

Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator

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Summary

1. There has been considerable debate over the past decade with respect to wildlife provisioning, especially resultant behavioural changes that may impact the ecological function of an apex predator. The controversy is exemplified by the shark diving industry, where major criticisms based on inference, anecdote and opinion stem from concerns of potential behaviourally mediated ecosystem effects because of ecotourism provisioning (*aka* 'chumming' or feeding).

2. There is a general lack of empirical evidence to refute or support associated claims. The few studies that have investigated the behavioural impacts of shark provisioning ecotourism have generated conflicting conclusions, where the confidence in such results may suffer from a narrow spatial and temporal focus given the highly mobile nature of these predators. There is need for studies that examine the potential behavioural consequences of provisioning over ecologically relevant spatial and temporal scales.

3. To advance this debate, we conducted the first satellite telemetry study and movement analysis to explicitly examine the long-range migrations and habitat utilization of tiger sharks (*Galeocerdo cuvier*) originating in the Bahamas and Florida, two areas that differ significantly with regards to the presence/absence of provisioning ecotourism.

4. Satellite telemetry data rejected the behaviourally mediated effects of provisioning ecotourism at large spatial and temporal scales. In contrast, to the restricted activity space and movement that were hypothesized, geolocation data evidenced previously unknown long-distance migrations and habitat use for both tiger shark populations closely associated with areas of high biological productivity in the Gulf Stream and subtropical western Atlantic Ocean. We speculate that these areas are likely critically important for *G. cuvier* feeding forays and parturition.

5. We concluded that, in the light of potential conservation and public awareness benefits of ecotourism provisioning, this practice should not be dismissed out of hand by managers. Given the pressing need for improved understanding of the functional ecology of apex predators relative to human disturbance, empirical studies of different species sensitivities to disturbance should be used to guide best-practice ecotourism policies that maximize conservation goals.

Key-words: feeding, migration, movement, optimal foraging, residency patterns, satellite tagging, site fidelity, tiger shark, tourism

Introduction

Ecosystems around the world are experiencing unprecedented losses in biodiversity and resilience because of a vari-

ety of anthropogenic threats (Jackson *et al.* 2001; Estes *et al.* 2011). Concomitantly, the value of non-consumptive usage of natural resources (e.g. catch-and-release sport fishing and wildlife tourism) is becoming increasingly popular and important in shaping conservation efforts (McNeeley *et al.* 1990; Perrings, Folke & Maler 1992; Brauer 2003;

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Ault 2008). As a result, understanding the ecological and population-dynamic consequences of modifications in wild animal behaviour arising from human interventions or disturbances has become an increasingly important and controversial topic in behavioural ecology and conservation biology (Gill, Sutherland & Watkinson 1996; Reynolds & Braithwaite 2001; Frid & Dill 2002; Kruger 2005). Provisioning ecotourism (i.e. the act of concentrating predators by offering a non-natural food source) has come under scientific scrutiny because it alters the spatial distribution of prey resources, thus attracting large predatory animals to aggregate and feed in close proximity to willing tourists (Scheyvens 1999; Orams 2002).

Numerous studies have investigated potential trade-offs in activity budgets promoted by human-mediated changes in the quality, quantity and delivery of food to wild animals by tracking changes in their stress physiology and metabolism, vitality, reproduction and movements (Knight & Cole 1995; Amo, Lopez & Martin 2006; Semeniuk & Rothley 2008). For example, wild populations of *Papio cynocephalus* (baboons), *Chlorocebus pygerythrus* (vervet monkeys) and *Cebus capucinus* (capuchin monkeys) all exhibited a nearly 50% decrease in activity and home range because of both direct and indirect food provisioning as compared to non-fed conspecifics (Musau & Strum 1984; Brennan, Else & Altmann 1985; Altmann & Muruthi 1988). Working in the marine environment, Semeniuk & Rothley (2008) found that *Dasyatis americana* (southern stingrays) in the presence of tourism-based provisioning resulted in lower fitness, increased susceptibility to ecto-dermal parasites and increased conspecific aggression because of heightened competition. Comparatively, few of these kinds of investigations have involved apex predators; however, this is of particular concern in the light of recent studies demonstrating that changes in abundance and behaviour of apex predators may have cascading impacts on a variety of ecological processes (Ripple & Beschta 2007; Creel & Christianson 2008; Estes *et al.* 2011).

