

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

## Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort

Received: 9 June 2005 / Accepted: 23 January 2006 / Published online: 25 February 2006  
© Springer-Verlag 2006

**Abstract** The tiger shark (*Galeocerdo cuvier* Peron and Lesueur 1822) is a widely distributed predator with a broad diet and the potential to affect marine community structure, yet information on local patterns of abundance for this species is lacking. Tiger shark catch data were gathered over 7 years of tag and release research fishing (1991–2000, 2002–2004) in Shark Bay, Western Australia (25°45'S, 113°44'E). Sharks were caught using drumlines deployed in six permanent zones (~3 km<sup>2</sup> in area). Fishing effort was standardized across days and months, and catch rates on hooks were expressed as the number of sharks caught h<sup>-1</sup>. A total of 449 individual tiger sharks was captured; 29 were recaptured. Tiger shark catch rate showed seasonal periodicity, being higher during the warm season (Sep–May) than during the cold season (Jun–Aug), and was marked by inter-annual variability. The most striking feature of the catch data was a consistent pattern of slow, continuous variation within each year from a peak during the height of the warm season (February) to a trough in the cold season (July). Annual growth rates of recaptured individuals were generally consistent with estimates

from other regions, but exceeded those for populations elsewhere for sharks > 275 cm fork length (FL), perhaps because mature sharks in the study area rely heavily on large prey. The data suggest that (1) the threat of predation faced by animals consumed by tiger sharks fluctuates dramatically within and between years, and (2) efforts to monitor large shark abundance should be extensive enough to detect inter-annual variation and sufficiently intensive to account for intra-annual trends.

### Introduction

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

Tiger sharks have been studied in a variety of locations, including the east coast of North America (e.g., Northwest Atlantic and Gulf of Mexico, Branstetter et al. 1987; western North Atlantic, Natanson et al. 1999; Northwest Atlantic, Baum et al. 2003), the Gulf of Mexico (Branstetter et al. 1987), the Hawaiian Islands

Communicated by J.P. Grassle, New Brunswick

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

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

M. R. Heithaus  
Department of Biological Sciences, Marine Biology Program, Florida International University, Biscayne Bay Campus AC1, 3000 NE 151 St, North Miami, FL 33181, USA

A. J. Wirsing  
Department of Biological Sciences,  
Florida International University,  
300 NE 151 St, North Miami, FL 33181, USA  
E-mail: wirsinga@fiu.edu  
Tel.: +1-305-9195819

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

Here, we present results from a 7 year (1997–2000, 2002–2004) study of tiger sharks in Shark Bay, Western Australia. Over the course of the investigation, which is an extension of the work of Heithaus (2001), sampling location, timing, and effort were held relatively constant. Thus, we were able to (1) determine whether the seasonal pattern of shark abundance documented by Heithaus (2001) remained consistent over a longer time interval, (2) test for variation in shark abundance within both warm and cold seasons, (3) address the magnitude of inter-annual variation in tiger shark abundance within a local area, and (4) compare growth rates of recaptured individuals to those of tiger sharks elsewhere. Because bait used in the study varied over time, we also (5) asked whether tiger shark catch rates were affected by different baits.

## Materials and methods

### Study site

This study was undertaken in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (25°45'S, 113°44'E). Shark Bay is a large (13,000 km<sup>2</sup>), semi-enclosed basin located roughly 900 km north of Perth, Western Australia (Fig. 1a, b). The study site (160 km<sup>2</sup>; Fig. 1b) features a patchwork of open embayment plains (6.5–15.0 m deep), swift-current

channels (6.5–12.0 m), and shallow banks ( $<4.0$  m). Most of the shallow habitat within the bay is dominated by extensive seagrass meadows (Walker 1989). In 1991, the Shark Bay region was listed as a World Heritage Area. The local tiger shark (*Galeocerdo cuvier* Peron and Lesueur 1822) population has been free from commercial fishing since 1994, and has never been subject to heavy harvest (Heithaus 2001). Thus, the study site has an intact and protected assemblage of tiger sharks and their major prey species (dugongs, *Dugong dugon*; pied cormorants, *Phalacrocorax varius*; sea snakes, primarily *Hydrophis elegans*; and sea turtles, *Caretta caretta*, *Chelonia mydas*; Heithaus 2001).

