

## The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem

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**Abstract.** The worldwide decline of large-bodied marine taxa has made it difficult to draw conclusions about the relative importance of top-down control, and the mechanisms through which it might operate, in coastal marine ecosystems. Since 1997, the Shark Bay Ecosystem Research Project has used the relatively pristine seagrass community of Shark Bay, Australia, to investigate the potential for tiger sharks, the apex predator in the ecosystem, to have an impact on their large-bodied prey through non-consumptive ('risk') effects. Here, we synthesise nearly 15 years of data to demonstrate that tiger sharks have widespread risk effects on both large-bodied herbivores and mesopredators in Shark Bay and explore the possibility that these impacts may cascade to lower trophic levels. Although much work remains to be done, our studies suggest that losses of top predators in subtropical estuaries may have greater consequences than generally appreciated and that efforts to conserve and restore their populations should be a priority. Furthermore, future management strategies and studies must explicitly consider the potential for predators to influence behaviour of even large-bodied marine taxa.

**Additional keywords:** behaviourally mediated indirect species interactions (BMII), community dynamics, dugong, Indo-Pacific bottlenose dolphin, non-consumptive effects, risk effects, tiger shark.

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### Introduction

Large-bodied marine predators have been declining worldwide for decades, including in coastal waters (e.g. Pauly *et al.* 1998; Jackson *et al.* 2001; Dulvy *et al.* 2008; Ferretti *et al.* 2010; Estes *et al.* 2011). Studies in terrestrial, freshwater and some marine ecosystems have demonstrated that predator declines and removals often are associated with large-scale changes to communities, leading Estes *et al.* (2011) to suggest that strong trophic cascades are likely to be a general rule of top-predator removals. Yet, further studies are needed to gain insights into the conditions under which predator removals are likely to trigger cascades and the mechanisms that might drive them (e.g. Heithaus *et al.* 2008a; Creel 2011). Such a mechanistic understanding of cascades is critical to predicting when and where they are likely to occur and to inform management and restoration strategies that might lessen the overall ecological consequences of anthropogenic disruption of cascades in marine ecosystems, including subtropical embayments.

Understanding trophic structure and the ecological role of top predators in subtropical embayments has been hampered by the realisation that current ecosystems probably bear little resemblance to those that existed historically (Heck and Valentine 2007). Seagrasses, which form the foundation of communities in many subtropical embayments, have been declining, and continue to decline, rapidly throughout much of the world (Waycott *et al.* 2009). Also, many of the widespread losses or severe population reductions of top predators (e.g. sharks, marine mammals) and large-bodied grazers (e.g. fishes, sea turtles and sirenians) occurred before the implementation of scientific investigation (e.g. Jackson *et al.* 2001).

In 1997, we initiated a long-term study of the dynamics of the relatively pristine seagrass ecosystem found in the Eastern Gulf of Shark Bay, Western Australia, with the goal of providing insights into the potential mechanisms and importance of top-down control in subtropical embayments and coastal marine ecosystems in general. Here, we review 15 years of research and

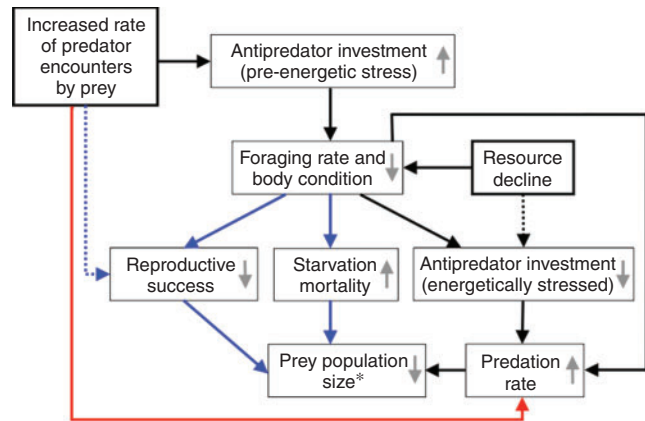
the inferences these studies have provided regarding ecosystem dynamics and management of such ecosystems.

### Mechanisms of top-down control

Until relatively recently, the majority of ecological literature regarding predator–prey interactions has assumed, either explicitly or implicitly, that predators influence prey primarily through the removal of prey individuals during predation events. Starting with early studies of behavioural responses of prey to the presence of predators (e.g. Lima and Dill 1990) and continuing with more recent explorations of the community and ecosystem consequences of these responses, ecologists have discovered that non-consumptive, or ‘risk’, effects of predators may equal or exceed the impacts of direct predation (Schmitz, Beckerman and O’Brien 1997; Lima 1998; Peacor and Werner 2000, 2001; Dill *et al.* 2003; Werner and Peacor 2003; Schmitz *et al.* 2004; Preisser *et al.* 2005; Wirsing *et al.* 2008a; Heithaus *et al.* 2008a, 2008b; Creel 2011). Indeed, some classic examples of predator impacts on prey may be the partially, or largely, the result of risk effects rather than direct predation (Peckarsky *et al.* 2008). Although somewhat counterintuitive, risk effects can be more important than direct predation because direct mortality usually removes a limited number of individuals from a population, which may result in decreased competition and enhanced reproduction or growth among remaining prey individuals (compensatory reproduction or growth), and an end result of no reduction in population size (Sinclair and Pech 1996; Creel 2011). In contrast, risk effects of predators, which may include leaving high-risk but profitable habitats, reduced foraging rates necessitated by vigilance, or increased stress, are generally experienced by a large proportion of the individuals in a population. These risk effects, be they behavioural or physiological, often result in lower access to food or compromised individual reproductive success that result in a reduction in the population’s reproductive potential (e.g. Biro *et al.* 2003; Creel *et al.* 2007). Importantly, most studies of the importance of top-down control provide correlations between changes in predator abundance and changes in abundances of other trophic levels (e.g. Myers *et al.* 2007; Estes *et al.* 2011). Although it is often assumed that increases in prey abundance following predator removal are due to reduced predation rates, these changes are actually the result of changes in direct predation, risk effects, and their interaction (e.g. Peacor and Werner 2001; Werner and Peacor 2003; Fig. 1). An important area of current investigation is understanding when a particular mechanism predominates (Heithaus *et al.* 2008a; Creel and Christianson 2008; Creel 2011).

