

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

Aaron J. Wirsing · Michael R. Heithaus ·
Lawrence M. Dill

Received: 7 November 2006 / Accepted: 18 June 2007 / Published online: 17 July 2007
© Springer-Verlag 2007

Abstract Predators can influence plants indirectly by altering spatial patterns of herbivory, so studies assessing the relationship between perceived predation risk and habitat use by herbivores may improve our understanding of community organization. In marine systems, the effects of predation danger on space use by large herbivores have received little attention, despite the possibility that predator-mediated alterations in patterns of grazing by these animals influence benthic community structure. We evaluated the relationship between habitat use by foraging dugongs (*Dugong dugon*) and the threat of tiger shark predation in an Australian embayment (Shark Bay) between 1997 and 2004. Dugong densities were quantified in shallow (putatively dangerous) and deep (putatively safe) habitats (seven

survey zones allocated to each habitat), and predation hazard was indexed using catch rates of tiger sharks (*Galeocerdo cuvier*); seagrass volume provided a measure of food biomass within each zone. Overall, dugongs selected shallow habitats, where their food is concentrated. Foragers used shallow and deep habitats in proportion to food availability (input matching) when large tiger sharks were scarce and overused deep habitats when sharks were common. Furthermore, strong synchrony existed between daily measures of shark abundance and the extent to which deep habitats were overused. Thus, dugongs appear to adaptively manage their risk of death by allocating time to safe but impoverished foraging patches in proportion to the likelihood of encountering predators in profitable but more dangerous areas. This apparent food-safety trade-off has important implications for seagrass community structure in Shark Bay, as it may result in marked temporal variability in grazing pressure.

Communicated by Peter Peterson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0802-3) contains supplementary material, which is available to authorized users.

A. J. Wirsing · L. M. Dill
Behavioural Ecology Research Group,
Department of Biological Sciences,
Simon Fraser University, Burnaby,
BC, Canada, V5A 1S6

A. J. Wirsing
Honorary Research Associate, School of Animal Biology,
University of Western Australia, 35 Stirling Highway,
Crawley, WA 6009, Australia

A. J. Wirsing (✉) · M. R. Heithaus
Department of Biological Sciences, Marine Biology Program,
Florida International University, Biscayne Bay Campus MSB,
3000 NE 151 St, North Miami, FL 33181, USA
e-mail: wirsinga@fiu.edu

Keywords Community structure · Foraging ·
Herbivory · Predator intimidation · Shark Bay

Introduction

Foraging by herbivores can lead to marked changes in plant biomass, distribution, and diversity (Crawley 1983). Thus, predators may affect plants indirectly 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 (nonconsumptively) if a positive correlation between resources and danger 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 trophic cascades within communities (e.g., Peacor and Werner 2001; Preisser et al. 2005). Consequently, studies focused on these changes should improve our understanding of ecosystem organization (Werner 1998). While the link between predator intimidation and space use by terrestrial herbivores is established (Lima and Dill 1990; Lima 1998; Brown et al. 1999; Laundré et al. 2001; Verdolin 2006), the extent to which large, marine herbivores (e.g., sea turtles, sirenians) trade food for safety has received little attention (Dill et al. 2003).

Exchanges of food for safety can be explored using consumer time allocation patterns and ideal free distribution (IFD) theory (Fretwell and Lucas 1970). According to IFD theory, consumer populations should be distributed across habitats in proportion to food supply. Thus, forager densities in all habitats should be equal after dividing by the food supply in each habitat. If predation risk influences habitat selection, however, then fewer consumers should be found in dangerous habitats than predicted by food availability, causing food-corrected forager densities in these habitats to fall below those in safer ones (van Baalen and Sabelis 1993). Therefore, spatial differences between forager densities that appear when antipredator defense is induced and are not explained by variance in food supply can be used to quantify the food foragers sacrifice by avoiding dangerous habitats (i.e., “hazardous duty pay”, Brown and Kotler 2004).

Using this theoretical framework, we asked whether perceived predation risk from tiger sharks (*Galeocerdo cuvier*) affects habitat use decisions of dugongs (*Dugong dugon*) in Shark Bay, Western Australia. Dugongs are seagrass specialists, and must forage for much of the day to offset metabolic costs (Marsh et al. 1982). In Shark Bay, seagrass grows primarily in shallow habitats (≤ 4.5 m in depth; Walker et al. 1988; Travers and Potter 2002; Heithaus 2004a), but these habitats also are used preferentially by tiger sharks (Heithaus et al. 2002), the dugong’s major local predator (Heithaus 2001; Simpfendorfer et al. 2001). Consequently, dugongs choosing between deep and shallow foraging patches may face a trade-off between energy acquisition rate and the risk of encountering and being killed by sharks. Tiger shark densities vary seasonally in Shark Bay, however, peaking in the austral warm season (January–February) and reaching a nadir during the cold season (July) (Heithaus 2001; Wirsing et al. 2006), so the magnitude of this trade-off should vary temporally.

