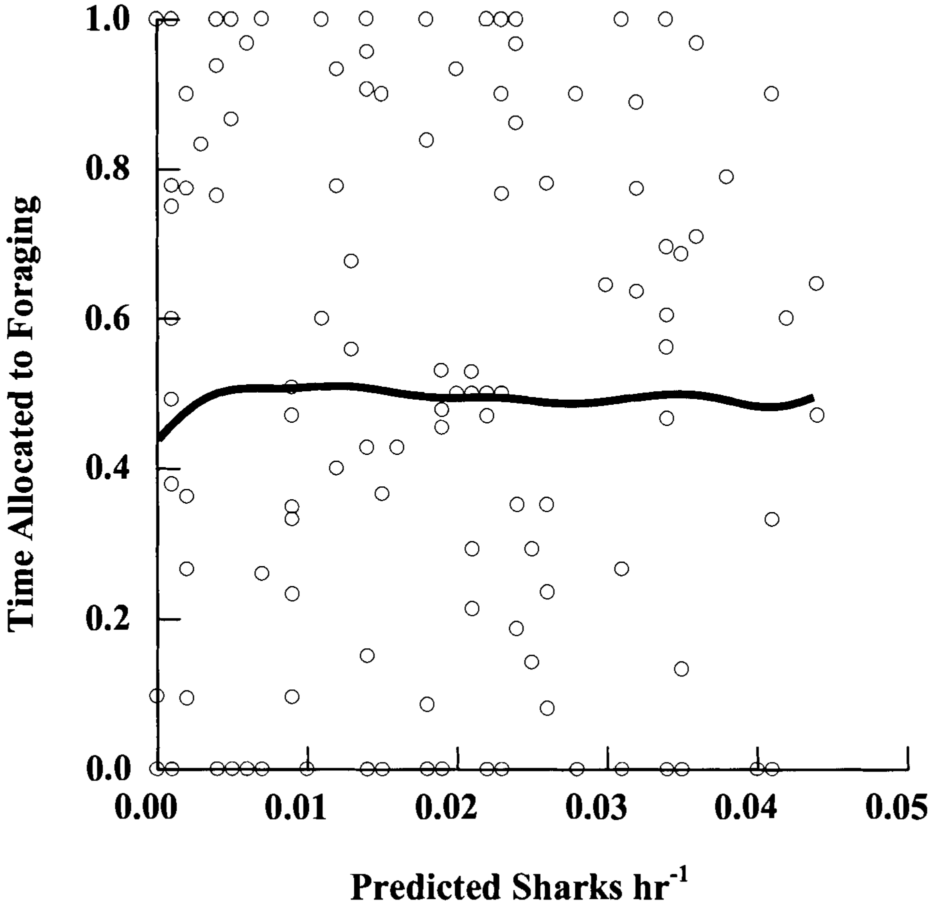

**Figure 6.1 Time allocated to foraging by dugongs versus large tiger shark catch rate.**

Relationship between the proportion of time allocated to foraging by dugongs during focal animal follows (*n* = 128) and large (> 3 m) tiger shark catch rate (h$^{-1}$; predicted using a maximum-likelihood model of the annual trend in raw daily catch values) over a period of three years (2002 – 2004). The trend line was generated using distance-weighted least squares smoothing (DWLS, tension 1.0).

**Table 6.2 Models of time devoted to foraging in deep water by dugongs in Shark Bay, Western Australia**

Models of the time devoted to foraging in deep water (i.e., the proportion of two-minute observation intervals during which animals engaged in foraging used water > 6.5 m in depth) by dugongs; follows that did not involve foraging for a minimum of five observation intervals (*n* = 30) were not considered. Models were generated using all linear combinations (*n* = 3) of two independent variables (large tiger shark abundance [S] and sea surface temperature [°C, T]), fit with binomial regression, and then ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$). See Table 1 caption for symbol definitions.

| Model | $K$ | $\Delta$ | $w$ | $R^2_L$ |
|---|---|---|---|---|
| **S** | **1** | **-** | **0.581** | **0.047** |
| S+T | 2 | 0.657 | 0.418 | 0.049 |
| T | 1 | 16.066 | 0.000 | 0.021 |

Note: *w* for the constant-only model was 0.000.