### The Shark Bay Ecosystem Research Project

The Eastern Gulf of Shark Bay is an ideal location to investigate the nature and relative importance of top-down control that is likely to have characterised other subtropical seagrass ecosystems in the absence of substantial anthropogenic impacts. Indeed, its remote location and small human population have contributed to healthy seagrass communities (e.g. Walker *et al.* 1988; Burkholder *et al.* in press), and large population sizes of many large-bodied taxa, including sea turtles (especially *Chelonia mydas* and *Caretta caretta*), dugongs (*Dugong dugon*),



**Fig. 1.** Simplified pathways illustrating how direct predator-induced mortality (consumption) and behavioural changes (risk effects) may combine synergistically with bottom-up forces (resource declines) to influence prey population size. Downward-facing arrows inside boxes indicate a negative response and upward-facing arrows indicate a positive response. Dotted lines emphasise the indirect effect of predators on reproductive success of prey, as mediated by the costs of antipredator behaviour, and the indirect effects of resource declines on predation rates, as mediated by reduced investment in costly antipredator behaviour. The red line indicates the only pathway by which direct predation mortality alone may influence prey populations (i.e. increases in predation rate driven by encounters and not enhanced risk-taking or decreased escape ability by energetically stressed prey). Solid blue lines indicate pathways through which predator risk effects operate independently of direct predation (i.e. prey starvation resulting from the combined effects of resource declines and antipredator behaviour, or condition-related losses of reproductive output) and solid black lines are those that involve an interaction of the effects of consumption and risk effects. Investment in anti-predator behaviour is predicted to depend on the species’ life-history characteristics (e.g. Clark 1994, Warner 1998, Frid *et al.* 2012), and therefore, the strengths of various linkages depicted should vary among taxa.

Indo-Pacific bottlenose dolphins (*Tursiops cf. aduncus*), rays and tiger sharks (*Galeocerdo cuvier*) (e.g. Preen *et al.* 1997; Heithaus 2001b; Heithaus *et al.* 2005; Wirsing *et al.* 2006; Vaudo and Heithaus 2009). The habitats of our study area are made up of near-shore shallows (usually <4 m in depth and up to several kilometres wide) that feature seagrasses along the seaward edges, offshore banks (1–4.5 m in depth) largely covered by seagrasses, and waters 6–12 m in depth that are primarily covered by sand (see Heithaus and Dill 2002; Vaudo and Heithaus 2009, for more detailed descriptions). For the purposes of our studies, we have broadly classified the deep waters and offshore banks into the following three microhabitats (Heithaus and Dill 2006): deep waters, interior areas of shallow banks (waters <2.5 m in depth and >75 m from water >4.5 m in depth) and bank edges (waters 2.5–4.5 m in depth or <2.5 m in depth and within 75 m of waters >4.5 m in depth).

When we initiated work in Shark Bay in 1997, relatively little was known about the importance of large marine predators in shaping the population dynamics and behavioural decisions of their prey. Indeed, there was a general assumption that large-bodied taxa, including sea turtles, sirienians, and odontocetes, had little to fear from predators (e.g. Jackson *et al.* 2001). We soon discovered, however, that several prey species were

**Table 1. Captures of elasmobranchs on drumlines in the Eastern Gulf of Shark Bay (1997–2011)**

TL = total length

Common name	Scientific name	<i>N</i>	TL (mean ± s.d.) (cm)	Range (cm)
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	3	125.0 ± 1.0	124–126
Pigeeye shark	<i>Carcharhinus amboinensis</i>	9	190.2 ± 11.7	173–208
Bronze whaler	<i>Carcharhinus brachyurus</i>	2	227.0	185–269
Nervous shark	<i>Carcharhinus cautus</i>	1		
Silky shark	<i>Carcharhinus falciformis</i>	1	235.0	
Blacktip shark	<i>Carcharhinus limbatus</i>	2	74.0	
Dusky shark	<i>Carcharhinus obscurus</i>	6	177.0 ± 17.0	158–199
Sandbar shark	<i>Carcharhinus plumbeus</i>	47	179.6 ± 10.5	150–198
Spottail shark	<i>Carcharhinus sorrah</i>	4	125.0 ± 28.3	96–154
Tiger shark	<i>Galeocerdo cuvier</i>	911	284.4 ± 55.2	101–445
Giant shovelnose ray	<i>Glaucostegus typus</i>	1	243.0	
Shortfin mako shark	<i>Isurus oxyrinchus</i>	3	255.5 ± 0.7	255–256
Sickle fin lemon shark	<i>Negaprion acutidens</i>	9	228.0 ± 57.9	89–261
Milk shark	<i>Rhizoprionodon acutus</i>	1		
Scalloped hammerhead	<i>Sphyrna lewini</i>	1	250.0	
Great hammerhead	<i>Sphyrna mokarran</i>	2	275.0	275–400