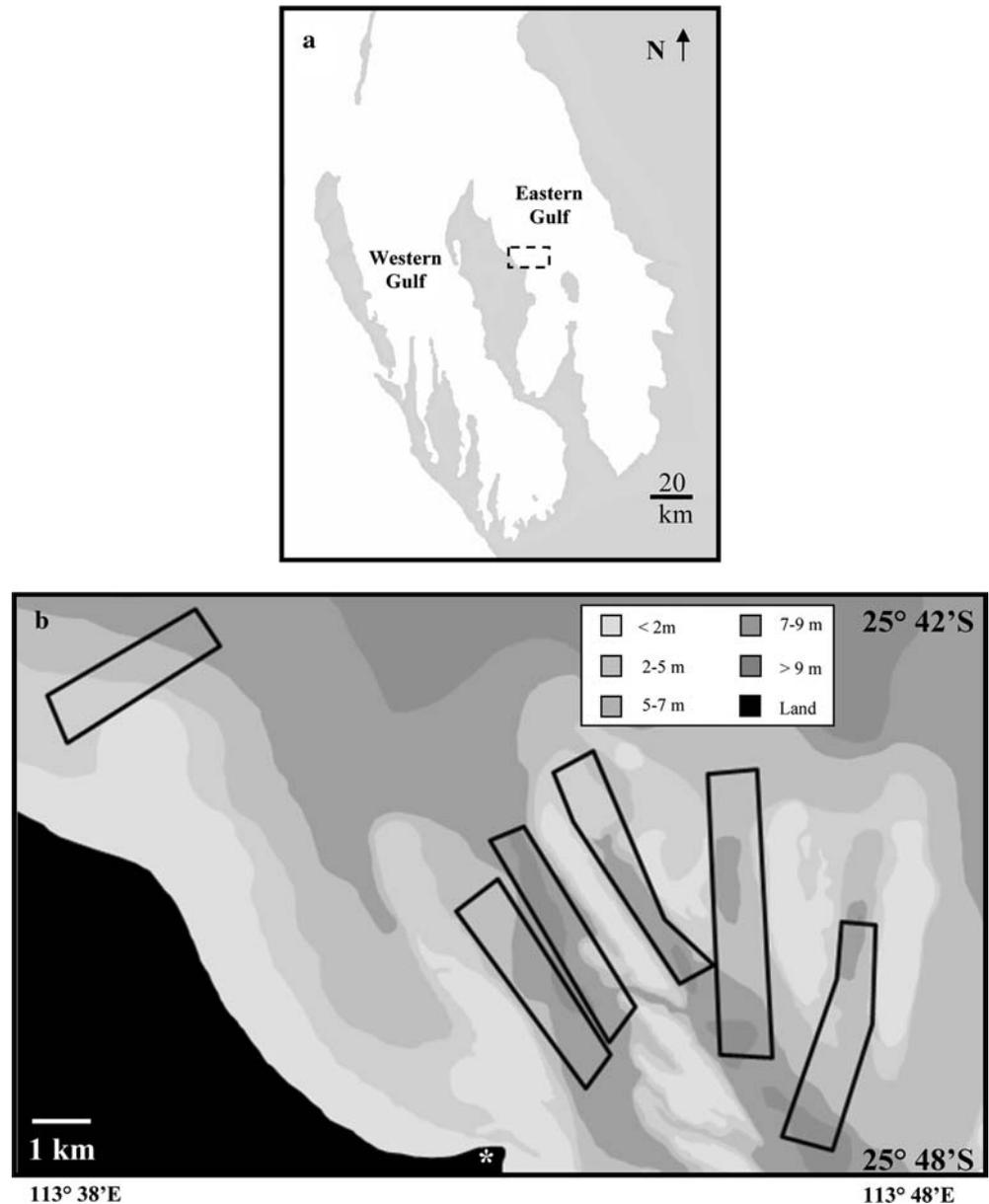
### Field methods

Over the course of the investigation (1997–2000, 2002–2004), we sampled tiger sharks in six deep-water fishing zones (Fig. 1b). Individual sharks were captured using drumlines equipped with a single hook (Mustad Shark Hook; size 13/0 used predominantly, with occasional use of sizes 12/0 and 14/0) fished at a depth of 0.7–2.0 m. Hooks were baited predominantly with Australian salmon (*Arripis truttaceus*, AS; 9,771 h; 70% of total fishing time). Between 2002 and 2004, four other bait species were used when AS was not available: baldchin groper (*Choerodon rubescens*, G; 189 h), sea mullet (*Mugil cephalus*, M; 256 h), pink snapper (*Pagrus auratus*, PS; 2,451 h), and tailor (*Pomatomus saltatrix*, T; 1,273 h). Ten drumlines were deployed concurrently in one or two zones and spaced 300 or 700 m apart (Heithaus 2001). Shark catch rates may in part be a function of sampling design (Heithaus 2001). However, catch rates (sharks h<sup>-1</sup>, see below) for the two deployment protocols (one zone with 300 m spacing versus two zones with 700 m spacing) did not differ (paired *t* test based on catch values for days falling within the same week during which one protocol was used exclusively,  $t_6 = -0.542$ ,  $P = 0.607$ ), so all catch rate data have been pooled for the purposes of this analysis.

