State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem

MICHAEL R. HEITHAUS, ALEJANDRO FRID*, AARON J. WIRSING*, LAWRENCE M. DILL*, JAMES W. FOURQUREAN†, DEREK BURKHOLDER, JORDAN THOMSON* and LARS BEJDER‡

*Department of Biological Sciences, Marine Biology Program, Florida International University, Biscayne Bay Campus ACI 371, 3000 NE 151 St, North Miami FL 33181, USA; *Behavioural Ecology Research Group, Department of Biological Sciences, 8888 University Drive, Simon Fraser University, Burnaby, BC V5A 1S6, Canada; †Department of Biological Sciences, Florida International University, 11200 SW 8th St, Miami FL 33199, USA; and ‡Department of Biology, Dalhousie University, Halifax, NS B3H 3J5, Canada*

Summary

1. A predictive framework of community and ecosystem dynamics that applies across systems has remained elusive, in part because non-consumptive predator effects are often ignored. Further, it is unclear how much individual-level detail community models must include.

2. Previous studies of short-lived species suggest that state-dependent decisions add little to our understanding of community dynamics. Body condition-dependent decisions made by long-lived herbivores under risk of predation, however, might have greater community-level effects. This possibility remains largely unexplored, especially in marine environments.

3. In the relatively pristine seagrass community of Shark Bay, Australia, we found that herbivorous green sea turtles (*Chelonia mydas* Linnaeus, 1758) threatened by tiger sharks (*Galeocerdo cuvier* Peron and LeSueur, 1822) select microhabitats in a condition-dependent manner. Turtles in poor body condition selected profitable, high-risk microhabitats, while turtles in good body condition, which are more abundant, selected safer, less profitable microhabitats. When predation risk was low, however, turtles in good condition moved into more profitable microhabitats.

4. Condition-dependent use of space by turtles shows that tiger sharks modify the spatio-temporal pattern of turtle grazing and their impacts on ecosystem dynamics (a trait-mediated indirect interaction). Therefore, state-dependent decisions by individuals can have important implications for community dynamics in some situations.

5. Our study suggests that declines in large-bodied sharks may affect ecosystems more substantially than assumed when non-lethal effects of these top predators on mesocon-sumers are not considered explicitly.

Key-words: marine conservation, non-lethal predator effects, predation risk, state-dependent behaviour, trait-mediated indirect effects (TMII).

Introduction

Interactions within communities and ecosystems are complex, and ecologists have struggled to develop frameworks for predicting their dynamics across systems and taxa. Part of the difficulty may be due to a lack of a functional understanding of relationships within communities (Ovadia & Schmitz 2004), such as non-consumptive effects of predators (Dill *et al.* 2003; Schmitz *et al.* 2004; Schmitz 2006). These non-lethal effects – which include prey changing their habitat use, activity level or diet – are pervasive in natural communities. A growing literature suggests that they may have greater impacts on prey populations than lethal effects

Correspondence: Michael Heithaus, 3000 NE 151 St, North Miami, FL 33181, USA. Tel.: +1 305 919 5234. Fax: +1 305 919 5896. E-mail: heithaus@fiu.edu

due to their propensity to affect many individuals within prey populations simultaneously (Werner & Peacor 2003; Preisser *et al*. 2005). Furthermore, transmission through food webs of non-lethal effects of predators (trait-mediated indirect interactions, TMII) may be stronger than the transmission of lethal effects (density-mediated indirect interactions) (see Preisser *et al*. 2005 for a review). However, tests of these ideas in complex natural communities are few. Therefore new data on the importance of TMIIs in diverse communities should aid in generating a general theory of community dynamics.