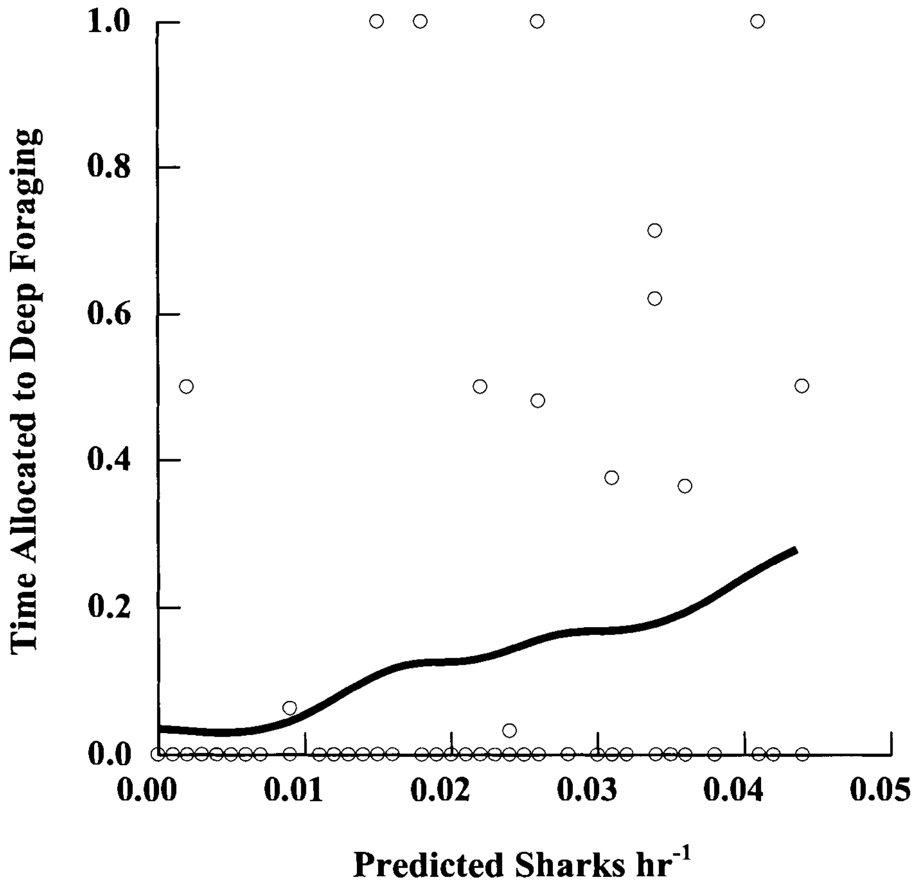

**Figure 6.2 Time allocated to foraging in deep water by dugongs versus large tiger shark catch rate.**

Relationship between the proportion of time allocated to foraging in deep habitat (> 6.5 m in depth) by dugongs during focal follows (*n* = 98) and predicted large (> 3 m) tiger shark catch rate (h$^{-1}$).

**Table 6.3 Models of time devoted to excavation foraging by dugongs in Shark Bay, Western Australia**

Models of the time devoted (i.e., proportion of two-minute observation intervals allocated) to excavation by dugongs foraging in shallow seagrass habitat (< 4.5 m in depth); follows that did not involve shallow foraging for a minimum of five observation intervals ($n$ = 36) were not considered. Models were generated using all combinations of tiger shark abundance (S) and sea surface temperature (°C) (T), fit with binomial regression, and then ranked using Akaike's Information Criterion, corrected for small sample size ($AIC_c$); non-linear (quadratic) transformation substantially improved the fit of all models (i.e., $\Delta AIC_c$ values > 2). See Table 1 caption for symbol definitions.

| Model | $K$ | $\Delta$ | $w$ | $R^2_L$ |
|---|---|---|---|---|
| **S + T** | **4** | **0.000** | **0.984** | **0.523** |
| T | 2 | 8.29 | 0.016 | 0.508 |
| S | 2 | 230.97 | 0.000 | 0.166 |

Note: $w$ for the constant-only model was 0.000.

quadratic transformation substantially improved the fit of the best model, $\Delta AIC_c$ value > 2). The coefficient estimate for the temperature variable in the best model was positive (23.28), meaning that dugongs excavated seagrass with greatest frequency during the warmest months (i.e., February – May) of the investigation; indeed, use of this tactic was not observed during months when temperatures typically fell below 20°C (June – October). The coefficient estimate for the shark abundance variable in this model was negative (-28.97), implying that, after accounting for the effects of temperature (i.e., during the warm period [temperatures ≥20°C] when excavation occurred), dugongs reduced their reliance on excavation as shark abundance rose (Fig. 6.3).