Accordingly, we tested whether dugongs minimize their risk of mortality by using safer, but energy-poor, foraging habitats to a greater extent as overall predator abundance

increases (predation risk sensitivity hypothesis). This hypothesis predicts that, after adjustment for spatial and temporal differences in food supply, the degree of inequality between foraging dugong densities in safe and hazardous habitats should be influenced by predator numbers. Under the assumption that shallow habitat is relatively dangerous, then, foragers should distribute themselves in proportion to food supply when sharks are scarce and use deep habitats more often than predicted by food availability when sharks are most abundant. If predation danger does not influence habitat use by foraging dugongs, then we should observe proportional forager densities in the two habitat types (i.e., input matching) throughout the year (food quantity hypothesis). To test our understanding of spatial variation in predation risk, we also asked whether dugongs select deep habitats while resting, when vulnerability to predation presumably is elevated and there is no benefit to using dangerous areas (Lima and Dill 1990).

Materials and methods

Study site

This study was undertaken in the Eastern Gulf of Shark Bay ($\sim 25^{\circ}45'S$, $113^{\circ}44'E$; Fig. 1). Listed as a World Heritage Area in 1991, Shark Bay features a mosaic of embayment plains (6.0–15 m deep), swift-current channels (6.0–12 m), shallow banks (<4.5 m), and sandy flats (generally <2.5 m and intertidal). Approximately one-third of its area ($\sim 4,000$ km²) is covered by seagrass meadows (Walker et al. 1988), which support 10,000–14,000 dugongs (Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004).

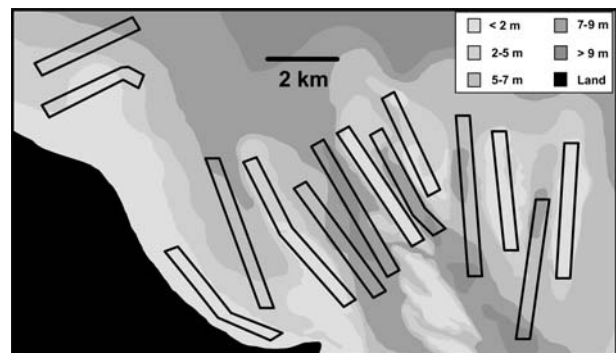


Fig. 1 This study was conducted in the Eastern Gulf of Shark Bay ($\sim 25^{\circ}45'S$, $113^{\circ}44'E$), Western Australia, between 1997 and 2004. Survey zones (i.e., 400-m sighting belts; $n = 14$) were stratified across shallow (2.5–4.5 m in depth) and deep (>6 m in depth) habitats throughout the 160 km² study area. Land is portrayed in black, while shades of gray depict water depth in categories ranging from <2 to >9 m deep

Food availability

We quantified food availability (biomass) in 14 survey zones, allocated evenly to deep (≥ 6 m in depth) and shallow (2.5–4.5 m deep) habitats (Fig. 1c). The survey zones did not incorporate intertidal sandy flats. 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 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 survey zone). At each station, seagrass species coverage and composition were estimated within a 1 m² 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 shark hazard to divers.

Food biomass was expressed as above-ground seagrass volume (area covered \times height; m³); measures from sampling points were pooled to generate overall values for each survey zone. Volume measures for survey zones consisted of two seagrass species: *Amphibolis antarctica* (mean = 82.7% of total volume) and *Posidonia australis* (mean = 17.3% of total volume). While *A. antarctica* is a food source for dugongs in the study area during both cold (Anderson 1986) and warm months (A. Wirsing, personal observation), the value of *P. australis* as a dietary item for dugongs is not known. The removal of this species from consideration, however, does not affect the results. We may also have incurred bias by failing to measure rhizomal (i.e., subsurface) biomass (de Iongh et al. 1995). Rhizomes of the dominant species (*A. antarctica*) are not available to dugongs as food (Anderson 1986), however, so such bias was likely modest. Finally, we were unable to quantify the biomass of tropical seagrass species since they are scarce during the winter in our study area. Nevertheless, we assumed that our biomass measure adequately captured differences in food availability between deep and shallow habitats because tropical species are always spatially concordant with *A. antarctica* and *P. australis* (Walker et al. 1988; D. Burkholder, unpublished data).

Dugong density and habitat use

We assessed patterns of dugong abundance using transect passes through the survey zones from 1997 to 2004 (2000–2001 excluded). To maintain sampling consistency, transect effort was allocated evenly across days ($n = 218$; mean = 7.52 passes day⁻¹, SD 2.42), months (mean =

44.17 \pm 18.24 passes month⁻¹; note, however, that surveys were not conducted during the months of November to January), and habitats (shallow survey zones: mean = 3.79 \pm 1.64 passes day⁻¹; deep survey zones: 3.86 \pm 1.65 passes day⁻¹). Survey zones within shallow and deep habitats were selected to ensure that all portions of the study area were monitored evenly, and no survey zone 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 ≤ 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 6–9 km h⁻¹. When dugongs were sighted at the surface within a survey zone (i.e., a 400-m sighting belt) before being passed by the boat, we recorded their position with a GPS and the water depth and substrate at their location. Between 2002 and 2004 ($n = 114$ days), we also determined the behavioral state (foraging, resting, and traveling) of all dugongs sighted at the surface based on direct observation and diagnostic surface behavior (Anderson 1986; Chilvers et al. 2004). Individual dugongs were distinguished using scarring patterns (Anderson 1995) and counted only once per day; individuals were rarely resampled during each year of the investigation.