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

We used a shark handling procedure consistent with that of Heithaus (2001). Briefly, hooked sharks were brought alongside a 4.5 m vessel and allowed to swim slowly while the boat idled forward. Each shark was then measured (pre-caudal length [PCL], fork length [FL], and total length [TL]), sexed, tagged (numbered rototag in the dorsal or pectoral fin), and released.

**Fig. 1** This study was conducted between 1997 and 2004 (2001 excluded) in Shark Bay, Western Australia (**a**). Tiger sharks were caught in the Bay's Eastern Gulf (*hatched box*) using drumlines deployed in six zones (**b**). All sampling zones were located in deep water (generally > 7 m). The Monkey Mia Dolphin Resort has been designated with an *asterisk*



Length measurements from recaptured sharks for which time at liberty exceeded 0.5 year were used to generate growth rates (previous year's growth [cm] year<sup>-1</sup>). We used the previous year's change in cm FL as the basis for growth calculations in order to facilitate comparisons with previous studies of tiger shark growth conducted elsewhere (Branstetter et al. 1987; Natanson et al. 1999; Wintner and Dudley 2000).

#### Statistical analyses

We expressed catch rates for tiger sharks as the number of sharks caught h<sup>-1</sup> of fishing effort (Heithaus 2001; Heithaus and Dill 2002). Catch rates were calculated for all hooks soaked on each day during which drumlines were deployed ( $n=241$ ), and then variation in catch

rates over the course of the entire study in relation to day-of-year (DOY), season (warm [September–May] versus cold [June–August]; Heithaus 2001), and year was analyzed using a generalized linear model with fishing effort as an offset. Sharks may show preferences for certain bait types over others, and rates of bait loss may be influenced by bait type as well (Heithaus 2001). Consequently, use of different baits may bias shark catch results, impeding group-specific and temporal comparisons (Heithaus 2001). Thus, bait type was included as a covariate in this analysis. The dependent variable consisted of non-negative integer values with a low mean and large variance, so a negative binomial error distribution served as the basis for statistical inference (White and Bennetts 1996). For the purposes of this temporal analysis, DOY was considered to be a continuous variable, whereas baits, seasons, and years were expressed as

discrete categories (Sokal and Rohlf 1995; Zar 1999). During all years of the study, fishing effort from November–January was minimal. Thus, we censored sampling data collected during these months from the temporal analysis. Many previous attempts to monitor shark demographic trends using catch rates have been plagued by uncertain or variable sampling effort (Xiao and Walker 2000; Kohler and Turner 2001). We believe, however, that the present analysis was robust to the problem of effort variability given that daily fishing times were relatively consistent (mean = 53.50 h of total bait soak time,  $s = 21.73$ ), and effort was distributed relatively evenly across the months during which fishing took place ( $n = 40$ , mean = 331.62 h of total bait soak time,  $s = 215.09$ ). Importantly, catch rates in our study area are believed to reliably index tiger shark abundance since the rate at which free-swimming sharks (tagged and untagged) are sighted is directly related to the frequency with which sharks are being hooked, the presence of acoustically tagged sharks ( $n = 8$ ) within the fishing zone has only been detected during periods when catch rates are high (Heithaus 2001), and tiger sharks have been caught even when water temperatures are at their lowest, indicating that feeding is not suspended during cold periods.

We evaluated the sex ratio of caught sharks (for all sharks and for large individuals  $\geq 300$  cm TL; see Heithaus 2001) against the null expectation of 1:1 using chi square contingency tables. Unless otherwise specified, reported means are accompanied by 95% confidence intervals.

## Results

Over the course of the investigation, a total of 492 sharks was caught, of which 449 were *Galeocerdo cuvier* (91.3%). Other species included dusky sharks, *Carcharhinus obscurus* ( $n = 5$ ), gray reef sharks, *Carcharhinus amblyrhynchos* ( $n = 1$ ), great hammerhead sharks, *Sphyrna mokarran* ( $n = 1$ ), lemon sharks, *Negaprion brevirostris* ( $n = 2$ ), mako sharks, *Isurus oxyrinchus* ( $n = 3$ ), nervous sharks, *Carcharhinus cautus* ( $n = 5$ ), sandbar sharks, *Carcharhinus plumbeus* ( $n = 23$ ), scalloped hammerhead sharks, *Sphyrna lewini* ( $n = 1$ ), and silky sharks, *Carcharhinus falciformis* ( $n = 2$ ). Among the tiger sharks for which reliable measurements were taken (excluding recaptures), sizes ranged from 148 to 445 cm TL, with mean TL for males ( $n = 115$ , mean = 300.6 cm, 95% CI = 290.7–310.5 cm) exceeding that for females ( $n = 281$ , mean = 284.2 cm, 95% CI = 277.4–290.9 cm) (two-sample  $t$  test,  $t_{394} = 2.63$ ,  $P = 0.009$ ). Among tiger sharks for which sex could be determined ( $n = 422$ ), the overall sex ratio was female biased (ratio = 2.6:1,  $\chi^2 = 69.59$ ,  $df = 1$ ,  $P < 0.001$ ). For sharks  $< 300$  cm TL ( $n = 235$ ), this skew was particularly strong (ratio = 3.7:1); all 7 years included in the study featured a female bias, four to a significant degree (Table 1). The overall sexual skew for larger sharks ( $\geq 300$  cm TL,  $n = 185$ ) was less pronounced