## 6.5 Discussion

The results of this investigation are consistent with the hypothesis that use of particular foraging tactics by dugongs is sensitive to the danger of predation. Overall levels of foraging by dugongs were temporally consistent. However, during warm months (February – May) when the seagrass species typically excavated by dugongs in Shark Bay (i.e., tropical species; *Halodule uninervis*, *Halophila ovalis*; Anderson 1986) were most available, individuals significantly reduced their use of this tactic (and devoted more time to cropping) when large tiger sharks were most abundant, presumably because the process of excavation inhibits vigilance and may even attract predators. Thus, I conclude that dugongs manage their risk of death by avoiding a profitable but risky feeding tactic when the likelihood of predator encounter is elevated.

Previous work has shown that tropical seagrass species are sparsely distributed, of low biomass, and generally unavailable during months when water temperatures are

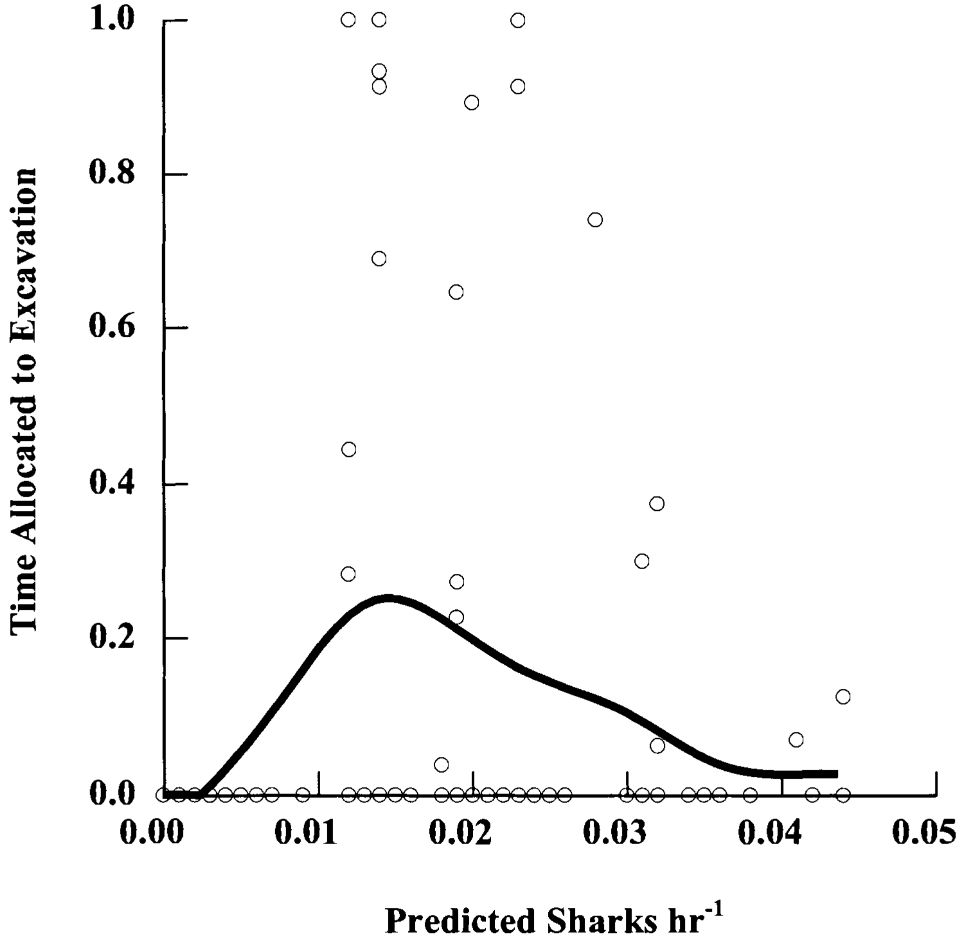

**Figure 6.3 Time allocated to excavation foraging by dugongs versus large tiger shark catch rate**

Relationship between the proportion of time allocated to excavation foraging in shallow habitat (< 4.5 m in depth) by dugongs during focal follows ($n$ = 92) and predicted large (> 3 m) tiger shark catch rate (h$^{-1}$). Note that days on which predicted shark catch rates fell below ~ 0.010 were always associated with water temperatures < 20°C (i.e., excavation was only observed during months when tropical seagrass were available for harvest, February – May of all y).