The development of a general predictive framework for community dynamics has also been limited by not knowing how much individual-level detail should be included in community models. Ovadia & Schmitz (2002, 2004) addressed this question by investigating whether knowledge of size-related differences in risk-taking by grasshoppers foraging under the risk of spider predation improved models of community dynamics. They found that, although grasshoppers adjusted foraging effort in a size-dependent manner, details on size-dependent decisions did not enhance predictions about community dynamics (grasshopper impacts on vegetation mediated by risk from spiders) (Ovadia & Schmitz 2002, 2004). However, the results of the grasshopper study may apply primarily to short-lived or semelparous species (Ovadia & Schmitz 2002, 2004). It is likely that long-lived, iteroparous species would be more risk-averse than grasshoppers (Warner 1998), and state-dependent decisions made under the risk of predation are more likely to have community-level effects. Also, state variables other than body size influence foraging–predation risk trade-offs, and variables that operate in all size and age classes of a population, such as energetic state, may be of greater importance in structuring communities (Luttbeg *et al*. 2003). Field studies have yet to address the effect of state-dependent risk-taking decisions on community dynamics (but for theoretical treatments see Luttbeg *et al*. 2003; Frid *et al*. 2006).

Behavioural ecologists have long been interested in the trade-off between foraging opportunities and the risk of predation. This interest stems in large part from widespread recognition that the behaviour of consumers under risk of predation can cause (and provide insights into the potential importance of) top-down effects that may shape spatial distributions and limit prey population sizes. In general, forager populations are unlikely to be influenced solely by bottom-up forces when individuals are willing to give up energy in order to be safe (through reduced activity levels, increased giving-up densities, selection of energy-poor but safe habitats for foraging, or restricting foraging locations or times: Houston *et al*. 1993; Walters & Juanes 1993; Brown 1999; Kotler *et al*. 2004; for a review see Brown & Kotler 2004). Top-down effects of predators on prey populations are enhanced when individuals in poor condition take greater risks in order to obtain greater foraging gains (condition-dependent risk taking: McNamara & Houston 1987, 1994; Anholt & Werner 1995; Sinclair & Arcese 1995;

Nelson *et al*. 2004). Therefore predators may influence community dynamics indirectly through condition-dependent risk-sensitive foraging by their prey, which would modify the overall intensity and spatio-temporal pattern of resource exploitation.

Since 1997, we have used Shark Bay, Western Australia as a model system for understanding the importance of non-consumptive effects of tiger sharks (*Galeocerdo cuvier*), including TMII, in a relatively undisturbed seagrass community. Here tiger sharks are predators on a variety of large vertebrates, including herbivorous green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon* Müller 1776) (Heithaus 2005; Heithaus & Dill 2006; Wirsing *et al*. 2007). Because there is marked temporal variation in shark abundance while the abundance of many of their prey species remains relatively constant, we are able to use temporal variation in risk as a natural experiment to assess the importance of predation risk in shaping consumer behaviours (*sensu* Biro *et al*. 2005). Given that green turtles are long-lived, suffer relatively low mortality rates, and can modify seagrass communities and nutrient composition as well as detrital cycles (Bjorndal 1980, 1997; Aragones 2000; Aragones *et al*. 2006), their condition-dependent variation in habitat use when threatened by predators could influence community and ecosystem dynamics.

Materials and methods

NATURAL HISTORY

The study was conducted in the relatively pristine Eastern Gulf of Shark Bay, Western Australia (*c*. 25°45′S, 113°44′E) (Fig. 1), which contains offshore subtidal seagrass beds (usually <4·0 m deep) covered primarily by the seagrass *Amphibolis antarctica* Labillardière and occasionally *Posidonia australis* Hooker 1858. The rest of the study area is deeper (generally 6·0–12·0 m) with little seagrass cover. There is a large population of green turtles in the study area that is not subject to substantial anthropogenic influences. Tiger sharks are the only predator on adult turtles in the area, but shark abundance fluctuates seasonally (Heithaus *et al*. 2002, 2005; Wirsing *et al*. 2006). Studies conducted concurrently with turtle sampling revealed that tiger sharks are abundant in summer (Septmber–May), but rare or absent during the winter (June–August) (Wirsing *et al*. 2006).