Predator abundance

Our assumption that tiger sharks are active predators of dugongs is based on several pieces of evidence. One, the frequency with which dugong remains occur in the stomachs of tiger sharks appears to be too high to be explained by scavenging alone: dugong tissue was found in 15 of 84 tiger sharks caught along the northwestern coast of Australia (Simpfendorfer et al. 2001) and in all six large sharks (>3.0 m) caught in our study area from which complete stomach contents were collected (Heithaus 2001; unpublished data). Two, some adult dugongs bear scars from unsuccessful attacks by sharks (Anderson 1995; A. Wirsing, personal observation). Three, tiger sharks have been sighted harassing, attacking, killing, and consuming dugongs of various ages, including adults, and healthy individuals (A. Wirsing, personal observation; D. Charles, Western Australia Department of Conservation and Land Management, personal communication). Four, when sharks are abundant, microhabitat shifts by dugongs (Wirsing et al. 2007) mirror those of other species subject to tiger shark predation (bottlenose dolphins, *Tursiops* sp., Heithaus and Dill 2006; green turtles, *Chelonia mydas*, Heithaus et al. 2007). Importantly, although other predators have been observed attacking dugongs in the Bay's Western Gulf (killer whales, *Orcinus orca*, Anderson and Prince 1985),

tiger sharks are the dugong's only potential predator in the study area.

The extent of tiger shark predation on dugongs in Shark Bay is unclear, and kill rates are unlikely to be high. Tiger sharks nevertheless have the potential to influence dugong behavior. Indeed, long-lived species like the dugong should invest in anti-predator behavior even if the risk of being killed is low (Warner 1998). For example, bottlenose dolphins (*Tursiops* sp.) are almost never found in the stomachs of tiger sharks in Western Australia (Simpfendorfer et al. 2001), but shift their habitat use at multiple spatial scales in response to tiger shark predation risk (Heithaus and Dill 2002, 2006).

Catch rates provide a reliable index of tiger shark abundance in Shark Bay (Heithaus 2001; Wirsing et al. 2006). 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 brought next to the vessel, measured for total length (TL), tagged, and released (for details, see Heithaus 2001; Wirsing et al. 2006). Because of an ontogenetic shift in the tiger shark's diet (Lowe et al. 1996), tiger sharks under 3.0 m TL are much less likely to pose a threat to dugongs. Thus, only sharks >3.0 m TL were used to generate daily catch rates. Note, however, that the inclusion of sharks falling below this size threshold does not change the results of the analyses (see "Electronic supplementary material").

Although our fishing effort was intensive and daily fishing effort varied little (Wirsing et al. 2006), fishing frequency (~ 6 fishing days month⁻¹) did not allow for a continuous evaluation of the relationship between daily dugong habitat use and predator numbers. Thus, we used a sinusoidal function with a period of one year to predict the annual trend in daily catch rates (sharks h⁻¹; Fig. 2). The catch data used in the model were combined for the years 2002–2004 because interannual variation was not detected after accounting for seasonal effects ($F_{(2,117)} = 0.97$,

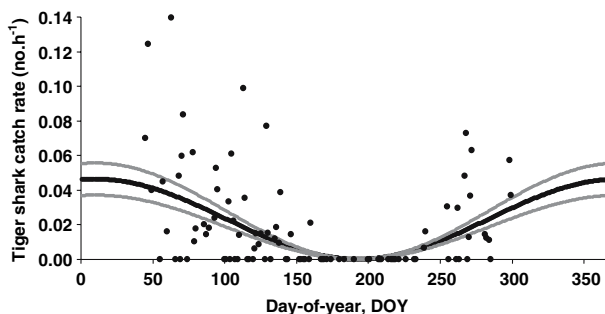


Fig. 2 Maximum likelihood model of tiger shark abundance based on daily catch rates (filled circles) pooled over three years (95% CI shown in gray lines). The model was fit using a sinusoidal function with a period of one year and a Poisson error distribution given the strong seasonal pattern and heterogeneity manifest in the raw catch data

$P = 0.38$). We fit the model using maximum-likelihood under the assumption of a Poisson error distribution since our data consisted of integer values for the number of sharks caught per day (we rarely caught more than one large shark per fishing day). The model was characterized by a good fit (i.e., tight confidence intervals; see Fig. 2), so we are confident that it furnished reliable daily estimates of large tiger shark abundance. Nevertheless, to assess the validity of the model's predictions and test whether pooling years introduced bias, we carried out a companion analysis involving running two-week averages of daily tiger shark catch rates centered on each day on which dugong density estimates were calculated; the results of this analysis did not differ from those presented below (see "Electronic supplementary material").

Statistical analyses

Dugong densities for individual survey zones were calculated by dividing the number of animals sighted by the area searched (ha). Densities for all survey zones 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 ($t_{118} = 2.19$, $P = 0.03$) (A. Wirsing et al., unpublished data). Thus, to ensure that dugong density estimates reflected actual patterns of habitat use, we multiplied deep habitat densities by the ratio between these two rates (1.14).

Foraging dugong densities for survey zones 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 (m³). This measure assumes that foraging animals should be distributed across habitats in proportion to food availability (van Baalen and Sabelis 1993).

Thus, after division by food supply, asymmetry between forager densities in two patch types serves as a proxy for the degree to which habitat choice is influenced by other factors, including perceived predation danger. Note that use of this habitat use metric requires that the analysis be restricted to foraging individuals; thus, only survey data from 2002 to 2004 were used to generate forager densities, as activity states were not determined between 1997 and 1999. Foraging dugong densities for survey zones 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. We sighted ten mother–calf pairs engaged in foraging while conducting transects. The behavior of dugong calves mirrors that of their mother, so we treated these pairs as one individual for purposes of analysis; removing them from consideration had no measurable effect.