below 20°C in the study area (Walker and McComb 1988; Walker et al. 1988). In accord with my assumption that dugongs use excavation to target these rare but nutritious species, I found that foragers tended to use this tactic in seagrass patches where the presence of tropical species has been documented (Walker et al. 1988), generally devoted little time to excavation while harvesting seagrass, and ceased using excavation between June and October. The comparatively heavy use of excavation by dugongs during the latter stages of the warm season (i.e., mid-April through May), when tropical seagrass species are still available and tiger shark abundance has dropped to intermediate levels (Chapter 2), suggests that foragers would likely spend more time harvesting the energy-rich rhizomes of these species throughout the warm season, despite their relative scarcity, were it not for the influence of risk from tiger sharks.

I was unable to determine whether dugongs under focal observation excavated seagrass while foraging in deep habitat. This methodological shortcoming could have biased the results presented herein if episodes of deep water excavation were missed frequently. I am confident, however, that use of this tactic was largely restricted to the shallows because (i) the tropical seagrass species putatively targeted by dugongs using this tactic are found primarily in shallow habitat (Anderson 1986; Walker et al. 1988), (ii) sediment plumes that often accompany excavation were never witnessed during observations of individuals feeding in deep water (even when water clarity was excellent and conditions were calm), and (iii) deep habitat foraging was relatively infrequent (i.e., < 10% of total foraging time; Fig. 6.2) during periods when excavation was used most often in the shallows (mid-April – May).

Despite marked variation in the abundance of their major local predator, on average dugongs budgeted approximately half of their time to foraging over the course of this investigation. This result, which is consistent with the findings of several previous dugong tracking studies (e.g., Churchward 2001; Chilvers et al. 2004), may mean that these sirenians do not sacrifice diurnal feeding time in order to be more vigilant during periods of high mortality risk. Dugongs may be unable to dramatically alter their feeding schedule given the generally poor quality of their diet (Best 1981; Marsh et al. 1984) and the fact that their relatively slow rate of digestion likely limits the amount of seagrass that can be ingested (Lanyon and Marsh 1995).

In a companion study based on data collected using transects (Chapter 4), I found that foraging dugongs shifted to deep habitats during periods when tiger shark abundance was elevated. Deep habitats in the study area offer increased safety from sharks (Heithaus et al. 2002), but only a fraction of the seagrass biomass available in shallow patches (Chapter 4). Thus, I concluded that this habitat shift represents an exchange of food for safety. Here, using data collected during focal observations, I present further evidence suggesting that dugongs manage their risk of mortality via adaptive habitat switching: though much of the individual variation in deep habitat foraging time I observed could not be explained by the model, the extent to which foragers used deep habitat was directly related to the abundance of tiger sharks, rather than to water temperature.

Predators often select unwary prey (Krause and Godin 1996). For prey animals that have been targeted, even slight delays in escape can mean the difference between life and death (Kaby and Lind 2003). Thus, in general, we would expect prey individuals to reduce their use of foraging tactics that, by virtue of their complexity or the body position they require, inhibit antipredator vigilance when the likelihood of predatory attack is high. Dugongs seem to conform to this expectation: individual foragers relied less on excavation, a tactic that enables dugongs to access the nutritious rhizomal portions of tropical seagrass species but precludes frequent scans of the environment, when large tiger sharks were abundant. This predator-mediated shift in the use of alternative foraging tactics by dugongs is noteworthy, as previous inquiries have discussed the feeding modes of this sirenian solely in relation to the availability of various seagrass species (e.g., Anderson and Birtles 1978; Anderson 1982; Anderson 1986; Preen 1995). It also has important implications for the relationship between dugongs and the seagrass meadows upon which they subsist. Excavation feeding by dugongs can radically disrupt the structure of seagrass meadows, leaving deep furrows and denuded patches that promote succession (de Iongh et al. 1995; Preen 1995; Nakaoka and Aioi 1999; Masini et al. 2001). In contrast, dugongs engaged in cropping are believed to be less disruptive as they only remove the terminal portions of seagrass plants, leaving the rhizomes intact (Anderson 1986). Thus, by influencing the time dugongs allocate to these two tactics, tiger sharks may exert a strong indirect influence on the dugong's food (i.e., the seagrass beds themselves). During periods when an abundance of sharks forces dugongs to allocate relatively high amounts of time to cropping, for example, the extent to which dugong feeding facilitates the intrusion of pioneering seagrass species may decline markedly. I surmise, then, that alterations in the dynamics of tiger shark populations where this predator coexists with dugongs are likely to have a profound effect on the composition of local seagrass meadows and, ultimately, benthic community structure and function.

