# Can measures of prey availability improve our ability to predict the abundance of large marine predators?

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

**Abstract** Apex marine predators can structure marine communities, so factors underlying their abundance are of broad interest. However, such data are almost completely lacking for large sharks. We assessed the relationship between tiger shark abundance, water temperature, and the availability of a variety of known prey over 5 years in Western Australia. Abundance of sharks in four size categories and the density of prey (cormorants, dugongs, sea snakes, sea turtles) were indexed using daily catch rates and transects, respectively. Across all sizes, thermal conditions were a determinant of abundance, with numerical peaks coinciding with periods of high water temperature. However, for sharks exceeding 300 cm total length, the inclusion of dugong density significantly improved temperature-based models, suggesting that use of particular areas by large tiger sharks is influenced by availability of this sirenian.

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

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,
North Miami, FL 33181, USA
e-mail: wirsinga@fiu.edu

We conclude that large marine predator population models may benefit from the inclusion of measures of prey availability, but only if such measures consider prey types separately and account for ontogenetic shifts in the diet of the predator in question.

## Introduction

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

Large sharks, which may play an important structural role in marine ecosystems (Heithaus 2004a; Shepherd and Myers 2005), are undergoing a global decline (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005). To date, little is known about the determinants of their abundance and distribution (Kohler and Turner 2001; Baum and

Myers 2004), hindering both predictions concerning population viability and the establishment of effective conservation measures. Some authors have proposed that large sharks use areas based primarily on abiotic conditions such as water temperature (e.g., Randall 1992), while others have argued that prey availability is also likely important (e.g., Heithaus 2004a). However, to our knowledge, no study has addressed the relative extent to which abiotic and biotic factors explain large shark abundance in one area. Accordingly, we explored the relationship between the abundance of tiger sharks (*Galeocerdo cuvier*), prey availability, and the thermal environment in the relatively pristine marine community of Shark Bay, Western Australia.

In the eastern gulf of Shark Bay, tiger shark numbers show strong annual periodicity, with peak levels of abundance coinciding with the height of the Austral summer (January–February) and troughs occurring during the cold season (July) (Heithaus 2001a; Wirsing et al. 2006). When assessed on a coarse (monthly) basis between 1997 and 1999, this trend in shark abundance showed strong, positive correlation with sea surface temperature (Heithaus 2001a). However, a substantial amount of variation in shark abundance was left unexplained (25%), and numbers of sharks in cool months sometimes exceeded those in warm months, leading to speculation that changes in tiger shark numbers within and between years may be driven in part by the availability of their major prey species (dugongs, *Dugong dugon*; pied cormorants, *Phalacrocorax varius*; sea snakes, *Aipysurus pooleorum*, *Disteria major*, *Hydrophis elegans*; and sea turtles, *Caretta caretta*, *Chelonia mydas*; Heithaus 2001a). Thus, using data collected systematically over a longer period (5 years 1998–2004, 2000–2001 excluded), we sought to address this possibility rigorously by comparing the predictive power of shark abundance models based solely on temperature to those including prey availability. Given that tiger sharks undergo ontogenetic dietary shifts (Lowe et al. 1996; Simpfendorfer et al. 2001), we also asked whether any predictive improvements stemming from the inclusion of large-bodied prey (i.e., dugongs and sea turtles) availability were restricted to models of large [$\geq$ 300 cm total length (TL)] shark abundance.

## Materials and methods

### Study site

This study was undertaken in the eastern gulf of Shark Bay ($\sim$ 25°45′S, 113°44′E). Shark Bay has been listed as a World Heritage Site since 1991, and the local tiger shark population is relatively undisturbed (Heithaus 2001a), enabling an assessment of the numerical relationship between tiger sharks and their prey under relatively pristine conditions.