Spatial variation in predation risk (the 'landscape of fear': Laundré *et al*. 2001) is influenced by predator encounter rates, intrinsic habitat risk (probability of prey death in an encounter situation; Lima & Dill 1990), and antipredator behaviour. Therefore it is best assessed using consumer behaviour (Brown & Kotler 2004). Risk from tiger sharks, to turtles and other species, is higher in shallow habitats than in deep ones within the study area (Heithaus & Dill 2006; Heithaus *et al*. 2006), but risk also varies across microhabitats within shallow habitat patches. Risk is highest in the middle of shallow banks (interior microhabitats far from bank edges) due
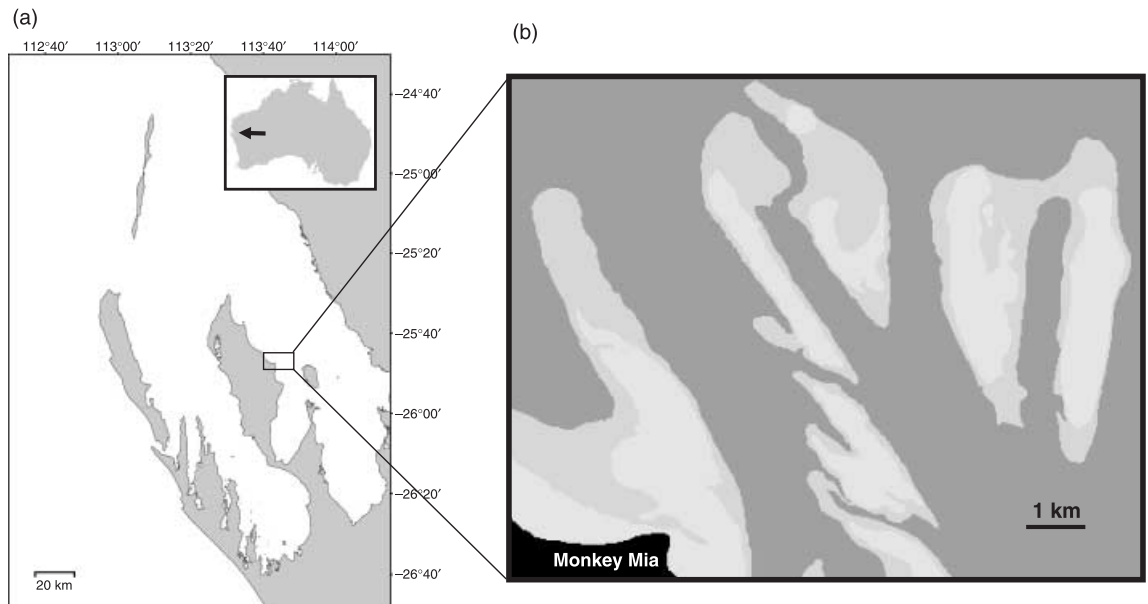
Fig. 1. The study was conducted in Shark Bay, Western Australia (a). Turtles were captured on shallow banks offshore of Monkey Mia (b). Shading represents waters at >4·5 m (dark grey); 4·5–2·0 m; <2·0 m (light grey); land is black.

to a lack of escape routes, and long distances to deeper water where turtles can outmanoeuvre tiger sharks (Heithaus *et al.* 2002, 2006; Heithaus 2004); this pattern of risk is supported by predation-sensitive microhabitat shifts in both dugongs and bottlenose dolphins (*Tursiops aduncus*) (Wirsing *et al.* 2007; Heithaus & Dill 2006), which use escape tactics similar to turtles (bursts of speed with very sharp turning manoeuvres). While foraging, both these species increase their use of edges relative to interior areas (corrected for spatial and temporal variation in food availability) as the density of tiger sharks in the study area increases (Heithaus & Dill 2006; Wirsing *et al.* 2007).