**Table 1** *Galeocerdo cuvier*. Sex ratios for tiger sharks caught over 7 years in Shark Bay, Western Australia

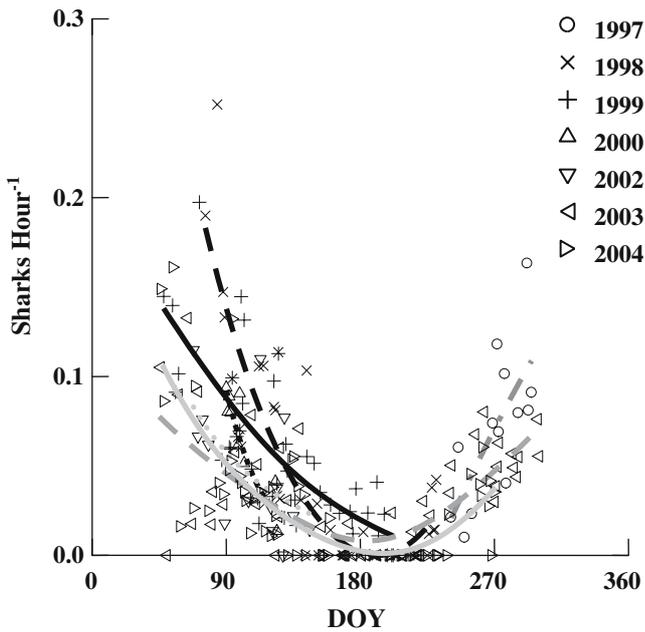
Year	Females	Males	Ratio	$\chi^2$	$P$
Small sharks (< 300 cm TL)					
1997	26	13	2.0	4.3	0.037
1998	16	10	1.6	1.4	0.24
1999	38	9	4.2	17.9	< 0.001
2000	10	4	2.5	2.6	0.11
2002	10	5	2.0	1.7	0.20
2003	55	7	7.9	37.2	< 0.001
2004	33	3	11.0	25.0	< 0.001
Large sharks ( $\geq 300$ cm TL)					
1997	16	16	1.0	0.0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

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

(ratio = 1.8:1). When large shark catch data were analyzed on a yearly basis, a significant bias was detected in only two of seven cases.

## Abundance

Tiger shark catch rates varied sharply over the 7 years of the study, with daily values (hooks pooled) ranging from 0 to 0.28 sharks  $h^{-1}$  (Fig. 2). However, the seasonal pattern observed by Heithaus (2001), with relatively high shark catch rates typifying the warm months of September–May and relatively low catch rates prevailing during the cold months of June–August, is clearly manifest in this extended dataset as well (Table 2, Fig. 2). The lack of a significant interaction between the season and year variables in our generalized linear model ( $P = 0.98$ ) indicates that this seasonal pattern was present in all years of the investigation. Day-of-year (DOY) also was retained as a significant factor in the model, implying that much of the observed heterogeneity in capture rates could not be explained by seasonal fluctuations alone. Rather, strong covariation existed between mean daily catch rate and DOY, and the lack of a significant season by DOY interaction ( $P = 0.20$ ) indicates that this pattern of covariation was a feature of both warm and cold periods. We detected significant yearly variation in tiger shark catch rates as well. Inter-annual catch rate variation was evident during both warm and cold periods (i.e., an interaction between year and season variables was not detected). However, the absence of a significant interaction between the year and DOY terms in the model ( $P = 0.41$ ) suggests that tight covariation between mean daily tiger shark catch rate and DOY was manifest in all years of the study. After accounting for temporal variation, catch rate was not influenced by bait type (Table 2).