### Tiger shark abundance

Tiger sharks were caught on single-hook drumlines ($n = 10$) deployed in six fishing zones throughout the study area (160 km²). All zones featured similar habitats and little variation in catch rates existed among them (Heithaus et al. 2006), so they were considered to be functionally equivalent. One zone was sampled per day, and all sharks caught were measured (TL), tagged, and released (for details, see Heithaus 2001a and Wirsing et al. 2006). Daily catch rates ($n = 204$ days spanning 32 months; all months represented save November and December) were expressed as the number of sharks hooked per baited hook hour. A measure of sea surface temperature (°C) was recorded at a constant location on each day of shark fishing.

### Prey availability

We assessed patterns of prey abundance using transect passes through 14 survey zones (SZ), which were allocated evenly to deep ($\geq$ 6 m depth) and shallow ($\leq$ 4 m) habitats within the study area. Each zone consisted of a 100-m sighting belt bisected by a central transect line, yielding an average sampling area of 0.71 km² (SD = 0.13). Transect effort was distributed evenly across days ($n = 189$, mean = 7.63 passes day$^{-1}$, SD = 2.45), months (mean = 45.61 $\pm$ 18.01 passes month$^{-1}$), and SZ (shallow mean = 3.96 $\pm$ 1.64 passes; deep 3.71 $\pm$ 1.68 passes). SZ within shallow and deep categories were selected haphazardly to ensure that all portions of the study area were monitored evenly, and each SZ was not visited more than once per day. To reduce the effects of tidal and diel variation, the order and direction in which transects were driven each day were haphazard. Transects were conducted in Beaufort wind conditions $\leq$ 2 to minimize sighting bias caused by poor weather.

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

Prey densities for SZ were calculated by dividing the number of animals sighted by the area searched (square kilometers). Dugongs are large and difficult to miss from close range (i.e., within 100 m), so all dugongs recorded ($n = 416$) during each pass through a SZ were used to generate density estimates. In contrast, cormorants, sea turtles, and sea snakes are more difficult to spot. Thus, we generated density estimates for cormorants ($n = 6,139$) and sea turtles ($n = 923$) using a 60-m sighting belt, and sea snakes ($n = 178$) using a 10-m sighting belt. Species-specific prey densities for all SZ visited on a given day were pooled into shallow and deep categories; daily densities for the study area were derived by summing the densities for shallow and deep habitats, weighted by the proportional coverage of each habitat category.

For air-breathing vertebrates, time spent at the surface may differ as a function of water depth. To account for this potential source of sighting bias, we multiplied our estimates of dugong and sea turtle density in deep SZ by the ratio of their surface times in the two habitats (A. J. Wirsing et al., unpublished data; Heithaus et al. 2002). Cormorant and sea snake counts in deep SZ were not converted because habitat-specific surface times were not available. To test for bias stemming from the use of raw deep-habitat density estimates for these two prey types, we conducted sensitivity analyses involving cormorant and sea snake count data from deep SZ multiplied by factors of 2 and 0.5 (i.e., factors of greater magnitude than those characterizing the conversions for dugongs and sea turtles). These analyses produced results matching those reported below.

Data analysis

Assessment of prey and shark numbers was rarely concurrent. Thus, daily estimates of shark and prey abundance were averaged into 2-week bins ($n = 58$) prior to analysis. Importantly, bins incorporated shark catch rate data from an average of 3.5 zones ($\pm 1.6$, SD), ensuring that catch rates for any given 2-week interval indexed numbers of sharks in the entire study area. Bi-weekly catch rates were generated for tiger sharks belonging to four size categories: (1) 241–270 cm; (2) 271–300 cm; (3) 301–330 cm; and (4) $\geq 331$ cm (maximum = 445 cm). Note that sharks < 241 cm TL were excluded from the analysis because of insufficient sample size. We assumed that sharks belonging to each successive category would be increasingly likely to kill and consume large-bodied prey (see Lowe et al. 1996; Simpfendorfer et al. 2001; Heithaus 2001a, b), and that sharks within particular categories would target similar prey. The categories contained large and approximately even proportions (0.23, 0.23, 0.21, and 0.32, respectively) of the overall number of sharks caught ($n = 303$).