regular recipients of tiger shark-inflicted injury (e.g. ~74% of bottlenose dolphins, Heithaus 2001a; ~25% of female loggerhead turtles, ~50% of male loggerhead turtles, Heithaus *et al.* 2002b, 2005), suggesting that these species at least had incentive to invest in safety from predators. In addition, studies in terrestrial systems suggested that even large-bodied predators would modify their habitat use patterns to reduce risk (e.g. African wild dogs, *Lycaon pictus*, Mills and Gorman 1997; desert baboons, *Papio cynocephalus ursinus*, Cowlshaw 1997), and a diverse theoretical and experimental literature (e.g. Werner and Hall 1988; Abrahams and Dill 1989; Brown 1992; Houston *et al.* 1993; Hugie and Dill 1994; Schmitz *et al.* 1997; Brown *et al.* 1999) provided a framework for generating testable predictions that could help elucidate the potential importance of predation risk, and predators, in structuring the behaviour of large-bodied taxa and, ultimately, the Shark Bay ecosystem.

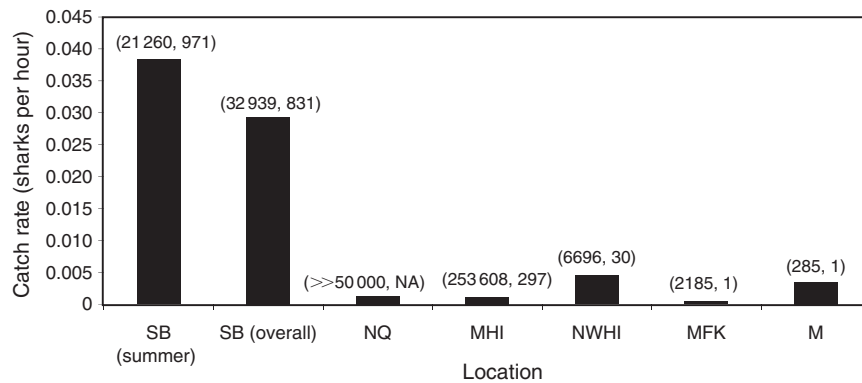
Our field studies have focused primarily on (1) understanding spatiotemporal variation in the abundance and size of tiger sharks and other large sharks (i.e. spatial and temporal patterns of potential predation risk to other large-bodied taxa), (2) elucidating the factors influencing habitat use decisions and other behaviours of key large-bodied taxa (e.g. food availability, predation risk), (3) trophic structure and (4) the potential for cascading impacts of top-down processes. Here, we focus on our results pertaining to the importance of risk effects in subtropical embayments.

### Top predator populations in Shark Bay

Since 1997, we have used quantitative drumline fishing to monitor relative abundances and size structure of large sharks in Shark Bay (see Heithaus 2001b; Wirsing *et al.* 2006, for details). We have captured more than 1000 sharks from 15 species. Tiger sharks make up 90.8% (911 of 1003) of the catches, and are the largest-bodied species captured in the study area (Table 1). More

than 97% of sharks longer than 2 m total length are tiger sharks. Sandbar sharks are the second-most commonly captured species ( $n = 47$ ). Although it is difficult to compare tiger shark abundances across studies because of variation in methodology, tiger shark catch rates in Shark Bay appear to be considerably higher than those from studies in other areas of the world that have targeted large sharks (Fig. 2). Tiger shark catch rates in the Shark Bay study area, however, show considerable temporal variation. Indeed, although catch rates between the months of September and May tend to be high, catch rates of tiger sharks drop considerably during the winter (June–August) (Heithaus 2001b; Wirsing *et al.* 2006). This seasonal variation is part of a sinusoidal pattern of daily catch rates with a peak in mid-summer (February; Wirsing *et al.* 2006). Tracking studies using passive acoustic telemetry and satellite telemetry (Heithaus 2001b, Heithaus *et al.* 2007c; M. Heithaus, unpubl. data) have demonstrated that most sharks have left the study area during the periods when catch rates are low, supporting the assumption that catch rates reflect relative abundance of sharks in the bay rather than reduced activity or foraging rates.

One important aspect of temporal changes in tiger shark abundance from the perspective of our studies of their impacts on prey is inter-annual variation in catch rates. Although always abundant in summer, tiger shark catch rates in winter vary from no captures at all to moderate abundances of large sharks remaining in the bay (Heithaus and Dill 2002; Wirsing *et al.* 2006; M. Heithaus, D. Burkholder, J. Vaudo and C. Bessey, unpubl. data). Inter-annual and seasonal variation in tiger shark catch rates, therefore, provide for a natural experiment (*sensu* Biro *et al.* 2005) to investigate behavioural variation in potential tiger shark prey that is independent of changes to water temperatures or seasonal reproductive cycles. In other words, our capacity to ask whether potential prey species respond to within- and between-year variation in tiger shark abundance with commensurate investment in safety is not confounded by other possible behavioural drivers.