**Fig. 2** *Galeocerdo cuvier*. Daily tiger shark catch rate (soak times for hooks fished each d pooled) as a function of day-of-year (DOY); estimates generated in Eastern Gulf of Shark Bay over 7 years using consistent fishing effort (mean total bait soak time = 53.50 h day<sup>-1</sup>, *s* = 21.73). Distance-weighted least squares (DWLS, tension 1.0) trend lines for each year are designated as follows: 1997 (gray broken line with dots), 1998 (solid broken line), 1999 (solid line), 2000 (dotted line), 2002 (gray dotted line), 2003 (gray broken line), 2004 (gray solid line)

**Recapture and growth rate**

Twenty-nine tiger sharks were recaptured, yielding a minimum recapture rate of 0.06. However, 12 additional tiger sharks bore clear evidence of tag loss (e.g., scars or loss of tissue along the leading edge of the dorsal fin near the point of tag insertion), implying a higher recapture rate (0.09). Recaptured sharks ranged in size between 219 and 394 cm TL (mean = 302.17, 284.28–320.06), and, like sharks caught for the first time, tended to be female (ratio = 2.2:1,  $\chi^2 = 4.17$ , *df* = 1, *P* = 0.04). Among those sharks for which reliable growth estimates could be generated (*n* = 19, mean time at liberty = 0.78 year, range = 0.5–1.37 year), annual growth rates ranged from

**Table 2** *Galeocerdo cuvier*. Generalized linear model of variation in tiger shark catch rates as a function of species of fish bait (*n* = 5) and three temporal variables: day-of-year (DOY, *n* = 241), season (warm vs. cold), and year

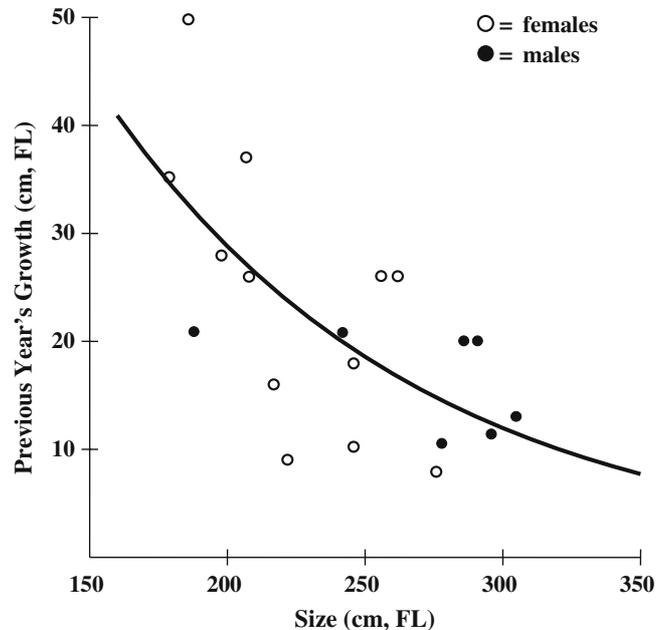
Factor	<i>df</i>	$\theta$	SE ( $\theta$ )	95% CI	<i>P</i>
Bait	4	0.063	0.039	-0.013, 0.138	0.104
DOY	1	-0.002	0.001	-0.003, -0.001	0.007
Season	1	1.757	0.156	1.451, 2.062	< 0.001
Year	6	-0.096	0.023	-0.141, -0.051	< 0.001

For all independent variables, coefficient estimates ( $\theta$ ) are accompanied by standard errors and 95% confidence intervals (CI). All interactions were excluded from the final model (all *P* ≥ 0.204)

7.9 to 49.8 cm FL (mean = 21.41 cm, 16.18–26.64). Growth rate declined significantly with size ( $r^2 = 0.40$ , *P* < 0.01; Fig. 3). A comparison of corrected Akaike’s Information Criteria (AIC<sub>c</sub>, Burnham and Anderson 1998) for linear and non-linear configurations of the independent variable revealed that an exponential decay function best fit the growth data (i.e., the AIC<sub>c</sub> for the linear model exceeded that for non-linear [exponential decay] model by > 2; Fig. 3). This model yielded growth estimates for the study population ranging from approximately 35 cm FL year<sup>-1</sup> for sharks 175 cm in length (FL) to roughly 12 cm FL year<sup>-1</sup> for sharks 300 cm in length (FL) (Fig. 3). The estimated growth rate for sexually mature tiger sharks (~250 cm FL; Heithaus 2001) was ~20 cm FL year<sup>-1</sup>.

**Discussion**

Large sharks are assumed to play important roles within marine ecosystems (Baum et al. 2003; Baum and Myers 2004; Heithaus 2004). Yet, trophic and behavioral interactions between sharks and their prey with the potential to produce community effects rarely have been documented (Heithaus 2004). This paradox could be due to a lack of area-specific information on the patterns of abundance of these apex predators. In the absence of localized numerical data required to estimate the likelihood of shark attack, for example, trends in the behavior of prey species consumed by large sharks have



**Fig. 3** *Galeocerdo cuvier*. Relationship between size (cm FL) and growth (year<sup>-1</sup>) in tiger sharks (*n* = 19) caught in the Eastern Gulf of Shark Bay, best explained by an exponential decay equation (previous year’s growth = 162.795 × e<sup>(-0.00866 × FL)</sup>;  $r^2 = 0.43$ , *P* < 0.005). Growth estimates used to generate equation based upon length measurements from recaptured individuals (mean time at liberty = 0.78 year)

been difficult to analyze in an antipredator context (Heithaus 2004). Similarly, the scarcity of numerical information concerning large sharks has hampered attempts to quantify large shark predation rates on particular prey species. Thus, systematic efforts to quantify the presence of large sharks in particular areas are needed to facilitate rigorous assessments of the influence of these predators on marine community dynamics.