The biomass of *A. antarctica*, which is the primary forage available to turtles in the study area, is similar between edge and interior microhabitats of banks (Wirsing *et al.* 2007).

Forage quality, however, varies spatially (Table 1). Inorganic carbon appears to be avoided by green turtles, while organic C and nitrogen are nutritionally important (Thayer *et al.* 1984). In our study area, the leaves of *A. antarctica* plants found along bank edges have higher inorganic C content, but lower organic C content, than those in the middle of banks. Thus turtles must select

whether to forage in microhabitats far from bank edges that are high in both food quality and predation risk, or in low-quality but low-risk microhabitats along the edges of banks. Based on state-dependent theory, we predicted that, during months when tiger sharks were abundant, turtles in relatively good condition would forage along bank edges, while turtles in relatively poor condition would accept higher predation risk far from the edges of banks in order to forage on higher-quality seagrass. Furthermore, we predicted that when shark abundance was lower, this pattern would be relaxed and turtles in good condition would move further from bank edges to take advantage of high-quality resources.

FIELD METHODS AND ANALYSIS

Turtles were captured by hand from March 1999– August 2006 during routine transect surveys of the study area and during searches of relatively shallow waters (Heithaus et al. 2002, 2005). Turtles were brought alongside the capture boat and their curved carapace length (CCL) was measured before they were individually tagged. Turtles were assigned to one of four condition classes based on external characteristics (Fig. 2). Turtles were considered to be in 'poor' condition when their undersides were extremely concave. These individuals also tended to exhibit sunken eyes and reduced body mass around the neck and base of the foreflippers, and were easily captured due to their slow escape responses. Turtles in 'fair' condition had concave or slightly concave undersides, but were usually active during capture, and other body parts were not obviously in deteriorating condition. Turtles in 'good' condition had flat undersides; turtles in 'very good' condition had convex undersides. This condition index has been validated by comparing field

Table 1. MANOVA results of arcsin-transformed data on the chemical composition of *Amphibolis antarctica* leaves within edge and interior microhabitats of shallow seagrass banks, collected at 40 sites during September 2004

Chemical composition	Edge (mean ± SE)	Interior (mean ± SE)	F	P
Nitrogen (%)	1·0 ± 0·03	1·1 ± 0·05	1·93	0·17
Inorganic carbon (%)	4·6 ± 0·2	3·7 ± 0·3	4·46	0·04
Organic carbon (%)	22·9 ± 0·8	26·0 ± 1·2	4·23	0·04