**Fig. 2.** Tiger shark catch rates (sharks per hour) in Shark Bay (SB), northern Queensland (NQ, Simpfendorfer 1992), the main Hawaiian Islands (MHI, Papastamatiou *et al.* 2006), north-western Hawaiian Islands (NWHI, Papastamatiou *et al.* 2006), main Florida Keys (MFK, Heithaus *et al.* 2007d) and the Marquesas FL (M, Heithaus *et al.* 2007d). Note that summer catch rates in SB have been presented separately because it is a seasonal system. Numbers in parentheses are total hours fished and sharks caught. All fishing programs specifically targeted large sharks; however, exact methodologies differed (i.e. longlines were employed in NWHI and MHI, drumlines in NQ and SB, single-hook bottom lines MFK, M). Catch rates for NQ are for Horseshoe Bay ( $0.008 \text{ sharks} \times \text{line-day}^{-1}$ ), which had maximum effort and the highest catch rates of six sites (low =  $0.0004 \text{ sharks} \times \text{line-day}^{-1}$ ). Although hooks were soaked for a day, to account for bait loss, we assumed that they fished only for 6 h to generate hourly catch rates. Also, fishing was not concurrent: MHI (1967–1969 and 1971–1976), NWHI (1978–1980), MFK and M (2002–2004), NQ (1964–1986) and SB (August 1997 – August 2011). Hence, these data are intended to provide only a rough comparison.

Catch rates could not be used to assess habitat preferences of tiger sharks because of differences in bait-loss rates among habitats. Indeed, bait-loss rates to teleosts (especially the north-west blowfish, *Lagocephalus sceleratus*) in shallow habitats were so high that we had to turn to the use of acoustic tracking and animal-borne imaging (Heithaus *et al.* 2001, 2002a, 2006) to elucidate the habitat use preferences of the tiger shark. Overall, we have found that tiger sharks show a preference for shallow habitats over deep ones, and are more common over shallow edges than in interior portions of seagrass banks. Therefore, from the perspective of potential prey species, we can characterise the probability of encounters with tiger sharks, which is one component of overall risk (see below), as shallow edges > shallow interior > deep channels = deep open waters (Heithaus *et al.* 2002a, 2006).

### Using spatiotemporal variation in predator abundance as a natural 'experiment': investigating the importance of risk effects in diverse taxa

Predation risk, or the probability that prey are killed by a predator per unit time, is the product of a series of probabilities during a predator–prey interaction. These include the probability of prey encountering a predator, the probability that prey are detected by the predator, the probability that the predator attacks the prey, and the probabilities that the prey is captured and killed if attacked (e.g. Lima and Dill 1990).

To determine the importance of food availability and predation risk from tiger sharks in structuring the habitat use and behaviour of their air-breathing prey, we established 10 long-term transects (~4–6 km long) that represent replicates of deep

**Table 2.** Primary species sampled along transects in the Eastern Gulf of Shark Bay

Only individuals found within the sighting distance from the boat are included in analyses

Common name	Scientific name	Distance (m)
Dugong	<i>Dugong dugon</i>	100
Indo-Pacific bottlenose dolphin	<i>Tursiops cf. aduncus</i>	300
Loggerhead turtle	<i>Caretta caretta</i>	30
Green turtle	<i>Chelonia mydas</i>	30
Pied cormorant	<i>Phalacrocorax varius</i>	30
Bar-bellied sea snake	<i>Hydrophis elegans</i>	5
Olive-headed sea snake	<i>Disteria major</i>	5
Shark Bay sea snake	<i>Aipysurus pooleorum</i>	5

and shallow habitats and cover a variety of microhabitats (deep channels, deep open waters, shallow edges, shallow interior). For 3 years, we also established transects along three banks that represented only interior and only edge microhabitats to gain further insights into small-scale habitat use by key species, and for studies of turtles and rays, additional transects have been employed in near-shore shallow habitats (e.g. Vaudo and Heithaus 2009). Between 1997 and 2011, we conducted more than 3700 passes along our primary transects. During these transects, we recorded all individuals from eight primary species within species-specific sighting belts (Table 2) that are designed to minimise the probability that individuals within the search area are missed. Detection probabilities are enhanced by the relatively slow speeds,  $6\text{--}9 \text{ km h}^{-1}$ , at which the 4.5–5.5-m

vessels traverse the sampling zones. For dugongs (2002–06) and dolphins (1997–2000), we collected detailed data on exact position, behaviour and group sizes of all groups and individuals sighted along transects.

For most species, the combination of slow vessel speeds and relatively short dive times makes it unnecessary to correct sightings data for spatiotemporal variation in dive–surface intervals. For sea turtles, however, such correction is necessary. Accordingly, we have conducted studies of sea turtle diving behaviour with time–depth recorders to create spatially and temporally explicit correction factors for our surface sightings (Thomson *et al.* 2012). Although dugongs in other locations exhibit diving and surfacing patterns that may result in similar confounds (Marsh *et al.* 2011), surfacing rates of dugongs in Shark Bay are high relative to our boat speed along transects (Wirsing *et al.* 2007a) and surfacing rates do not change significantly with shark abundance in either habitat, except among individuals engaged in excavation foraging in the shallows (Wirsing *et al.* 2011). However, excavators actually increase their surfacing rate in the shallows as shark abundance rises, running counter to trends in abundance (see below) and making our results conservative (Wirsing *et al.* 2011).