Here, we present catch data from a *Galeocerdo cuvier* population study employing a standardized and long-term sampling protocol in the Eastern Gulf of Shark Bay. Our results show that seasonal periodicity in catch rates is a consistent feature of the study population: over 7 years, shark catch rates were always higher during the warm season (September–May, days 45–151 and 244–300; Fig. 2), when surface water temperatures (measured daily from a constant location; Heithaus 2001) tend to be  $>20^{\circ}\text{C}$ , than during the cold season (June–August, days 152–243). Furthermore, within both seasons, significant yearly variation was detected. However, even after accounting for the effects of season and year, we found a strong and remarkably consistent pattern of covariation between day-of-year (DOY) and catch rate. During all years of the study and within the range of months sampled, both catch values and catch variance tended to (1) be greatest at or near the peak of the warm season (February through early March,  $\sim$  days 40–75), (2) decline continuously thereafter, reaching a minimum in July (the mid-point of the cold season), and (3) increase steadily again beginning in late August (near the end of the cold season, generally between days 230 and 245). The consistent temporal trend in shark catch rates reported here has two important implications for studies of both tiger shark-prey interactions and shark-mediated community effects in the Eastern Gulf of Shark Bay: (1) those potential prey individuals remaining in the study area during the cold season can be assumed to experience a temporal refuge from predation, or at least reduced predation risk; and (2) in so far as relative predator abundance serves as a metric of predation danger (i.e., the likelihood of predator encounter and, by extension, mortality; Holling 1959; Gilliam and Fraser 1987), we should expect the magnitude of antipredator behavioral responses by prey to vary with shark catch rate throughout the year, given that within-season catch rates are not constant. Such responses have been observed in bottlenose dolphins (*Tursiops aduncus*) and pied cormorants (*Phalacrocorax varius*) in Shark Bay (Heithaus and Dill 2002; Heithaus 2005).

Recaptured sharks from which reliable measures of fork length (FL) were taken were all at least three years old, based upon the aging criteria of Natanson et al. (1999) and Wintner and Dudley (2000). For Shark Bay tiger sharks just beyond this lower age limit (175 cm FL), our growth equation suggests a growth rate of approximately  $35\text{ cm FL year}^{-1}$ , which is generally consistent with growth estimates for similarly aged tiger sharks in populations in the Gulf of Mexico (31 cm FL year $^{-1}$ ), along the east coast of North America (32 cm

FL year $^{-1}$ ) and the east coast of South Africa (32 cm FL year $^{-1}$  [note: estimated from PCL measurements, which are closely correlated with FL,  $r^2=0.999$ , see Compagno 1984], Wintner and Dudley 2000). However, the estimated growth rate for our study population declines less rapidly as a function of size than in populations elsewhere. Although initially small, the magnitude of this disparity in growth rate is notable for sharks  $\geq 275$  cm in FL, with the estimated value for the Shark Bay population ( $\sim 15\text{ cm FL year}^{-1}$ ) exceeding those calculated for populations in the Gulf of Mexico, Northwestern Atlantic (Branstetter et al. 1987), waters along North America's eastern seaboard, and South Africa by factors of 1.5 to 2.2 (Table 3). Similarly, among the largest size class available for comparison (300 cm FL), the growth estimate of the study population ( $\sim 12\text{ cm FL year}^{-1}$ ) was 1.7- to 2.8-fold higher than those for other populations.