We 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 varying degrees of freedom, and therefore facilitates rigorous evaluation of competing hypotheses (Burnham and Anderson 1998; Anderson et al. 2000). Four primary competing models of food-corrected forager density were evaluated: (1) a model based on large tiger shark abundance (S), to test whether variation in predator numbers was accompanied by changes in foraging dugong density but neither a habitat shift nor a habitat preference (i.e., to challenge the food quantity hypothesis); (2) a model based on both shark abundance and habitat category (deep versus shallow; H), to assess whether foraging dugongs consistently overused one habitat after accounting for changes in overall dugong and predator abundance (i.e., to challenge the food quality hypothesis); (3) a model incorporating shark abundance and its interaction with habitat category (H × S), to test whether fluctuation in predator numbers was accompanied by changes in dugong density and a habitat shift (i.e., to test for an exchange of food for safety and thereby challenge the predation risk sensitivity hypothesis); and (4) a full model including shark abundance, its interaction with habitat, and habitat type to test whether foragers evinced a threat-sensitive shift but nevertheless maintained an overall habitat preference. In our study area, sea surface temperature (T) and shark abundance covary (Heithaus 2001). Thus, we also evaluated four secondary models, each replacing shark abundance with temperature (i.e., T, T + H, T + H × T, and T + H × T + H), to ensure that any statistical relationships

between predator abundance and foraging dugong habitat use were not a spurious consequence of correlation between shark numbers and temperature. 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). We 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 the best among a set of competitors, and the change in AIC_c between models (Δ AIC_c), were used to assess model uncertainty (Burnham and Anderson 1998). The predictive strengths of individual explanatory variables were evaluated using coefficient estimates with 95% confidence intervals (Burnham and Anderson 1998).

Note that nonlinear transformation of the continuous independent variables in our analyses of dugong and foraging dugong density (DOY, shark catch rate, temperature) did not improve the performance of any of the linear models considered (Δ AIC_c ≤ 2, Burnham and Anderson 1998). Thus, only linear models are presented.

Results

Dugong density

We sighted 528 dugongs while conducting transects. Most sightings (320 of 398) were of solitary animals, and group size averaged 1.33 (±0.09, 95% CI) individuals, facilitating robust estimation of survey zone (and overall) densities. The density of dugongs in the study area varied temporally, with warm season estimates (September–May) exceeding those for the cold season (June–August) (Fig. 3a). 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 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 1; Fig. 3b). After blocking for spatial (i.e., survey zone) effects, average seagrass biomass estimates for quadrat samples from shallow habitats (0.17 m³ ± 0.01, 95% CI) greatly exceeded those for deep areas (0.01 m³ ± 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 1; Fig. 3c). Finally, after accounting for temporal and habitat effects, sea surface temperature was a significant predictor of dugong density (Table 1).

Fig. 3a–d **a** Daily estimates of overall dugong density (*open circles*, number per ha^{-1}) in relation to day-of-year (DOY; three years pooled); the cold season (June–August) is marked with a *gray line*. **b** Annual trends in dugong density (each trend line is labeled with a year). **c** Daily estimates of dugong density in shallow (*open circles*, *gray line*) and deep (*filled circles*, *black line*) habitat. **d** Daily estimates of dugong density in relation to sea surface temperature ($^{\circ}\text{C}$). *Trend lines* were generated using distance-weighted least squares smoothing (DWLS, tension 1.0, SYSTAT 10.2)

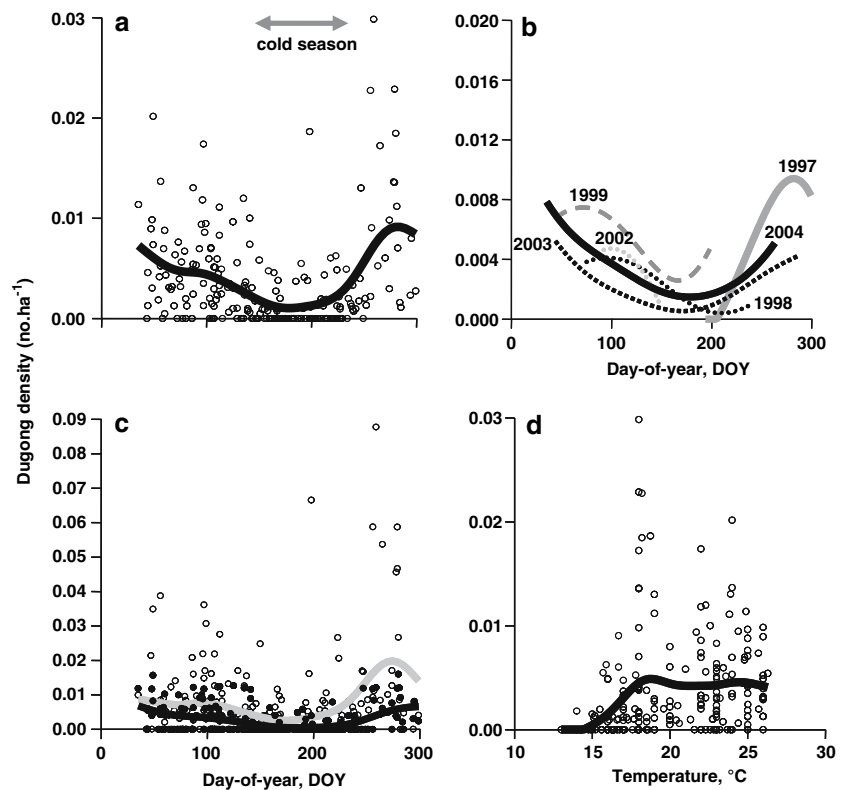


Table 1 Generalized linear model of dugong density (day^{-1}) in Shark Bay, Western Australia, as a function of day-of-year (DOY, expressed continuously), year, habitat (shallow versus deep), and sea surface temperature ($^{\circ}\text{C}$)