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# Chapter 7

# General Conclusions

## 7.1 Discussion

Traditionally, behavioural studies focused on large marine mammals have been hindered by logistical obstacles and the tendency of these species to range widely and spend little time at the surface (Bowen 1997). Thus, little is known about the space use and foraging behaviour of most marine mammal species, especially in the context of predation risk. This thesis provides a rare demonstration of predation-sensitive foraging behaviour in a marine mammal, the dugong, and, to my knowledge, the only such example involving a marine mammal herbivore.

Dugongs adjusted their foraging behaviour at three spatial scales in a manner consistent with mortality risk reduction during periods of heightened danger: when large tiger sharks were abundant, individual foragers (i) increased their use of safe but relatively impoverished deep habitats (i.e., manifested a habitat switch on the order of 100s of m to several km; Chapter 4), (ii) increased their use of safe but low-quality microhabitats (feeding sites) along the edges of shallow seagrass meadows (i.e., manifested microhabitat switches on the order of 10s of m; Chapter 5), and (iii) increased their use of a foraging tactic, cropping, that allows for simultaneous anti-predator vigilance (i.e., switched foraging tactics at feeding sites; Chapter 6). Use of an array of behavioural responses may allow prey species to minimize the sublethal effects of predation danger on their feeding while incurring only a small increase in mortality risk (Holbrook and Schmidt 1988). It is noteworthy that other vertebrates in Shark Bay also appear to utilize a diversity of anti-predator behaviours over multiple spatial scales. For example, Indian Ocean bottlenose dolphins (*Tursiops* sp.) employ habitat shifts (Heithaus and Dill 2002), microhabitat shifts (Heithaus and Dill, *in review*), and shifts between foraging tactics at feeding sites (Sargeant 2005) to cope with the threat of tiger shark attack. Similarly, green sea turtles (*Chelonia mydas*) adjust both their use of safe and dangerous foraging microhabitats (Heithaus et al., *in review*) and their dive profiles (A. Frid and M. R. Heithaus, *unpublished material*) to reduce their probability of tiger shark-induced mortality. Thus, anti-predator behaviour characterized by marked spatial and temporal flexibility may be common in marine systems. By extension, failure to detect responses to predators at a particular scale in these systems should not be used as a basis for ignoring the influence of predation risk.

Changes in patterns of dugong foraging at the habitat, microhabitat, and tactical level that are induced by predators all have the capacity to influence the biomass and composition of seagrass meadows. For example, when dugongs avoid productive but perilous shallow habitats, seagrass meadows growing in these areas are likely to experience reduced herbivory. Such periods of relaxed dugong herbivory are in turn likely to foster the recovery of over-harvested seagrass species, and impede the growth and establishment of species that rely on disturbance. Similarly, dangerous interior portions of seagrass meadows (feeding microhabitats) that are avoided by dugongs during periods of shark abundance are likely to be exploited less heavily than seagrass meadow peripheries (i.e., edge microhabitats), which provide added safety. Consequently, over the course of a year, interior and edge microhabitats are likely characterized by different patterns of seagrass colonization, growth, and persistence, yielding heterogeneity that might not otherwise exist within seagrass meadows. Finally, given that dugongs engaged in cropping and excavation affect seagrass differently (Anderson 1986), variation in the use of these two tactics elicited by the presence of tiger sharks likely results in spatial and temporal patterns of seagrass removal that differ from those caused by dugongs in areas where these predators are rare or absent. Thus, by inducing changes in dugong foraging at each of these spatial scales, tiger sharks likely exert a powerful indirect influence on Shark Bay's seagrass meadows and, ultimately, on the diverse fauna these meadows support.