Generalized linear models of tiger shark abundance within each size category were built using backwards elimination ($\alpha = 0.05$) and bi-weekly averages of cormorant, dugong, sea snake, and sea turtle density, and sea surface temperature as independent variables. We invoked temperature as a continuous variable. Given the possibility that this factor might instead act seasonally (i.e., as a threshold effect), however, we also ran an analysis with water temperature expressed discretely as warm season (> 20°C) versus cold season ($\leq 20$°C). The results of this analysis were equivalent to those presented below (S1). Correlation between the independent variables was low enough (all Pearson correlation coefficients $\leq 0.48$, mean = 0.25) to allow for independent assessment (Burnham and Anderson 1998). The dependent variable for the models, bi-weekly shark catch rate, consisted of non-negative integer values (i.e., counts of sharks) divided by the number of hours fished. Moreover, within each shark size category, catch rates were characterized by a low mean and large variance. Thus, models were fit using maximum-likelihood under the assumption of a Poisson error distribution and, therefore, with a log link function (Selvin 1995). For each size category, the predictive strengths of explanatory variables included in the final model of shark abundance were evaluated using coefficient estimates with 95% confidence intervals; variables with confidence intervals not encompassing zero were considered to be both statistically significant and biologically meaningful (Burnham and Anderson 1998). $R^2$ analogues for models analyzed using maximum-likelihood ($R^2_L$; calculated as one minus the percent difference in the negative log likelihood value for the model in question and the constant-only model) were used to index the amount of variation in the dependent variable explained by each final model. In cases where final models incorporated measures of prey availability, $R^2_L$ values for the temperature-only model are also presented for purposes of comparison. We checked for the presence of temporal autocorrelation in the residuals of all final models using the Durbin–Watson test statistic (Durbin and Watson 1950). In all cases, the null hypothesis of no autocorrelation was supported.

Results

Tiger sharks 241–270 cm TL

The abundance of tiger sharks between 241 and 270 cm TL was best explained by a model incorporating sea surface temperature (Table 1). This model was highly significant (Table 1), and explained 16% of the observed bi-weekly variation in the abundance of these sharks ($R^2_L$). The temperature variable featured a positive coefficient estimate with a 95% confidence interval not encompassing zero

**Table 1** Generalized linear models of tiger shark abundance for each of four size categories (divisions based on total length (*TL*; cm). Independent variables are sea surface temperature (*T*; °C) and the density of cormorants, dugongs (*D*), sea snakes, and sea turtles. Models were fit under the assumption of a Poisson error distribution, and only final models with significant main effects ($\alpha = 0.05$) are presented[a]. Main effects are accompanied by coefficient estimates (*β*) with 95% confidence intervals and *P*-values

| Shark size class (TL; cm) | Term | *β* | 95% CI | *df* | *P* |
|---|---|---|---|---|---|
| 241–270 | *T* | 0.20 | 0.12, 0.27 | 1 | 0.002 |
| 271–300 | *T* | 0.21 | 0.12, 0.30 | 1 | < 0.001 |
| 301–330 | *D* | 238.83 | 162.67, 314.98 | 1 | < 0.001 |
|  | *T* | 0.18 | 0.09, 0.27 | 1 | < 0.001 |
| ≥ 331 | *D* | 128.44 | 62.94, 193.94 | 1 | < 0.001 |
|  | *T* | 0.26 | 0.18, 0.33 | 1 | < 0.001 |

[a] Note, variables for cormorants, sea snakes, and sea turtles were eliminated from all final models (*P* always > 0.05)

(Table 1), meaning that the abundance of sharks within this size category increased as ambient temperature rose.

## Tiger sharks 271–300 cm TL

The final model of the abundance of tiger sharks 271–300 cm TL included sea surface temperature (Table 1). This model explained 18% of the observed variation in the abundance of these sharks. The positive coefficient estimate and confidence interval for the temperature variable indicate that increases in the abundance of sharks within this size category coincided with elevated water temperature.