C and N content were determined with an elemental analyser (Fisons NA 1500). Organic C content was determined by subtracting the C content of the ash remaining after combusting the sample at 500 °C from the total C content.
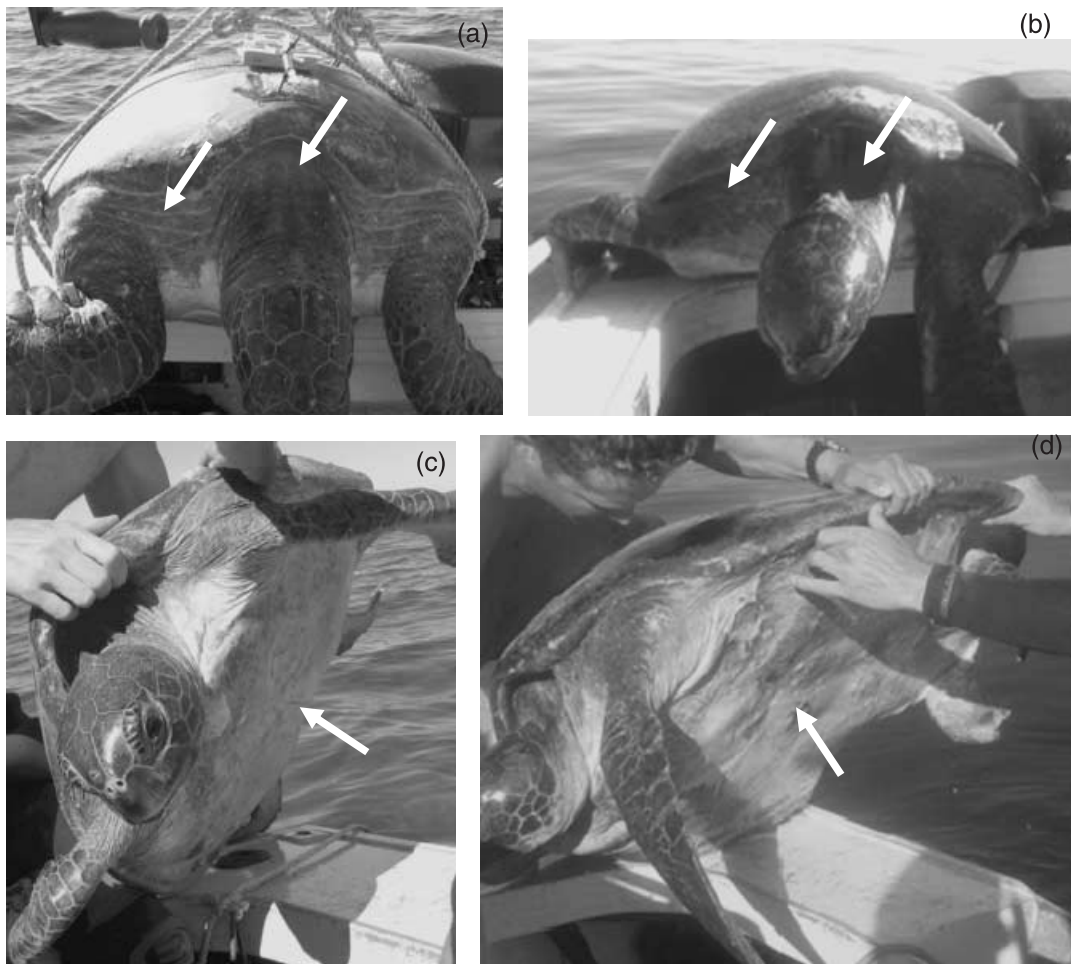
Fig. 2. Comparison of turtles in (a) very good condition (convex underside and large fat reserves near neck); (b) poor condition (very concave underside, deteriorated condition around neck). Comparison of ventral surfaces of a green turtle in (c) good condition (flat underside); (d) poor condition (very concave underside).

measurements of body condition index (mass/CCL3; Bjorndal et al. 2000) to our condition classifications, assigned before masses were measured, for a subset of 38 green turtles (J.T., unpublished data).

During the winters of 1999–2005, tiger sharks were caught in low numbers during the austral winter, but none was captured in the winter of 2006 (Wirsing *et al.* 2006). We did not analyse the winter months of 2006 separately because of relatively low sample sizes (*n* < 10) for turtles in good, poor and fair condition during the months when no sharks were present. Therefore we defined two seasons based on monthly average shark catch rates ('low', <0·03 sharks per bait h and 'high', >0·03 sharks per bait h). Because we had an adequate sample size for turtles in very good condition, which should be most responsive to changes in the intensity of predation risk (Clark 1994; Clark & Mangel 2000; Luttbeg *et al.* 2003), we conducted a companion analysis of their microhabitat selection with seasons broken into high (>0·03 sharks per bait h), low (>0, <0·03 sharks per bait h), and very low (0 sharks per bait h) shark abundance.

Analyses included only turtles that were captured within the shark study area, excluding turtles captured in near-shore shallows primarily covered by sand. Also, we

used only the first capture of an individual within the restricted study area in analyses of microhabitat use, leaving 138 turtles for analysis (15 adult males and 123 females and juvenile males, which cannot be easily distinguished in the field). We mapped the location of each turtle into a GIS (MapInfo, MapInfo Corp., Troy, NY) and measured the distance between the turtle's position and the bank edge, defined as the point at which water depth exceeded 4·5 m. Condition was treated as an ordinal variable, and we used ANOVA on $\log(x + 1)$-transformed distance-from-edge data to determine the effects of condition and relative shark density on the distance turtles were found from edges.