These growth comparisons must be interpreted cautiously, as the studies on which they are based used different means to estimate yearly growth (vertebral banding patterns were used by Branstetter et al. (1987) and Wintner and Dudley (2000) to estimate age). Moreover, the growth estimate for the Shark Bay population may have been biased by sampling error and/or a lack of large individuals ( $> 300\text{ cm FL}$ ). Finally, comparisons of populations from different regions may be confounded by variation in population-specific aging patterns. Nevertheless, it appears that large Shark Bay tiger sharks (and in particular those  $\geq 275\text{ cm FL}$ ) grow more swiftly than large tiger sharks in other regions. This putative regional disparity may stem from differences in local temperature regimes, with sharks inhabiting warm waters achieving relatively high growth rates. However, tiger sharks in the coldest region (South Africa) manifested growth rates second only to those of Shark Bay (Table 3). Alternatively, it may derive from differences in diet. Reliance on large-bodied prey (e.g., sea turtles and marine mammals) by sexually mature tiger sharks ingest is generally low (De Crosta 1984; Simpfendorfer 1992; Lowe et al. 1996). For example, the occurrence of sea turtle remains in the stomachs of large tiger sharks off New Caledonia (Rancurel and Intes 1982), eastern Australia (Simpfendorfer 1992), and the main Hawaiian Islands (Lowe et al. 1996) was always  $< 15\%$  (Lowe et al. 1996), though  $\sim 50\%$  of large tiger sharks caught off the Northwestern Hawaiian Islands had ingested sea turtle tissue (De Crosta 1984; Lowe et al. 1996). Marine mammal occurrence in large tiger shark stomachs ranged from 0 to 20% in the same four areas (Lowe et al. 1996). In contrast, large tiger sharks in Shark Bay appear to rely heavily on large-bodied prey: 60% of large sharks ( $n=5$ ) caught just outside Shark Bay contained sea turtle remains, and 20% contained marine mammal (dugong) remains (Simpfendorfer et al. 2001); similarly, 80% of large sharks ( $n=5$  individuals for which stomach contents could be fully catalogued) caught in the Bay's Eastern Gulf (the study area) had recently ingested sea turtles, and 100% of these sharks

**Table 3** *Galeocerdo cuvier*. Growth estimates (cm FL year<sup>-1</sup>) for tiger sharks

Location	Growth (cm FL) year <sup>-1</sup>					
	175 cm	200 cm	225 cm	250 cm	275 cm	300 cm
Shark Bay <sup>a</sup>	36	29	23	19	15	12
Gulf of Mexico <sup>b</sup>	31	25	20	15	10	5
Northwestern Atlantic <sup>b</sup>	18	15	12	10	8	4
East coast of North America <sup>c</sup>	32	27	22	17	12	7
South Africa <sup>d</sup>	32	28	22	17	11	6

Note that estimates for Eastern Gulf of Shark Bay were derived from a growth equation based upon length measurements from recaptures ( $n = 19$ , mean time at liberty = 0.78 year), while remaining estimates were back-calculated using population-specific von Bertalanffy growth parameters. Growth estimates given for six sizes ranging from 175 to 300 cm FL

<sup>a</sup>In the present study

<sup>b</sup>Branstetter et al. (1987)

<sup>c</sup>Natanson et al. (1999)

<sup>d</sup>Wintner and Dudley (2000)

contained dugong tissue (Heithaus 2001). Large prey items, and in particular marine mammals, represent a relatively energy-rich food source (Robbins 1993), so regular consumption of these prey types by sexually mature sharks may lead to heightened net energy intake rates and elevated growth.

We recorded a female bias for both tagged and recaptured sharks. This trend is consistent with most previous studies based on tiger shark catch data (e.g., Clark and von Schmidt 1965; Stevens and McLoughlin 1991; Simpfendorfer 1992; Krogh 1994; Wintner and Dudley 2000; Simpfendorfer et al. 2001). However, in contrast to these studies and in accord with the more limited results presented by Heithaus (2001), we also found that the degree of this bias was strongly size dependent. The tendency for small sharks (<300 cm TL) to be female was approximately twice that for larger sharks, and when years were analyzed individually, a female bias was detected more frequently for small sharks than for large ones. Moreover, for both small and large sharks, the degree to which catches were female biased varied considerably from year to year. The reasons for this size-dependent trend, and its marked variability, remain to be determined.

Populations of macropredatory fishes, including the tiger shark, are undergoing a global decline, due in large part to the effects of commercial harvest (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005). Given the putatively important role played by these species in marine ecosystems, there is much interest in their conservation (Baum et al. 2003), but reliable baseline numerical data upon which effective conservation protocols might be based are lacking (Xiao and Walker 2000; Kohler and Turner 2001; Baum and Myers 2004). Our data provide a baseline for the dynamics of a protected tiger shark population in a highly productive area (Shark Bay), which might be used to assess the status of tiger shark populations in less pristine regions. Our results suggest that catch rates for large sharks may vary markedly both within and between years. Consequently, we argue that monitoring programs designed to assess shark population status and promote recovery

must not only be long-term and standardized across years, but also intensive enough to account for within-year numerical patterns.