Factor	df	θ	SE (θ)	95% CI	P
DOY	1	0.009	0.002	0.006 to 0.012	<0.001
Year	5	-0.062	0.027	-0.115 to -0.009	0.001
Habitat	1	-0.859	0.143	-1.139 to -0.578	<0.001
Temperature	1	0.270	0.036	0.199 to 0.340	<0.001

For all independent variables, coefficient estimates (θ) are accompanied by standard errors and 95% confidence intervals (CI). All interactions were excluded from the final model (all $P \geq 0.15$)

Although the relationship between water temperature and dugong abundance was positive, the highest density estimates coincided with intermediate temperatures (19–20 $^{\circ}\text{C}$) (Fig. 3d).

Foraging dugong habitat use

Between 2002 and 2004, we sighted 151 foraging dugongs while conducting transects. Most encounters (83 of 113) involved solitary animals, and group size averaged 1.34 (± 0.33) individuals, facilitating reliable estimation of forager densities for survey zones, 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 ($H \times S$; Table 2);

this model explained 21% of the observed daily variation in forager density across the two habitat types (Table 2). The Akaike weight (w) for this model (0.86) suggested that its probability of being superior to the others under consideration was high; indeed, its closest competitor was approximately eight times less likely to be preminent (Table 2). Furthermore, the 95% confidence intervals for the coefficient estimates of shark abundance (7.40–23.86) and its interaction with habitat (18.23–109.51) did not encompass zero, suggesting that the relationships between these parameters and forager density were statistically significant. The coefficient estimate for shark abundance was positive (15.63), indicating that foraging dugong density increased with shark numbers. The inclusion of the interaction between shark abundance and habitat in the best model, however, means that the degree to which food-adjusted forager densities and predator abundance were associated differed as a function of habitat type: increases in shark abundance corresponded with marked elevation in the use of only deep habitat by foraging dugongs (Fig. 4). On days when foragers were sighted ($n = 69$), the extent to which use of deep survey zones exceeded that of shallow survey zones following food adjustment (i.e., preference for deep patches) correlated positively with tiger shark abundance (linear regression, $r^2 = 0.17$, $t_{67} = 3.73$, $\beta = 6.41$, $P < 0.001$; Fig. 5). By implication, input matching occurred when sharks were scarce, while the tendency of foragers to overuse deep habitats was greatest when sharks were most abundant (Figs. 4, 5).

Table 2 Competing models of the density of foraging dugongs across two habitat types (shallow and deep)

Model	K	Δ	w	R^2_L
S + (H × S)	3	0.000	0.864	0.208
S + H + (H × S)	4	4.124	0.110	0.204
S + H	3	7.692	0.018	0.196
T + (H × T)	3	10.392	0.005	0.191
T + H + (H × T)	4	11.870	0.002	0.192
T + H	5	13.994	0.001	0.186
S	3	36.609	0.000	0.147
T	5	48.093	0.000	0.129
Constant	1	127.643	0.000	–

Forager densities within each habitat were expressed as counts within survey zones ($n = 14$, replicated seven times per habitat category) divided by food supply (seagrass volume, m^3). Models were generated using linear combinations of habitat (H), an estimate of large (>3 m) tiger shark abundance (S), sea surface temperature ($^{\circ}C$) (T), the interaction between habitat category and shark abundance ($H \times S$), and the interaction between habitat and water temperature ($H \times T$), 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 pre-eminence), and R^2_L is the R^2 analog for models analyzed using maximum-likelihood

Resting dugong habitat use

We sighted 31 resting dugongs while conducting transects, all of which were solitary. Only four individuals (12.9%) were observed resting in shallow habitat, indicating a strong tendency to select deep (safe) habitats among individuals engaged in this potentially dangerous behavior (logistic regression, $t_{229} = 3.67$, and $P < 0.001$).

Discussion

Consumers are predicted to match their resources when predation risk is low and to trade food for safety by avoiding dangerous habitats when risk is high (Power 1984a, 1984b; Abrahams and Dill 1989; van Baalen and Sabelis 1993). Habitat use patterns of this nature are difficult to document in the field, however, especially when the consumer of interest is highly mobile and manipulative experimentation is implausible. Here, using predictable numerical variation in predator abundance to conduct a natural experiment, we show that the habitat use decisions of a large, wide-ranging marine herbivore match this theoretical expectation. After adjustment for food supply, foraging dugong densities were not proportional in shallow and deep habitats throughout the year (rejecting the food availability hypothesis). Rather, the degree of similarity between