## Tiger sharks 301–330 cm TL

The final model for tiger sharks between 301 and 330 cm TL included both dugong density and sea surface temperature (Table 1), and explained 33% of the variation in the abundance of these sharks. Both variables were highly significant and featured positive coefficient estimates and 95% confidence intervals (Table 1), implying that increases in the abundance of sharks within this size category corresponded with elevated dugong density and water temperature. The $R^2_L$ for the model based solely on water temperature (0.15) was less than half that of the final model.

## Tiger sharks ≥ 331 cm TL

The final model of the abundance of tiger sharks > 330 cm TL included dugong density and sea surface temperature (Table 1), and explained 32% of the observed variation in the abundance of these sharks. Both variables were highly significant and associated with positive coefficient

estimates and 95% confidence intervals (Table 1), meaning that increases in the abundance of these large sharks coincided with increased dugong density and water temperature. The $R^2_L$ for the model based solely on water temperature (0.17) was approximately half that of the final model.

## Discussion

The degree to which abiotic and biotic factors influence use of particular areas by large sharks has been a matter of much speculation (e.g., Klimey 1994; Heithaus 2001a; Simpfendorfer et al. 2001), but has not been the subject of rigorous empirical assessment (Heithaus 2004a). Consequently, our capacity to predict the distribution and abundance of these top predators is limited, hindering efforts to monitor their populations and evaluate their ecological role (Heithaus 2004a). Here, we present the first empirical demonstration that large shark abundance in particular areas is linked to both abiotic conditions (sea surface temperature) and the availability of prey. Specifically, using census data collected systematically over 5 years in a relatively pristine subtropical embayment (Shark Bay), we show that: (1) local changes in the abundance of tiger sharks can be predicted from measures of sea surface temperature, (2) the inclusion of measures of prey availability can markedly improve predictive models of tiger shark abundance based solely on temperature, and (3) the degree to which the inclusion of prey information improves the performance of temperature-based models depends on the shark size class and prey species considered. Our findings have important implications for the conservation of tiger sharks and the communities of which they are a part, and more generally for efforts to predict large marine predator numbers using abiotic conditions and prey-availability data.

The inclusion of prey density failed to improve upon temperature-based models of shark abundance for the two smallest size categories. This result may indicate that use of particular areas by tiger sharks < 300 cm TL (small sharks) is driven exclusively by changes in their thermal environment—cold temperatures may slow the metabolism of small sharks to a level precluding efficient prey capture, and thereby force habitat shifts. However, the relatively low $R^2_L$ values associated with the final models for both size categories (0.16 and 0.18, respectively) suggest that use of our study area by small sharks may be linked to changes in the availability of prey species that we failed to monitor and/or to factors other than local prey availability and temperature that were not incorporated in the models (e.g., prey availability and thermal patterns elsewhere).

The presence of large tiger sharks near dugong aggregations in Shark Bay has been noted (Anderson 1982), and