**Acknowledgements** We thank C. Lowe, R. McAuley, C. Simpfendorfer, and the crew of the Fisheries Western Australia R/V Flinders for their aid in initiating this project by providing bait, fishing gear, and advice. Field assistance was provided by R. Abernethy, V. Alla, L. Barre, L. Bejder, F. Bretos, S. Buchannan, T. Bujas, J. Burghardt, S. Burghardt, D. Charles, C. Chow, M. Davis, H. Finn, A. Frid, C. Genrich, P. Green, A. Greenley, K. Harper, L. Heithaus, M. Kerford, S. Kowalewsky, A. Krickan, J. Laski, L. Marshall, K. Martin, J. McLash, R. McPhie, B. Stalvey, J. Wilder, and K. Wirsing. Grants and support were provided by Australian Geographic, the Burghardt family, Eurocom Computers, Green Cape Wildlife Films, Humminbird, Mercury Marine Australia, the Monkey Mia Dolphin Resort, Monkey Mia Wildsights (Shotover), National Geographic Society Expeditions Council research grants to M. R. Heithaus and A. J. Wirsing, National Geographic Remote Imaging, the National Science Foundation, NSERC Canada grant A6869 to L.M. Dill, PADI Foundation, Shakespeare Electronics, the Shark Bay Fish Factory, Singapore Airlines, Tradewinds Supermarket, the 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 providing logistical support throughout the project's duration. Special thanks go to D. Charles for providing mechanical help and advice, to D. Massey for providing extra field accommodation, to H. Raven for daily water temperature data, and to B. Black, J. Heyman, and R. Holst for their generosity and hospitality. This manuscript benefited from helpful reviews by J. Baum, E. Elle, B. Sargeant, R. Ydenberg, and an anonymous referee. This study was performed under a Simon Fraser University Animal Care permit (639B), and under the authority of Fisheries Western Australia permits 69/97 and 08/01, and Western Australia Department of Conservation and Land Management permits SF002347, NE001808, SF003818, SF004228, and SF004542 and renewals, and therefore was in compliance with the current laws of the country in which it was conducted. This is contribution #21 of the Shark Bay Ecosystem Research Project.

## References

- Baum JK, Myers RA (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol Lett* 7:135–145
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299:389–392
- Branstetter S, Musick JA, Colvocoresses JA (1987) A comparison of the age and growth of the tiger shark, *Galeocerdo cuvier*,

- from off Virginia and from the northern Gulf of Mexico. Fish Bull 85:269–279
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, Berlin Heidelberg New York
- Clark E, von Schmidt K (1965) Sharks of the Central Gulf coast of Florida. Bull Mar Sci 15:13–83
- Compagno LJV (1984) FAO Species catalogue, volume 4. Sharks of the world. Part 1. Hexanchiformes to Lamniformes. FAO Fish Synop 125:1–655
- De Crosta MA (1984) Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. MS Thesis, University of Hawaii: Honolulu, Hawaii
- Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151–1157
- Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862
- 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. Env Biol Fish 61:25–36
- Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Musick J, Heithaus MR (eds) The biology of sharks, skates, and rays. CRC Press, Boca Raton, 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, Marshall GJ, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar Biol 140:237–248
- Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Mar Biol 134:665–673
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320
- Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. Env Biol Fish 60:191–223
- Krogh M (1994) Spatial, seasonal and biological analysis of sharks caught in the New South Wales protective beach meshing programme. Mar Freshwater Res 45:1087–1106
- Lima SL (2002) Putting predators back into behavioral predator-prey interactions. Trends Ecol Evol 17:70–75
- Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Env Biol Fish 47:203–211
- Natanson LJ, Casey JG, Kohler NE (1999) Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging. Fish Bull 97:944–953
- Polovina JJ, Lau B (1993) Temporal and spatial distribution of catches of tiger sharks, *Galeocerdo cuvier*, in the Pacific longline fishery around the Hawaiian Islands. Mar Fish Rev 55:1–3
- Rancurel P, Intes A (1982) Le requin tigre, *Galeocerdo cuvier* Lacépède, des eaux Néocalédoniennes examen des contenus stomacaux. Tethys 10:195–199
- Randall JE (1992) Review of the biology of the tiger shark (*Galeocerdo cuvier*). Mar Freshwater Res 43:21–31
- Robbins CT (1993) Wildlife feeding and nutrition. Academic Press, San Diego
- Simpfendorfer C (1992) Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. Mar Freshwater Res 43:33–43
- 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. Env Biol Fish 61:37–46
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman and Company, New York
- Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Mar Freshwater Res 42:151–199
- Walker DI (1989) Regional studies – seagrass in Shark Bay, the foundation of an ecosystem. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. Elsevier, New York, pp 182–210
- Ward P, RA Myers (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86:835–847
- White GC, RE Bennetts (1996) Analysis of frequency count data using the negative binomial distribution. Ecology 77:2549–2557
- Wintner SP, Dudley SFJ (2000) Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa. Mar Freshwater Res 51:43–53
- Xiao Y, Walker TI (2000) Demographic analysis of gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) off southern Australia by applying a generalized Lotka equation and its dual equation. Can J Fish Aq Sci 57:214–222
- Zar JH (1999) Biostatistical analysis. Prentice Hall, New Jersey