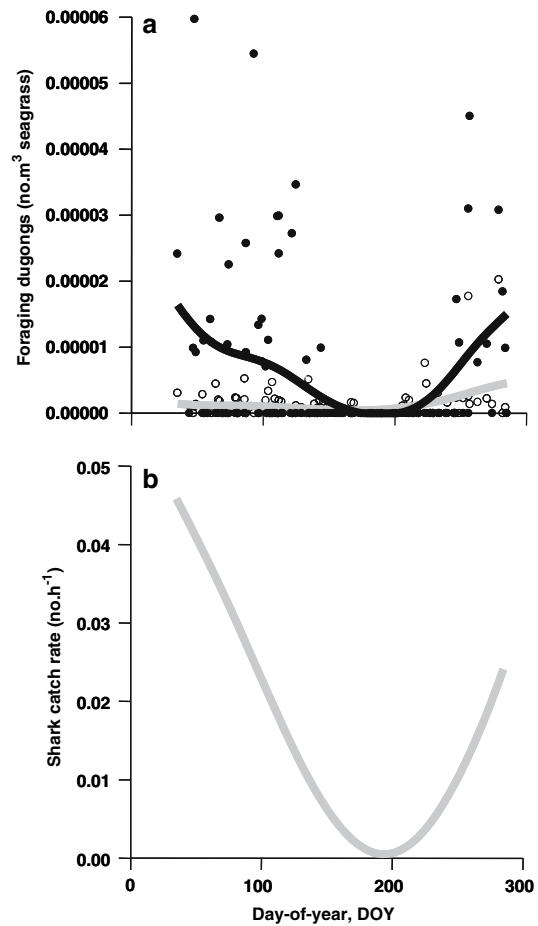


Fig. 4a–b Relationships between day-of-year (DOY) and **a** daily estimates of foraging dugong counts divided by seagrass volume (m^3) in shallow (open circles, gray line) and deep (filled circles, black line) habitats and **b** predicted large (>3 m) tiger shark catch rate. Trend lines created using DWLS smoothing (tension 1.0)

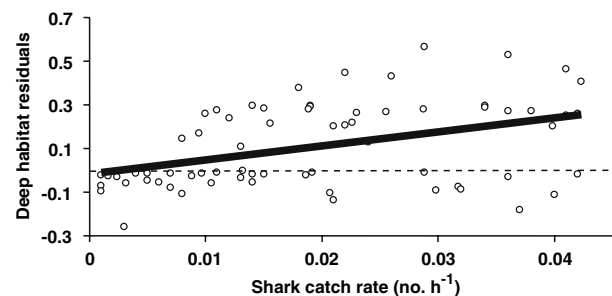


Fig. 5 Residual counts of foragers in deep habitat (observed counts—expected counts based on food supply) versus daily large tiger shark catch rate (open circles, no. caught h^{-1}). Residuals were $\log(x + 1)$ -transformed to homogenize variances. Equality between observed and expected deep counts (i.e., residual values equaling 0; dashed line) signifies proportional habitat use by foragers, after adjustment for food biomass (input matching). Large, positive residual values signify over-use of deep habitat

forager densities relative to food in shallow and deep habitats was correlated with large tiger shark abundance: we observed input matching (i.e., an ideal free distribution) when sharks were scarce, overuse of deep habitats when sharks were common, and strong association between daily measures of shark abundance and the extent to which deep habitats were overused. Thus, dugongs apparently (1) are sensitive to variation in predation risk across habitats, (2) perceive deep patches to be safe relative to shallower patches, and (3) manage their probability of death by allocating time to inherently safe but impoverished foraging patches in proportion to the overall danger associated with their surroundings.

Our conclusion that dugongs perceive deep foraging areas as havens from predation is corroborated by the tendency of animals at rest (a high-risk activity providing no benefit when undertaken in dangerous habitat) to use deep habitat almost exclusively, the fact 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), and the tendency of other prey species of tiger sharks (bottlenose dolphins, *Tursiops* sp.; pied cormorants, *Phalacrocorax varius*) to also shift into deep foraging habitats when sharks are abundant (Heithaus and Dill 2002; Heithaus 2005). We 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 our study area, deep water foraging likely entails a substantial nutritional cost. Given that the rhizomes of *A. antarctica* are inaccessible to dugongs (Anderson 1986), and that aboveground seagrass biomass was extremely low in deep survey zones, it is highly likely that individuals feeding in the deep habitats we surveyed experience depressed intake rates. Furthermore, deep substrates in our study area are composed primarily of sand and silt (Travers and Potter 2002; Heithaus 2004a), and are largely devoid of tropical seagrass species (Walker et al. 1988; A. Wirsing, 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) (Ward et al. 2000). We consider this scenario to be unlikely since territorial behavior has not been observed in our study area and foraging dugongs often

congregate in preferred feeding areas (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 distribution of tropical seagrass species is consistent with that of *A. antarctica*, but changes in tropical seagrass availability in the shallows also could have contributed to the observed habitat shift. This scenario lacks support because the availability of tropical species in the shallows decreases during the winter in our study area (D. Burkholder, unpublished data). If dugongs adjust their relative use of deep and shallow habitats in response to tropical seagrass biomass, then we would have expected them to reduce, rather than increase, their relative use of shallow banks as tiger shark numbers dropped.