For sea turtles, studies based on transects have been supplemented with at-sea captures using the rodeo technique (see Heithaus *et al.* 2005). These captures have provided otherwise unattainable information about the behaviour of green and loggerhead turtles. For example, the long dive times that typify both green and loggerhead turtles in Shark Bay (Thomson *et al.* 2012) and the inability to determine behavioural states when turtles are at the surface make it difficult to gain robust insights from transects regarding potential habitat shifts in response to predation risk. Captures allow us to obtain data on capture locations and body condition of turtles. Using a rapid visual assessment of the shape of a turtle's plastron provides a reliable indicator of body condition for green turtles (Thomson *et al.* 2009). When used in conjunction with capture location, these body condition measurements have allowed us to explore the relationship between tiger shark predation risk and green turtle behaviour. Specifically, we were able to examine use of dangerous seagrass microhabitats (seagrass interiors with high encounter rates) by individual turtles with variable energetic states to test the hypothesis that turtles in good condition, and therefore with assets to protect, would avoid these areas (see below; Heithaus *et al.* 2007a).

We used behavioural ecological theory to develop testable predictions to investigate potential responses of prey to tiger sharks (see Heithaus *et al.* 2007b). Briefly, on the basis of the ideal free distribution (IFD; Fretwell and Lucas 1969), foragers are predicted to be distributed across habitats proportional to food supply when not at risk of predation. Empirical studies and modification of IFD theory show that forager abundances relative to their food (e.g. the proportion of foragers in a habitat divided by the portion of food resources in a habitat) should increase in safer habitats and decrease in dangerous habitats as the overall risk of predation increases (e.g. Abrahams and Dill 1989, Hugie and Dill 1994, Heithaus 2001c, Krivan *et al.* 2008). Therefore, by monitoring forager distributions (using transect data) relative to that of their food as predation risk changes, it is

possible to examine the effects of predation risk on forager habitat use.

Quantifying food availability or quality can be difficult in large-scale marine settings, especially for herbivores (see individual papers for full considerations of assumptions of food abundance metrics). For example, we have based most of our inferences of dugong habitat shifts on spatiotemporal variation in seagrass biomass (Wirsing *et al.* 2007a, 2007b). Although dugongs in other locations have been shown to select seagrasses on the basis of more fine-scale features (e.g. nutrient content of seagrass species; Sheppard *et al.* 2010), spatiotemporal shifts in seagrass nutrient content and seagrass species composition cannot explain spatiotemporal variation in foraging–dugong habitat use in our study area (Wirsing *et al.* 2007a, 2007b).

Dolphins, dugongs and pied cormorants all modify their use of deep and shallow habitats in response to spatial and temporal variation in the abundance of tiger sharks (Heithaus and Dill 2002; Heithaus 2005; Wirsing *et al.* 2007a). When tiger sharks are largely absent from the study area, foraging individuals of all three species are distributed across habitats approximately proportional to that of their food. However, as tiger shark predation risk increases, all three species shift to foraging more in safer deep habitats than would be expected on the basis of the abundance of food. This shift results in all species giving up considerable foraging opportunities to be safer. Dugongs, however, are more constrained to continue using at least portions of shallow banks when tiger sharks are abundant because of the general lack of foraging opportunities (i.e. seagrass) in deep habitats (Wirsing *et al.* 2007a). Therefore, numbers of foraging dugongs remain reasonably high in shallow habitats during high-risk periods, compared with those of bottlenose dolphins. Interestingly, there was variation among age–sex classes in the use of dangerous habitats by bottlenose dolphins; juvenile males used high-risk but high-reward shallow habitats more than did adults (Heithaus and Dill 2002). We have not been able to test for similar age–sex variation in other prey species.

By investigating changes in how a variety of potential tiger shark prey species modify their use of the different portions (microhabitats) of shallow banks as shark abundance varies, we have begun to unravel the particular factors that influence the nature of predator risk effects (e.g. Heithaus *et al.* 2009; Wirsing *et al.* 2010). Indeed, we have found that in Shark Bay, the interaction of physical features of the habitat (in this case, depth) and escape probabilities of prey if they encounter predators is critical to determining how prey modify their use of relatively dangerous shallow areas. All of the species we have investigated are distributed across the middle of banks (interior microhabitats) and bank edges approximately in proportion to that of their food when sharks are scarce in the study area. However, different types of prey shift among interior and edge microhabitats in different ways as tiger sharks increase in overall numbers. Escape probabilities for pied cormorants and olive headed sea snakes, if they encounter a shark, should not vary between edge and interior microhabitats because of their escape tactics (fly away and escape into seagrass, respectively). Accordingly, when tiger sharks are abundant, both species greatly decrease their use of bank edges (where shark encounters are most likely) and use bank interiors (where shark encounters

are less likely) more often than expected on the basis of food abundance alone (Heithaus *et al.* 2009; Wirsing and Heithaus 2009).

In contrast to cormorants and sea snakes, dugongs, turtles and dolphins escape by out-maneuvring tiger sharks. Therefore, the deeper waters available in edge microhabitats provide greater escape probabilities for individuals that encounter a shark than do interior microhabitats, in which the manoeuvrability advantage enjoyed by these species is reduced. Consistent with predictions, when tiger shark abundance increases, those dugongs and dolphins that use shallow banks shift out of interior microhabitats and prefer bank edges where they are likely to encounter sharks more often but are more likely to escape them (Heithaus and Dill 2006; Wirsing *et al.* 2007b). They also prefer banks that have a higher proportion of edge microhabitat over those that have lower proportions (Heithaus *et al.* 2007b). Green turtles show a similar shift, but individual decisions in turtles are mediated by their body condition. The quality of the dominant seagrass species in Shark Bay, *Amphibolis antarctica*, is highest in the interior of seagrass meadows (Heithaus *et al.* 2007a). This spatial pattern of food quality apparently leads green turtles in good body condition to select generally safer but less profitable areas of banks (edges) and those in poor condition, whose need for nourishment is greater, to select high-risk but energetically more favourable interior microhabitats (Heithaus *et al.* 2007a).