Despite the criticisms associated with such activities, wildlife tourism remains a booming global industry. Marine shark provisioning, for instance, has become an increasingly popular attraction. For example, over a 20-year period (between 1987 and 2007), the Bahamas offered over 1 million shark-diver interactions, contributing an estimated gross of US\$800 million to the Bahamian economy (Gallagher & Hammerschlag 2011). Generally, fish parts are used to attract and sometimes feed these otherwise elusive animals for viewing by divers (i.e. 'chumming'). As sharks exhibit associative learning behaviours similar to those of land mammals (Guttridge *et al.* 2009), provisioning has generated significant concern as to the potential for negative influences on wild behaviours and natural ecology of free-ranging sharks. Additionally, there are tremendous fears that shark chumming poses significant safety hazards for recreational divers, beach-goers and water enthusiasts (Orams 2002), which has resulted in prohibitions on shark provisioning tourism in many jurisdictions (e.g. Florida and Hawaii, USA). However, at present, the debate has been largely rhetorical because of lack of sufficient

quantitative data to either support or refute various hypotheses regarding apex predator conditioning and behaviourally or ecologically mediated effects (Meyer *et al.* 2009b; Brunnschweiler & McKenzie 2010).

Studying effects of provisioning ecotourism on marine predatory fishes, especially sharks, present unique challenges because of their high degree of mobility as well as the inherent difficulties of working in underwater environments (Austin, Bowen & McMillan 2004). Traditional statistical ecological study approaches, which generally employ sophisticated experimental designs with controlled experiments and replicated measures, cannot be applied to large highly mobile marine predators. Accordingly, at present, more 'descriptive' approaches are required.

Several studies have used *in situ* visual surveys to examine occurrence, behaviour and abundance of sharks at ecotourism feeding sites (e.g. Clua *et al.* 2010; Smith, Scarr & Scarpaci 2010). However, recent work has demonstrated that observational techniques may be prone to some bias (Meyer *et al.* 2009a,b; Brunnschweiler & Baensch 2010; Brunnschweiler & McKenzie 2010) and reinforce the need for remote monitoring tools, particularly acoustic and satellite telemetry, to evaluate the ecological impacts of ecotourism on shark behaviour (Sims 2010; Hammerschlag, Gallagher & Lazarre 2011). To our knowledge, only four published studies have used telemetry to address these issues, with conflicting results. Laroche *et al.* (2007) reported that provisioning ecotourism in South Africa had negligible effects on *Carcharodon carcharias* (white shark) foraging behaviour at a popular shark cage-diving site. Clarke, Lea & Ormond (2011) documented short-term restricted movements of acoustically tagged *Carchahinus falciformis* (silky sharks) at provisioning sites in the Red Sea. Working in the Bahamas, Maljkovic & Cote (2011) conducted field experiments on a provisioned aggregation of *Carcharhinus perezii* (Caribbean reef sharks) and reported minimal behavioural impacts. Lastly, Fitzpatrick *et al.* (2011) examined diel vertical behaviour of *Triaenodon obesus* (whitetip reef sharks) in response to regular ecotourism and found evidence for alterations in habitat use associated with the presence of boats conducting provisioning.

The aforementioned acoustic telemetry studies generally focused on relatively short-term (days to months) and small-scale (tens of km) behavioural modifications of relatively small site-attached reef species (i.e. not apex predators, with the exception of Laroche *et al.* 2007). No previous work has applied satellite telemetry to investigate potential impacts of provisioning ecotourism on marine predators, although this technology permits long-term and large-scale remote monitoring of behaviour and habitat use.

The Atlantic tiger shark (*Galeocerdo cuvier*, Peron & Lesueur 1822) is a model candidate for investigating potential behavioural impacts of provisioning ecotourism. The tiger shark is the largest (maximum size *c.* 600 kg) apex predatory fish found throughout tropical seas (Compagno, Dando & Fowler 2005; Simpfendorfer 2009); however, published telemetry studies to date on tiger shark behavioural ecology have been conducted in the Indian or Pacific Oceans (e.g. Holland

et al. 1999; Heithaus *et al.* 2007; Meyer, Papastamatiou & Holland 2010; Nakamura *et al.* 2011; Papastamatiou *et al.* 2011; and references therein), highlighting a particular knowledge gap for the Atlantic. Studies from Western Australia have revealed that changes in tiger sharks functional ecology can induce behavioural changes in prey that may influence community dynamics (Heithaus *et al.* 2008); and finally, they are listed as 'near threatened' by the International Union for Conservation of Nature (IUCN) (Simpfendorfer 2009).

The objective of this article was to employ satellite telemetry to explicitly evaluate the potential effects of provisioning ecotourism on behaviour, habitat use and movements of tiger sharks in two areas of the subtropical Atlantic (Florida and the Bahamas) that differed markedly with respect to shark provisioning ecotourism. Specifically, we tested the hypothesis that in comparison with *G. cuvier* satellite-tagged off Florida, where feeding is illegal, sharks tagged in the Bahamas at a popular provisioning site would show comparatively restricted activity space and high site fidelity within close proximity of the original tagging location.

Materials and methods

Tiger sharks were tagged in two general areas of the western central Atlantic: (i) a popular ecotourism dive site in the Bahamas, (nicknamed 'Tiger Beach'); and (ii) within Florida state marine waters. Tiger Beach is known as an area where food (fish carcasses, mostly Serranidae, devoid of meat) is offered year-round to sharks by different commercial shark tourism operators. Dive operators claim that a resident population of conditioned *Galeocerdo cuvier* is present year-round in the vicinity of the provisioning site, with many known individual sharks resighted throughout the year (see <http://www.scuba-adventures.com>). In contrast, Florida state law strictly prohibits both fish feeding and shark provisioning for ecotourism purposes (<http://www.myfwc.com>).