Interestingly, while ambient thermal conditions did not affect the patch choices of foraging dugongs within the study area, they did influence the extent to which dugongs used the study area itself (i.e., larger-scale space use). Specifically, the periodic pattern of overall dugong abundance we observed was inversely related to sea surface temperature. This trend is consistent with previous studies of dugong distribution in Shark Bay, which have shown that dugongs using our study site during the warm season tend to shift northward and/or to the Western Gulf during the cold season (e.g., 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 we sighted dugongs with some regularity even when water temperatures were as low as 16 °C. Thus, while dugong densities apparently are influenced by water temperature over large spatial scales, individuals can use particular areas where ambient temperatures are 19 °C or less (see also Lanyon et al. 2005; Sheppard et al. 2006).

The possibility that large marine predators like sharks exert top-down effects on marine communities has received some empirical support (e.g., Myers et al. 2007) but remains contentious (Heithaus 2004b). 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 (bottlenose dolphins and pied cormorants), 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, are found primarily in shallow areas. Thus, it is possible that their presence leads sharks to hunt predominantly in the shallows and initiates this indirect relationship between sharks and teleosts (Dill et al. 2003). The results from the present study suggest that tiger sharks elicit a similar habitat

shift by dugongs. Although the impact of dugongs on the temperate seagrasses of Shark Bay is not known, grazing by dugongs can alter the composition and structure of seagrass meadows, seagrass nutrient content, and detrital cycles (de Iongh et al. 1995; Preen 1995; Nakaoka and Aioi 1999; Masini et al. 2001; Aragonés et al. 2006). Hence, this shift may in turn affect the distribution and abundance of other species (e.g., invertebrates, teleosts) that rely on seagrass for shelter and subsistence and the quality of forage available to mesograzers. We can speculate, then, that tiger sharks may not only exert an 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 trigger trophic cascades within seagrass communities. Collectively, these results suggest that apex predators such as tiger sharks may help to structure marine ecosystems, and further that overexploitation of these predators may have consequences for prey distributions and ecosystem dynamics. 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.

Finally, our results help to underscore the potentially broad scope of intimidation by predators in marine environments. Despite wide interest in the implications of fear for ecological communities (Brown and Kotler 2004), to date its effects on consumers in marine systems have rarely been demonstrated (Dill et al. 2003). One notable example involves several zooplankton taxa, which appear to shift from shallow to deep, relatively nutrient-poor strata of the water column during the day as a means of minimizing their vulnerability to visually orienting predators (Hays 2003). Our studies in Shark Bay show analogous exchanges of food for safety in bottlenose dolphins (Heithaus and Dill 2002, 2006), sea birds (Heithaus 2005), and now dugongs. In all of these cases, observed prey behavioral adjustments (i.e., habitat shifts) were substantial, and consistent with expectations based on spatial and temporal patterns of food distribution and predation risk. Thus, we conclude that (1) the influence of predator intimidation in marine environments is apparently widespread, and that its implications should be considered even for species, like the dugong, that are long-lived and do not suffer heavy predation rates, and (2) spatial responses by marine prey to fear in at least some communities can be predicted using a combination of habitat characteristics and the first principles of behavioral ecology.

Acknowledgments We thank R. Abernethy, V. Alla, L. Barre, F. Bretos, S. Buchannan, T. Bujas, J. Burghardt, S. Burghardt, C. Chow, M. Davis, H. Finn, C. Genrich, P. Green, A. Greenley, K. Harper, L. Heithaus, M. Kerford, S. Kowalewsky, A. Krickan, J. Lasky, L. Marshall, K. Martin, J. McLash, R. McPhie, B. Stalvey, J. Wilder, and K.

Wirsing for field assistance. This material is based in part upon work supported by the National Science Foundation under Grant Number 0526065. Other grants and support were provided by Australian Geographic, Humminbird, Mercury Marine Australia, Monkey Mia Dolphin Resort, Monkey Mia Wildsights (Shotover), National Geographic Society Expeditions Council, National Geographic Remote Imaging, NSERC Canada grant A6869 to L.M. Dill, PADI Foundation, Shakespeare Electronics, Shark Bay Fish Factory, University of Western Australia, and public donations. We are grateful to I. Anderson, B. Barton, C. Beck, K. Crane, A. Fraser, I. Gordon, D. Rose, R. Swann, and D. Witt for logistical support. Special thanks go to D. Charles for advice, D. Capewell, and the Yadgalah Aboriginal Corporation for information about dugongs, D. Massey for extra field housing, H. Raven for temperature data, E. Elle, J. Estes, G. Hays, P. Peterson, B. Sargeant, R. Ydenberg, and anonymous reviewers for helpful comments, B. Smith, and T. Steury for statistical help, B. Black, J. Heyman, and R. Holst for their hospitality, and the Dill lab for helpful suggestions. This research was conducted under Fisheries Western Australia permits 67/97 and 08/01, Western Australia Department of Conservation and Land Management permits NE001808, SF002347, SF003818, SF004228, and SF004542, SW008085, and renewals, and Simon Fraser University Animal Care permits 639B and 653B, and complied with the current laws of the country in which it was performed. This is contribution number 27 of the Shark Bay Ecosystem Research Project.