Results

Turtle condition was dynamic over periods of weeks to months. Of 34 turtles recaptured, the condition of 18 did not change, nine had lost condition, and seven had improved their condition. None of six turtles recaptured within 14 days had changed in condition, but two of seven (28·6%) recaptured after 15–30 days were in a different condition category, as were seven of 10 (70%) and seven of 11 (63·6%) turtles recaptured after 31–180 and 181–2197 days, respectively.
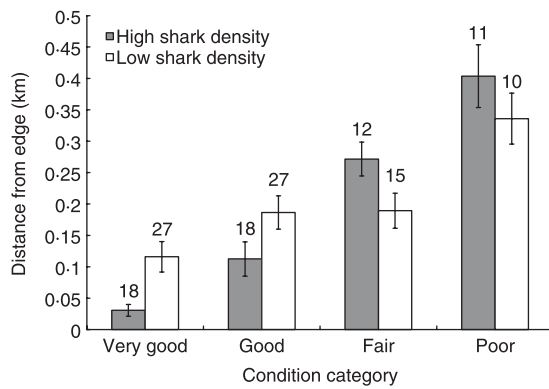
Fig. 3. Mean distances from turtle locations to bank edges (4·5-m isobath). Areas further from bank edges are more dangerous and have higher-quality seagrass. Error bars ± SE. Numbers over bars are sample sizes.
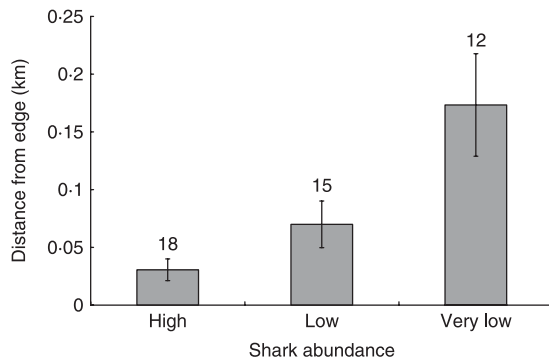

Fig. 4. Mean distances from turtle locations to bank edges (4·5-m isobath) for turtles in very good condition broken down into periods of high (>0·03 sharks/h), low (<0·03 sharks/h) and very low (0 sharks/h) shark-catch rates. Error bars ± SE. Numbers over bars are sample sizes.

Turtles in better condition were found closer to bank edges than those in poorer condition ($F_{3,137} = 32\cdot3$, $P < 0\cdot0001$), but the strength of this trend was much stronger when tiger sharks were abundant than when they were relatively scarce (condition × shark density, $F_{3,137} = 4\cdot4$, $P = 0\cdot005$). Turtles in fair and poor condition did not greatly change their relative distance from the edges of banks as shark density increased, while turtles in very good and good condition moved closer to edges when sharks were more abundant (Fig. 3). When data for good-condition turtles were partitioned into seasons when sharks were absent, present in low numbers, and present in high numbers, there was a continuous pattern of increasing distance from bank edges as shark abundance increased ($F_{2,44} = 8\cdot4$, $P = 0\cdot0008$; Fig. 4). There was no relationship between turtle CCL and distance at which turtles were found from banks ($F_{1,135} = 0\cdot02$, $P = 0\cdot89$), or between CCL and turtle condition ($F_{1,137} = 1\cdot7$, $P = 0\cdot19$).