Abiotic factors also may play an important role in mediating the impacts of sharks on the behaviour of their prey. For example, bar-bellied sea snakes (*Hydrophis elegans*) foraging in near-shore waters are found only over sand, where their prey is more abundant but also where capture by tiger sharks is more likely, when tides are low and access by sharks is limited. When tides are high, and sharks can access near-shore habitat, snakes are found almost exclusively within seagrass patches where they can hide from would-be predators (Kerford *et al.* 2008). Similarly, a variety of ray species may use very shallow waters near-shore to reduce encounters with tiger sharks and other potential predators, such as great hammerheads (*Sphyrna mokarran*) (Vaudo and Heithaus 2009).

While the majority of our initial work in Shark Bay focused on spatial shifts in response to predation risk, it is not surprising that the species we have investigated employ multiple tactics besides spatial shifts to reduce the risk of predation from sharks. For example, cowtail stingrays (*Pastinachus atrus*) in shallow waters generally rest alone when visibility is good, but they form groups when visibility, and their ability to visually detect predators, is low (Semeniuk and Dill 2005). Further, cowtail stingrays preferentially rest with reticulate whiprays (*Himantura uarnak*), which respond earlier to simulated predator encounters, thereby facilitating earlier detection of potential predators (Semeniuk and Dill 2006). Finally, rays resting in groups tend to form with individuals' heads oriented towards each other and tails pointing out. When disturbed, these groups display coordinated escape responses that may confuse a potential predator (Semeniuk and Dill 2005). Bottlenose dolphin group sizes also vary in a manner consistent with reducing predation risk; groups were larger in dangerous shallow waters (which may, however, also be explained by higher food availability in these habitats) and during resting, the most dangerous behavioural state (Heithaus and Dill 2002).

The best-studied species with respect to multiple layers of anti-predator behaviour in Shark Bay is the dugong. In addition to modifying their use of habitats (Wirsing *et al.* 2007a), microhabitats (Wirsing *et al.* 2007b) and patches (Heithaus *et al.* 2007b), they also modify their feeding modes, diving behaviour and duration of behavioural bouts in response to predation. These responses, however, tend to be concentrated in high-risk, shallow habitats and are less pronounced, or even absent, in safer, deep waters. As tiger shark numbers increase, dugongs largely switch their foraging behaviour in shallow habitats from excavation, which allows them to access more nutritious seagrass rhizomes but at the cost of creating large plumes of sediment that could mask the approach of a tiger shark, to cropping the less nutritious leaves of *A. antarctica*, a feeding mode that does not inhibit anti-predator vigilance (Wirsing *et al.* 2007c). Dugongs observed using the excavation feeding tactic make more and shorter dives during periods of high tiger shark abundance than during periods of low shark abundance, whereas dugongs using cropping do not change their diving behaviour as tiger shark catch rates vary (Wirsing *et al.* 2011). This change in diving behaviour is likely to allow excavating dugongs to be vigilant for tiger sharks more often by rising above sediment clouds. A final anti-predator behaviour identified in dugongs is modification of behavioural sequencing. Dugongs in dangerous shallow habitats, but not in deep habitats, more frequently switch between foraging and traveling, and resting and traveling, during periods of high shark abundance (Wirsing and Heithaus 2012). This sequencing adjustment results in individual dugongs avoiding long, continuous bouts of foraging and resting, during which their capacity to detect sharks is inhibited. Interestingly, the multiple layers of anti-predator behaviour in dugongs closely mirror those of elk (*Cervus elaphus*) foraging under the risk from grey wolves (*Canis lupus*) (Wirsing and Ripple 2011).

Like dugongs, pied cormorants modify their diving behaviour to reduce risk, but only in the most dangerous habitat (Dunphy-Daly *et al.* 2010). As predicted by theory (Heithaus and Frid 2003; Frid *et al.* 2007), cormorants in shallow habitats reduce their time spent at the surface (the most dangerous component of the dive cycle; see Heithaus and Frid 2003) as tiger shark catch rates increase (Dunphy-Daly *et al.* 2010). Interestingly, cormorants accomplish this by maintaining similar surface times per dive cycle but increasing dive duration rather than rearranging all components of their dive cycles. This suggests that cormorants work harder in dangerous habitats during dangerous times of the year, so as to spend less time at sea foraging (i.e. less time exposed to risk; see Frid *et al.* 2007). Ongoing studies in Shark Bay are investigating whether sea turtles modify their diving behaviour in response to spatiotemporal variation in risk from tiger sharks.

### **Behaviourally mediated indirect species interactions and the possibility of behaviour-mediated cascades in Shark Bay**

Our studies of tiger sharks and their prey have revealed that tiger sharks are likely to be important in transmitting behaviourally mediated indirect interactions (BMII) among their potential prey species. For example, we combined transect data with

those from shark fishing to demonstrate that the abundance of dugongs in the study area explains a considerable amount of the variation in shark catch rates (Wirsing *et al.* 2007d), while our tracking studies of sharks suggest that their preference for shallow habitats is influenced by the abundance of prey, including dugongs, in these habitats (Heithaus *et al.* 2002a). As a result, dolphins largely abandon the shallow waters where the highest densities of their prey are found in a behavioural analogue of apparent competition (Heithaus and Dill 2002; Dill *et al.* 2003).