References

- Abrahams MV, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999–1007
- Abrams PA (1995) Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *Am Nat* 146:112–134
- Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. *J Wildl Manage* 64:912–923
- Anderson PK (1986) Dugongs of Shark Bay, Australia—Seasonal migration, water temperature, and forage. *Natl Geogr Res* 2:473–490
- Anderson PK (1995) Scarring and photoidentification of dugongs (*Dugong dugon*) in Shark Bay, Western Australia. *Aq Mam* 21:205–211
- Anderson PK, Prince RIT (1985) Predation on dugongs: attacks by killer whales. *J Mammal* 66:554–556
- Aragonés LV, Lawler IR, Foley WJ, Marsh H (2006) Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? *Oecologia* 149:635–647
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014
- Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *J Mammal* 80:385–399
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York
- Chilvers BL, Delean S, Gales NJ, Holley DK, Lawler IR, Marsh H, Preen AR (2004) Diving behaviour of dugongs, *Dugong dugon*. *J Exp Mar Biol Ecol* 304:203–224
- Crawley MJ (1983) Herbivory. University of California Press, Los Angeles, CA
- de Iongh HH, Wenno BJ, Meelis E (1995) Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aq Bot* 50:1–19
- Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* 84:1151–1157
- Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distributions in birds: I. Theoretical developments. *Acta Biotheor* 19:16–36

- Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Cons Ecol* 6(1):11 (<http://www.consecol.org/vol6/iss1/art11>)
- Gales N, McCauley RD, Lanyon J, Holley D (2004) Change in abundance of dugongs in Shark Bay, Ningaloo and Exmouth Gulf, Western Australia: evidence for large-scale migration. *Wildl Res* 31:283–290
- Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–170
- Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet and seasonal changes in catch rates. *Environ Biol Fish* 61:25–36
- Heithaus MR (2004a) Fish communities of seagrass meadows and associated habitats in Shark Bay, Western Australia. *B Mar Sci* 75:79–99
- Heithaus MR (2004b) Predator-prey interactions. In: Carrier JC, Musick J, Heithaus MR (eds) *The biology of sharks, skates, and rays*. CRC Press, Boca Raton, FL, pp 487–521
- Heithaus MR (2005) Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Mar Biol* 147:27–35
- Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480–491
- Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* 114:257–264
- Heithaus MR, Dill LM, Marshall GJ, Buhleier BM (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a subtropical seagrass ecosystem. *Mar Biol* 140:237–248
- Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Bejder L (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J Anim Ecol* (in press). doi:10.1111/j.1365-2656.2007.01260.x
- Lanyon J, Johns T, Sneath HL (2005) Year round presence of dugongs in Pumicestone Passage, south-east Queensland, examined in response to water temperature and seagrass distribution. *Wildl Res* 32:361–368
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elf, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Can J Zool* 79:1401–1409
- Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27:215–290
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ Biol Fish* 47:203–211
- Marsh H, Channells PW, Heinsohn GE, Morrissey J (1982) Analysis of stomach contents of dugongs from Queensland. *Aust Wildl Res* 9:55–67
- Marsh H, Prince RIT, Saalfeld WK, Shepherd R (1994) The distribution and abundance of the dugong in Shark Bay, Western Australia. *Wildl Res* 21:149–161
- Masini RJ, Anderson PK, McComb AJ (2001) A *Halodule*-dominated community in a subtropical embayment: physical environment, productivity, biomass, and impact of dugong grazing. *Aq Bot* 71:179–197
- McNamara JM, Houston AI (1987) Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850
- Nakaoka M, Aioi K (1999) Growth of the seagrass *Halophila ovalis* at the dugong trails compared to existing within-patch variation in a Thailand intertidal flat. *Mar Ecol Prog Ser* 184:97–103
- Peacor SD, Werner EE (2000) Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. *Ecology* 81:1998–2010
- Peacor S, Werner E (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc Natl Acad Sci USA* 98:3904–3908
- Power ME (1984a) Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *J Anim Ecol* 53:357–374
- Power ME (1984b) Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* 65:523–528
- Preen A (1995) Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Mar Ecol Prog Ser* 124:201–213
- Preen AR, Marsh H, Lawler IR, Prince RIT, Shepherd R (1997) Distribution and abundance of dugongs, turtles, dolphins, and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildl Res* 24:185–208
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509
- Schmitz OJ (2003) Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* 6:156–163
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163
- Sheppard JK, Preen AR, Marsh H, Lawler IR, Whiting SD, Jones RE (2006) Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. *J Exp Mar Biol Ecol* 334:64–83
- Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043
- Simpfendorfer CA, Goodreid AB, McAuley RB (2001) Size, sex, and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Environ Biol Fish* 61:37–46
- Travers MJ, Potter IC (2002) Factors influencing the characteristics of fish assemblages in a large subtropical marine embayment. *J Fish Biol* 61:764–784
- van Baalen M, Sabelis MW (1993) Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *Am Nat* 142:646–670
- Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav Ecol Sociobiol* 60:457–464
- Walker DI, Kendrick GA, McComb AJ (1988) The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aq Bot* 30:305–317
- Ward JF, Austin RM, Macdonald DW (2000) A simulation model of foraging behaviour and the effect of predation risk. *J Anim Ecol* 69:16–30
- Warner RR (1998) The role of extreme iteroparity and risk-avoidance in the evolution of mating systems. *J Fish Biol* 53(Suppl A):82–93
- Werner EE (1998) Ecological experiments and a research program in community ecology. In: Reseritis WJ, Bernardo J (eds) *Experimental ecology: issues and perspectives*. Oxford University Press, Oxford, UK, pp 3–26
- White GC, Bennets RE (1996) Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549–2557
- Wirsing AJ, Heithaus MR, Dill LM (2006) Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. *Mar Biol* 149:961–968
- Wirsing AJ, Heithaus MR, Dill LM (2007) Dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Anim Behav* 74:93–101