Two individuals were recaptured in the same condition, but in different seasons of shark abundance. In both cases, the turtles were further from bank edges when shark abundance was low than when sharks abundance was high. Two other individuals were recaptured during periods of high shark abundance, but in different conditions. The first was captured in fair condition 0·35 km from the edge, but was in good condition and 0·2 km from the edge 80 days later. After another 164 days, the turtle was in poor condition and 0·58 km from the edge. The second individual was captured twice in fair condition 0·24 and 0·25 km from the edge. Twenty-seven days later, it was captured in poor condition and 0·44 km from the edge.

Discussion

The use of microhabitats by green turtles in Shark Bay was consistent with a predicted condition-dependent response to the trade-off between foraging rewards and predation risk, and not consistent with alternative explanations (Appendix S1, see Supplementary material). When tiger sharks were abundant, turtles in poor condition were found far from bank edges, where both seagrass quality and the risk of tiger shark predation are greater, while more turtles, especially those in very good condition, were found in safer habitats with lower forage quality. Moreover, turtles in good condition moved into areas of higher food quality, far from bank edges, when shark abundance dropped: turtles in good condition were found more than twice as far from bank edges during months of low shark density than they were when shark abundance was high, and five times as far from bank edges during months when sharks were at very low densities. Also, all four individuals recaptured during the study shifted their distances from the edges of banks in accordance with predictions. Finally, changes in the body condition of individual turtles occurred over relatively long periods (weeks) rather than over individual foraging bouts, suggesting that changing body condition is due to long-term behavioural tactics rather than short-term ones (e.g. vigilance over the course of a foraging bout). Recently developed GPS tags, which allow fine-scale tracking of individual movements (Schofield *et al.* 2007), could provide even more detailed information on condition-dependent behaviour (e.g. residence times in microhabitats) and how individual turtles modify their use of microhabitats in response to changes in their body condition.

Condition-dependent predation risk-sensitive decisions by turtles suggest that predation risk from tiger sharks influences turtle population sizes, and thus the overall intensity of turtle herbivory. The predation-sensitive food hypothesis (McNamara & Houston 1987, 1994) predicts that both food and predators will limit prey populations because, as food becomes limiting, individuals in poor condition will take greater risks when foraging and suffer high predation rates (e.g. wildebeest, *Connochaetes taurinus*, Sinclair & Arcese 1995; vertically migrating copepods, *Metridia pacifica*, Hays *et al.* 2001). This may lead to differential effects of predation within turtle populations. For example, green turtles, especially females, returning to foraging grounds after breeding, are likely to be in poorer condition than individuals

that remained in feeding areas (Hays *et al.* 2002). Thus these post-reproductive turtles may be forced to take greater risks to improve their condition, and suffer higher mortality from predators as a result. However, turtles need not incur higher predation rates when in poor condition for tiger sharks to influence their population size through non-lethal mechanisms. If access to food limits turtle populations, as has been assumed implicitly in previous studies (Jackson *et al.* 2001), then turtles giving up foraging opportunities or high-quality food to be safe would lead to reduced population sizes through non-lethal (behavioural) mechanisms (Walters & Juanes 1993; Nelson *et al.* 2004; Creel *et al.* 2007).

Green turtles are long-lived and suffer low predation rates, while tiger sharks have diverse diets and low feeding rates. Thus predator-inflicted mortality and possible density-mediated indirect effects of tiger sharks are probably modest. In contrast, condition-dependent decisions by green turtles probably result in TMII playing a prominent role in community and ecosystem dynamics in Shark Bay. Turtle cropping can alter the community composition of seagrasses, and alters ecosystem dynamics by short-circuiting the detrital cycle and modifying seagrass chemical composition (Bjorndal 1980; Aragones 2000; Aragones *et al.* 2006). The reduced organic C content and increased inorganic content of segrasses along the edges of banks, relative to interior areas, may be attributable to intense herbivory by turtles in very good and good condition (Bjorndal *et al.* 2000). In contrast, seagrass communities in the middle of banks experience relatively low grazing pressure, at least when sharks are present. Grazing in these areas during high-risk periods is by turtles in poor condition, which represent only 7% of individuals in the study area (Heithaus *et al.* 2005). The apparent TMII between sharks and seagrasses would be enhanced in Shark Bay by predation-sensitive foraging by dugongs (another long-lived megaherbivore), which shift their foraging locations from interior to edge microhabitats as shark density increases (Wirsing *et al.* 2007). TMII involving sharks could be transmitted further through the ecosystem because changes in the structure of seagrass communities and detrital cycles may affect the community of resident small-bodied consumers (Hyndes *et al.* 2003).