these sharks incorporate dugongs in their diet, leading to speculation that large tiger shark abundance within particular regions of the bay may be linked to the availability of this sirenian (Heithaus 2001a). Accordingly, we found that the abundance of tiger sharks greater than 300 cm TL (large sharks) was best predicted by the combination of sea surface temperature and dugong density rather than temperature alone. Tiger sharks are wide-ranging predators whose movements and habitat use patterns are undoubtedly dictated by multiple factors operating over large spatial scales (Randall 1992; Heithaus 2004a). Indeed, individual tiger sharks leaving Shark Bay have been shown to travel up to thousands of kilometers (Heithaus et al. 2007), and the time they allocate to our study site may well be influenced by patterns of food availability along these excursion paths. In that case, tight and temporally consistent associations between the use of particular areas by tiger sharks and local conditions (e.g., prey availability) would not necessarily be expected. Thus, the degree to which models incorporating only water temperature and dugong density explained observed variation in large shark abundance ($R^2_L$ values equaling 33 and 32%, respectively) is remarkable, in particular because our analysis was based on bi-weekly catch estimates characterized by substantial sampling error (e.g., the failure of even one hook to set in a shark attacking the bait during a 2-week interval would dramatically change its associated catch estimate). So, too, is the extent to which the inclusion of dugong density information improved strictly temperature-based models: the amount of variation explained increased by 120 and 88%, respectively. While dugong numbers were characterized by marked temporal variability over the course of this investigation, an overall decline was not observed (Wirsing et al. 2006), indicating that large sharks varied their use of our study area in response to both inter- and intra-annual variation in dugong abundance. The fact that sea turtle density was not retained in the best predictive model implies that large sharks use areas in relation to the availability of dugongs in particular, rather than large-bodied prey in general, perhaps because dugongs represent an especially energy-rich food source (Robbins 1993). Our finding that large tiger shark abundance is influenced strongly by the local availability of dugongs runs counter to the popular notion that tiger sharks are purely opportunistic feeders (Randall 1992), and suggests instead that the habitat use patterns of large individuals of this species may allow them to exploit spatial and temporal patterns in the abundance of favored prey.

Might our results have been influenced by interactions among tiger sharks of different sizes and the habitat use patterns of repeatedly caught individuals? We consider both of these possibilities to be unlikely. First, correlation between the numbers of sharks in each size class was always positive, and the numerical relationship between large and small sharks was weak (Pearson's $r = 0.16$). By implication, large sharks did not exclude smaller conspecifics from the study area, and the presence of small sharks (i.e., those within the smallest two size classes) did not attract larger ones. Second, tiger shark catch rates in Shark Bay are high across all of the size classes considered by this study (Heithaus 2001a; Wirsing et al. 2006). Moreover, recaptures are rare: of the 303 sharks caught, only 21 (7%) were recaptures, and only 12 (4%) were caught twice within the same year. Accordingly, we suggest that the influence of any one individual on the patterns of tiger shark abundance we observed would have been negligible.

Tiger sharks appear to be declining globally (Baum et al. 2003; Myers et al. 2007), yet information required to preserve this species is lacking, in part because logistical obstacles have precluded effective regional monitoring efforts. By taking advantage of an unprecedented opportunity to simultaneously evaluate trends in tiger shark abundance and the availability of known prey over 5 years, we have shown that, after accounting for the effects of the thermal environment, use of particular areas by large tiger sharks is influenced by the density of an energy-rich prey species (dugongs). Thus, we surmise that the abundance of dugongs is a determinant of habitat quality for these sharks and, more generally, that the abundance and distribution of tiger sharks throughout the species' range are likely influenced by the availability of locally important prey. Consequently, models assessing the viability of tiger shark populations may benefit from the inclusion of measures of the availability of major prey species, in particular if sharks within given size classes are matched to appropriate prey. The link between dugong and large shark abundance illuminated here also suggests that declines in dugong density could lead to dramatic reductions in the presence of large tiger sharks. Such reductions, which are occurring throughout much of the dugong's distribution (Preen 1998), could threaten the persistence of tiger shark populations where these two species coexist.

Finally, our study suggests that future efforts to predict the abundance of large marine predators should avoid making two key simplifying assumptions: (1) that individual predators respond to overall levels of prey availability, and (2) that all members of the predator population being investigated are functionally equivalent. We found that full models based on the availability of all prey species performed poorly, and only those incorporating numbers of specific prey species (i.e., dugongs) improved on simpler, temperature-based models. Accordingly, we suggest that approaches accounting for the possibility that large marine predators are exploiting particular prey species rather than overall prey abundance should be used whenever possible. We also found that measures of prey availability helped to predict the abundance of some shark size classes, but not

others. In general, then, we offer the suggestion that predictive models of abundance accounting for ontogenetic shifts in the diet of the predator species of interest may outperform those failing to address such shifts.

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