More important to understanding the overall dynamics of subtropical estuaries and other communities is whether anti-predator behaviours of large herbivores and upper trophic-level predators (e.g. dolphins) might trigger cascades in the Shark Bay ecosystem that parallel those suggested on land (e.g. Ripple and Beschta 2004). Studies from other subtropical and tropical ecosystems have shown that large-bodied herbivores can modify the nutrient dynamics, above- and below ground biomass, and species composition of seagrass communities. Dugongs are major grazers in many subtropical and tropical seagrass ecosystems throughout the Indo-Pacific region and may have a major impact on the structure and function of these seagrass communities (de Iongh *et al.* 1995, Preen 1995; Nakaoka and Aioi 1999; Aragonés 2000; Aragonés and Marsh 2000; Masini *et al.* 2001). For example, dugong grazing off Queensland, Australia, reduced shoot density by 65–95%, above-ground biomass by 73–96% and below-ground biomass by 31–71% (Preen 1995). Heavy grazing led to an ~12-fold increase in the shoot density of an early pioneering seagrass species (*Halophila ovalis*) and a six-fold decrease in the density of the dominant, although less preferred, species (*Zostera capricornis*). On control sites, *Z. capricornis* densities were four times greater than those of *H. ovalis*, whereas on heavily grazed sites, *H. ovalis* densities were 16 times higher. Growth dynamics of seagrass, and thus patch dynamics, may also be influenced by grazing. Branching rates of *H. ovalis*, for example, are 1.5 times greater in areas grazed by dugongs (Nakaoka and Aioi 1999). Green turtles may have similar impacts (e.g. Aragonés 2000; Aragonés and Marsh 2000; Moran and Bjørndal 2005; Lal *et al.* 2010). Patterns of nutrient composition of *A. antarctica* leaves in Shark Bay are consistent with risk-induced heavy grazing by dugongs and green turtles in edge microhabitats leading to reduced plant quality, with increased quality in less intensely grazed interior microhabitats (Heithaus *et al.* 2007a). However, ongoing experiments should reveal whether seagrass communities are in fact indirectly structured by spatiotemporal variation in tiger shark abundance and induced anti-predator behaviour. Of particular interest is the possibility that risk-sensitive foraging by teleost grazers might be as important as that by dugongs and sea turtles (e.g. Burkholder *et al.* 2012).

### Implications for community dynamics, conservation and management

By conducting a longitudinal study focusing on a suite of large-bodied species under relatively pristine conditions, we have gained insights into the dynamics of marine communities. Some of these insights are important for management of subtropical embayments.

*Large-bodied marine species, including those that have been considered largely immune to the effects of predators, respond to predation risk*

Large-bodied and long-lived marine taxa that are characterised by a high adult-survival probability (e.g. sea turtles, sea cows, odontocetes) generally are assumed to be little affected by predators, at least as adults (e.g. Preen 1995; Jackson *et al.* 2001). Our studies, however, suggest that, as in many terrestrial systems, even large-bodied taxa respond behaviourally to their predators and their populations may be, at least partially, influenced by predation, predation risk, and their interaction even if predation rates are low (Wirsing *et al.* 2008a; Heithaus *et al.* 2008a, 2008b, 2009; Creel and Christianson 2008; Creel 2011). Indeed, because most of these species are relatively long-lived and highly iteroparous, they are expected to invest heavily in anti-predator behaviour (e.g. Clark 1994; Warner 1998; Frid *et al.* 2012) and risk effects may be greater than those of direct predation. By extension, strong behavioural effects of predators on prey cannot be ruled out in cases where prey species comprise only a small proportion of the predator's diet. In Shark Bay, for example, bottlenose dolphins are very rarely found in the stomach contents of tiger sharks (Heithaus 2001b; Simpfendorfer *et al.* 2001), yet they are frequently attacked (Heithaus 2001a) and respond markedly to risk of tiger shark predation (Heithaus and Dill 2002). Traditional methods of estimating effects of predators would overlook the importance of tiger sharks to dolphins. Yet, theoretical (Abrams 1993; Brown *et al.* 1999; Creel and Christianson 2008) and empirical (Biro *et al.* 2003; Creel *et al.* 2007) studies have suggested that when many individuals give up access to considerable resources in order to be safe, overall population numbers often are lower than they would be in the absence of predators. By inference, the presence of tiger sharks in Shark Bay is likely to reduce the ecosystem's carrying capacity for dolphins, as well as other potential prey species.

*The nature of risk effects can be influenced by interactions of landscape features, predator hunting mode and anti-predator tactics and capabilities of prey*

From the perspective of predicting the potential risk effects of predators, our studies – when synthesised with results from other research – have helped to build a framework for understanding the factors that might influence the strength and intensity of risk effects (for detailed discussion see Heithaus *et al.* 2009). Particularly relevant is the importance of the interaction of predator hunting mode with landscape features. Recent literature has suggested that roving predators should have lesser impacts on habitat use decisions of prey than sit-and-wait predators (e.g. Preisser *et al.* 2007; Schmitz 2008; Kauffman *et al.* 2010). This assumption stems from the idea that sit-and-wait predators usually are more easily detected and avoided than are roving predators. In other words, prey cannot easily make behavioural adjustments to reduce encounters with roving predators, whereas they can avoid the easily detected halo of predator cues from sit-and-wait predators (Preisser *et al.* 2007; Schmitz 2008). Our tiger shark research, however, shows that roving predators can have major impacts on prey behaviours because prey can make spatial shifts to reduce encounter rates or improve escape

probabilities. If tiger shark–prey interactions were occurring in a homogeneous landscape, spatial shifts would not be predicted (although other anti-predator behaviours, such as shifts in foraging modes, with the potential to initiate behavioural cascades, might still occur). Therefore, assumptions about the relative importance of predator risk effects in ecological interactions and dynamics should not be made solely on the basis of predator hunting mode (see also Heithaus *et al.* 2009; Wirsing *et al.* 2010; Creel 2011). Also, as evidenced by differential shifts in space use by prey with divergent escape responses, using predator abundance or encounter rates as a proxy for overall predation risk may not be appropriate in some situations.