In terrestrial systems, community changes have been linked to the consumption and intimidation of important prey species by apex predators. For example, predation by arctic foxes (*Alopex lagopus*) introduced to the Aleutian archipelago appears to have triggered reductions in seabird abundance, which in turn reduced the rate of nutrient transfer from sea to land and, ultimately, converted the islands from grasslands to maritime tundra (Croll et al. 2005). The reintroduction of wolves (*Canis lupus*) to Yellowstone National Park has altered the foraging behaviour of resident ungulates, leading to dramatic changes in the structure of the Park's plant communities (Fortin et al. 2005). In marine environments, community changes have been linked to the consumptive effects of top predators as well. For instance, consumption of sea otters (*Enhydra lutris*) by killer whales (*Orcinus orca*) in nearshore communities off western Alaska may have released sea urchin populations, leading to the impoverishment of kelp forests (Estes et al. 1998). However, examples of changes in community structure triggered by behavioural responses to apex predators are absent from the marine literature, despite the likelihood that these changes are common (Dill et al. 2003). The paucity of such examples stems largely from the fact that few investigations of the behaviour of prey under risk of predation have been conducted in marine settings, especially where large vertebrate prey species are concerned. Using standardized sampling methodology and a behavioural ecology framework, I showed that tiger sharks affect the foraging decisions of one of Shark Bay's primary herbivorous vertebrates, the dugong. Thus, documentation of risk-averse behaviour by large marine vertebrates is possible if rigorous research approaches are employed in tractable systems. Similar research approaches have demonstrated that tiger sharks alter the behaviour of other locally abundant herbivores (e.g., green sea turtles) and piscivores as well. Thus, I suggest that studies of the possible indirect effects on seagrass and fishes that Shark Bay's tiger sharks transmit through their prey are likely to reveal much about the role of apex predators in marine ecosystems.

The dugong is an imperilled species, having been reduced or extirpated throughout much of its range (Preen 1998). Thus, there is great interest in its conservation. To date, efforts to manage and predict the viability of dugong populations have focused on the protection of seagrass habitat (Preen 1998) and the mitigation of anthropogenic impacts (e.g., harvest, Heinsohn et al. 2004); the effects of predation have not been addressed. The results of this thesis have three major implications for the conservation of dugongs. First, my results suggest that areas designated as dugong protection zones should incorporate not only feeding habitats (i.e., seagrass meadows) but also habitats providing refuge from large predators like tiger sharks (i.e., deep channels). Second, my results suggest that dugong population viability models would benefit from the inclusion of metrics of predation risk (possibly indexed in terms of predator abundance), since individual anti-predator decisions can have important consequences at the population level (Lima and Dill 1990), and that models failing to include such information must be interpreted with caution. Third, my results suggest that boat traffic should be controlled in areas used by dugongs, given that the approach of a marine vessel may elicit costly anti-predator behaviour in much the same way as attacks by predators (e.g., termination of feeding bouts and/or the abandonment of productive feeding areas; see Frid and Dill 2002).

Large sharks, too, are experiencing a global decline (Baum et al. 2003). Though interest in their conservation is growing, data required to underwrite effective protective measures are lacking (Kohler and Turner 2001). In Chapter 2, I show that large shark numbers within particular areas can be characterized by dramatic and temporally patterned fluctuations, implying that regional efforts designed to effectively monitor large shark populations must be based on intensive and long-term census methods rather than short-term investigations involving infrequent and non-standardized surveys. Then, in Chapter 3, I demonstrate that large shark abundance can be influenced heavily by both water temperature and the availability of particular prey types. Thus, measures of these two variables should be used to help predict the viability of imperilled large shark populations.

Marine ecosystems have been heavily modified by humans, and the pace at which anthropogenic disturbance is altering these systems seems to be increasing (Jackson et al. 2001; Western 2001). Consequently, there is great pressure on ecologists and conservation biologists to predict the effects of human activities on marine environments. The results presented in this thesis warrant such a prediction. Namely, changes in the size and dynamics of Shark Bay's tiger shark population induced by humans, courtesy of global warming and/or overfishing, will undoubtedly elicit alterations in the foraging behaviour of prominent local herbivores like dugongs and, potentially, a cascade of indirect ecosystem effects. Clearly, therefore, the persistence of Shark Bay's pristine seagrass ecosystem, as well as the restoration of more exploited seagrass communities elsewhere, will depend on the existence of intact populations of apex predators and the herbivores on which they subsist.

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