Previous studies have sought to determine the level of individual detail necessary for understanding community dynamics. It has become increasingly apparent that community models can benefit greatly from the inclusion of non-consumptive effects of predators (Bolker *et al.* 2003). Indeed, the similarity in the dynamics of the predator–herbivore systems in Shark Bay, and terrestrial systems involving interactions between wolves and moose, and between grasshoppers and spiders (Schmitz 2006), is striking and suggests that simple behavioural rules apply across systems and are important to the dynamics of communities in general. However, the general importance of state-dependent decisions in community and ecosystem dynamics is still a matter of debate. Studies of a short-lived species (grasshoppers) suggest that state-

dependent decisions made under risk of predation may not add significantly to our understanding of communities (Ovadia & Schmitz 2002, 2004). However, the brief period available for grasshopper development and reproduction may reduce the community-level effects of their state-dependent decisions. Our results suggest that condition-dependent behaviour by long-lived species may be more likely to influence community dynamics, and that the importance of understanding individual decisions for making predictions about community dynamics may vary with life-history traits (e.g. longevity, parity). Consequently, further consideration is needed of the types of state variables, life-history characteristics and general ecological conditions that produce community- and ecosystem-level effects.

Our results have important implications for the conservation and management of marine ecosystems. Recent studies have revealed that marine communities have been greatly modified by human activities in modern and historical times (Jackson *et al.* 2001; Lotze *et al.* 2006). One of the most conspicuous changes is the dramatic decline, and sometimes ecological extinction, of 'highly interactive species', including large herbivores and top predators such as sharks (Jackson *et al.* 2001; Baum *et al.* 2003). Yet there are few empirical data regarding the ecological role of large sharks (but see Heithaus 2004; Myers *et al.* 2007), and few empirical studies of the possible impacts of predators on population sizes of large marine herbivores and their spatial patterns of grazing.

Here, taking advantage of a rare opportunity to study interactions between relatively intact populations of sharks and a large marine herbivore, we have demonstrated the importance of tiger sharks in shaping turtle behaviour and, probably, turtle populations. Given the antipredator responses of turtles, dugongs and other tiger shark prey species in Shark Bay (Heithaus 2005; Heithaus & Dill 2006; Wirsing *et al.* 2007), it is likely that tiger sharks play a critical role in marine ecosystems through multiple TMII. By extension, the reductions of large-bodied shark populations in other areas of the world would be predicted to have substantial community-level consequences. Indeed, some of the recent increases in turtle populations around the world (Balazs & Chaloupka 2004) may have been facilitated by reductions in shark populations that would allow turtles to forage free of energy intake–predation risk trade-offs. While such rebounds in populations may appear to be beneficial for turtle populations in the short term, the community and ecosystem consequences of unrestricted grazing without the spatial variation in herbivory that might be imposed by predation risk remain unclear. The loss of turtle predators could result in negative impacts on seagrass beds. Indeed, recent declines in seagrasses offshore of Bermuda may be linked to increases in turtle populations (Murdoch *et al.* 2007) that coincide with steep declines in tiger shark populations in the same region (Baum *et al.* 2003). Together, these findings suggest that recent declines in large shark populations may have more widespread ecological impacts than are

generally appreciated, and conservation strategies should explicitly consider the potential lethal and non-lethal effects of sharks, both direct and indirect.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Evidence against alternative explanations for state-dependent habitat use by green turtles.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01260.x

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