*Habitats with high animal abundances may serve as a relative refuge from predation rather than being critical foraging habitat*

Habitat use patterns of large-bodied marine taxa are increasingly being used to infer foraging hotspots and designate protected areas (e.g. Yen *et al.* 2004; James *et al.* 2005); however, understanding potential patterns of predation risk is important for making such links. For example, without detailed studies it might be predicted that deep habitats offer the best foraging rewards for dolphins in Shark Bay if they had been studied in months when tiger sharks were present and no data were collected on spatial variation in prey abundance and predation risk. Diving behaviour also is being used as a behavioural indicator of the quality of prey patches (e.g. Burns *et al.* 2004; Mori *et al.* 2007). Although this approach is certainly valid in some circumstances, our studies of cormorants would have incorrectly identified rich patches, had we not explicitly considered risk. Therefore, the potential effects of predators should be explicitly considered before using such data for management decisions (e.g. Frid *et al.* 2007; Dunphy-Daly *et al.* 2010).

*Risk effects may provide insights into documenting and assessing the impacts of human disturbance*

There is a diverse literature showing the potential reproductive, demographic, population and ecosystem consequences of risk effects in small-scale and some large-scale systems (e.g. Schmitz *et al.* 2004; Preisser *et al.* 2005; Creel and Christianson 2008). In many ways, human disturbance is analogous to predation risk, with animals responding to disturbance events in a manner similar to their response to natural predators, and with similar consequences (see Frid and Dill 2002, for a review). Our studies of responses to natural predators provide some potential behavioural indicators for human disturbance and lessons for drafting strategies for minimising its impacts. For example, using modifications to ideal free distribution theory, as we have in Shark Bay, it is possible to measure changes in foraging distributions relative to that of food resources across gradients in disturbance (Heithaus *et al.* 2007b). Habitats perceived as safer from disturbance should experience an increase in relative abundances, whereas more disturbed habitats (i.e. those perceived as more dangerous) would have fewer individuals than expected on the basis of food resources. Importantly, depending on the perception of escape ability across habitats, their own condition, and impacts of disturbance on their predators (Muhly *et al.* 2011), animals may actually shift *into* habitats with higher disturbance rates. Although this may, on the surface, appear to

suggest that impacts of disturbance are minimal, microhabitat shifts of dugongs, dolphins and green turtles in response to tiger sharks demonstrate that this is not necessarily the case.

Our ongoing work also highlights changes in the duration and/or sequence of behavioural states as a subtle yet costly behavioural response to human disturbance (Wirsing and Heithaus 2012). If dugongs perceive boats as a form of predation risk, and previous work suggests that this is the case both for sirenians (e.g. Miksis-Olds *et al.* 2007) and other large marine taxa (e.g. sea turtles; Wirsing *et al.* 2008b), then increasing boat traffic may induce dugongs to exhibit the same costly behavioural shift. Importantly, because behavioural sequences can be adjusted without any change to overall behavioural time budgets, shifts to behavioural sequences triggered by human disturbance are likely to be missed, if they are not the specific focus of impact assessment.

*The loss of marine top predators may have greater impacts than are generally appreciated*

An interesting aspect of our work in Shark Bay is the similarity of our results to other predator–prey systems in diverse ecosystems. For example, the anti-predator behaviours of prey in our system mirror those of grasshoppers at risk from spiders (Schmitz 2008), terrestrial ungulates at risk from large mammalian predators (e.g. Sinclair and Arcese 1995; Wirsing and Ripple 2011) and small freshwater taxa at risk from a variety of fish and invertebrate predators (e.g. Werner and Hall 1988; Abrahams and Dill 1989; Power 1984; Biro *et al.* 2003). This similarity suggests that lessons learned from Shark Bay can be applied to other subtropical embayments, and even to other aquatic and terrestrial ecosystems (e.g. Heithaus *et al.* 2009). In these other systems, it has become apparent that direct effects of predators that manifest through risk effects may be mediated solely by spatiotemporal shifts in foraging locations or changes in foraging mode that could cascade to other trophic levels despite no obvious changes in population sizes of mesopredators (e.g. Creel and Christianson 2008; Heithaus *et al.* 2008a, 2010). On the basis of the prevalence of tiger shark risk effects in Shark Bay, it is important that risk effects be explicitly considered, including adaptive variation in response to predators, in modelling ecosystem dynamics. In addition, our work strengthens the argument that top-predator populations should be preserved and, in many cases, restored even in systems where we have yet to conclusively determine their ecological roles (e.g. Heithaus *et al.* 2008a; Estes *et al.* 2011). Finally, drawing on results from Shark Bay and locations where tiger sharks have declined (e.g. Bermuda; Murdoch *et al.* 2007; Fourqrean *et al.* 2010), it appears that a failure to retain tiger sharks at ecologically meaningful densities could result in ecosystem disruptions, affecting even foundation species, such as seagrasses.

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