Between May 2010 and February 2011, we conducted satellite-tagging operations along the west coast of Florida and the Florida Keys (Fig. 1), as well as the West End of the Bahamas (Fig. 2). Sharks were captured using baited drumlines and tagged as described by Hammerschlag *et al.* (2011). Drumlines were left to soak for 1-0 h before being checked for shark presence, and upon capture tiger sharks were secured alongside the stern of the boat using cables; however, a salt-water hose and pump was inserted in the shark's mouth to pump water over the gills while temporarily immobilized. Shark sex was recorded, total length (TL) in cm was measured, and thereafter the shark's first dorsal fin was affixed with a Smart Position and Temperature Transmitting (SPOT) tags (SPOT5, Wildlife Computers; <http://www.wildlifecomputers.com>). Tags were coated with Prospeed, a non-toxic, non-metallic anti-fouling agent, to minimize biofouling. Transmitters were attached using titanium bolts, neoprene and steel washers, and high carbon steel nuts. This method was used to prevent any metallic corrosion from contact with the fin as well as to ensure that the steel nuts eventually corrode, resulting in eventual tag detachment (Hanson 2001).

Geographic location of each shark was determined by Doppler-shift calculations made by the ARGOS Data Collection and Location Service (<http://www.argos-system.org>) whenever an orbiting satellite received messages from the tag's antennae at the surface. In 2011, Argos began processing Doppler derived data using kalman filtering (KF) to improve location accuracy.

Accuracies are indicated by a location class (LC), ranging in decreasing accuracy from LC 3, 2, 1, 0, A, B, and Z. Argos provides the following radius of error for each position: LC 3 < 250 m, 250 m < LC 2 < 500 m, 500 m < LC 1 < 1500 m. The median error for LC 0, A, and B ranges from 1 to 3 km (Bernard and Belbeoch 2010). Data collected before implantation of KF were reprocessed, such that all transmissions were based on KF processing. Class Z indicates positions are highly inaccurate and were removed from the data set. Remaining transmissions were filtered to eliminate locations on land and those related to swimming speeds > 2 m s⁻¹ (following Weng *et al.* 2005, 2008). Additionally, to account for variable intervals at which SPOT-derived positions are attained, gaps in data and autocorrelations because of successive locations (Katajisto & Moilanen 2006), tracks were standardized to 12-h intervals (midnight and noon), using piecewise Bézier interpolation methods similar to Tremblay *et al.* (2006), but adapted with the algorithm by Lars Jensen (<http://ljensen.com/bezier/>). All quantitative metrics of habitat use were generated based on the filtered Bézier-interpolated locations. We employed the modified algorithm to eliminate unnatural loops in the tracks that may occur with the Bezier method used in Tremblay *et al.* (2006). We did not interpolate gaps in the data that exceeded 3 days (following Weng *et al.* 2008).

To evaluate differences in area utilized (i.e. 'activity space') by Florida and Bahamas sharks, we used two metrics: spatial residency time and kernel density. To determine spatial residency, we calculated the number of tracking days within 100 km radius of each 12-h location. We also calculated kernel density according to the algorithms in Worton (1995) and plotted using Interactive Data Languages (<http://www.itvis.com>) software. Kernel density values are cumulated from the highest to lowest density areas (Worton 1989). Thus, the 25% kernel area contours represent areas of the top highest observed densities, while the 95% contours represent up to 95% density areas. We evaluated the maximum distance from the tagging location during each regularized 12-h interval. We determined the 'record' distance for each fish by recording for each day the greatest distance moved from the tagging location. Dispersion rates were calculated as the record distance divided by days at liberty.

Results

Eleven *G. cuvier* (nine female, two male), ranging from 184 to 295 cm TL, were tagged in Florida state waters (hereafter 'Florida sharks') and generated geolocation data over deployments ranging from 26 to 297 days that were suitable for movement analyses (Table 1A). Fourteen female *G. cuvier* ranging from 280 to 403 cm TL were tagged at the Bahamas provisional site (hereafter 'Bahamas Sharks') and transmitted position data for periods ranging between 40 and 182 days (Table 1B). Ten of the Bahamas sharks provided valid geolocations for use in subsequent movement analysis.

Florida sharks were distributed from the coast to the outer continental shelf edge, spanning from the Gulf coast of Florida (north of Sanibel Island) to North Carolina (Fig. 1). Residency times ranged from < 5 to ≥ 60 days. However, highest residency times (> 60 days) were mostly found within close proximity (150–300 km) to the tagging sites (white stars in Fig. 1a). Florida sharks exhibited a core occupancy area (i.e. 25% kernel) centred on the tagging sites (Fig. 1b). The calculated activity space was 1945 km².

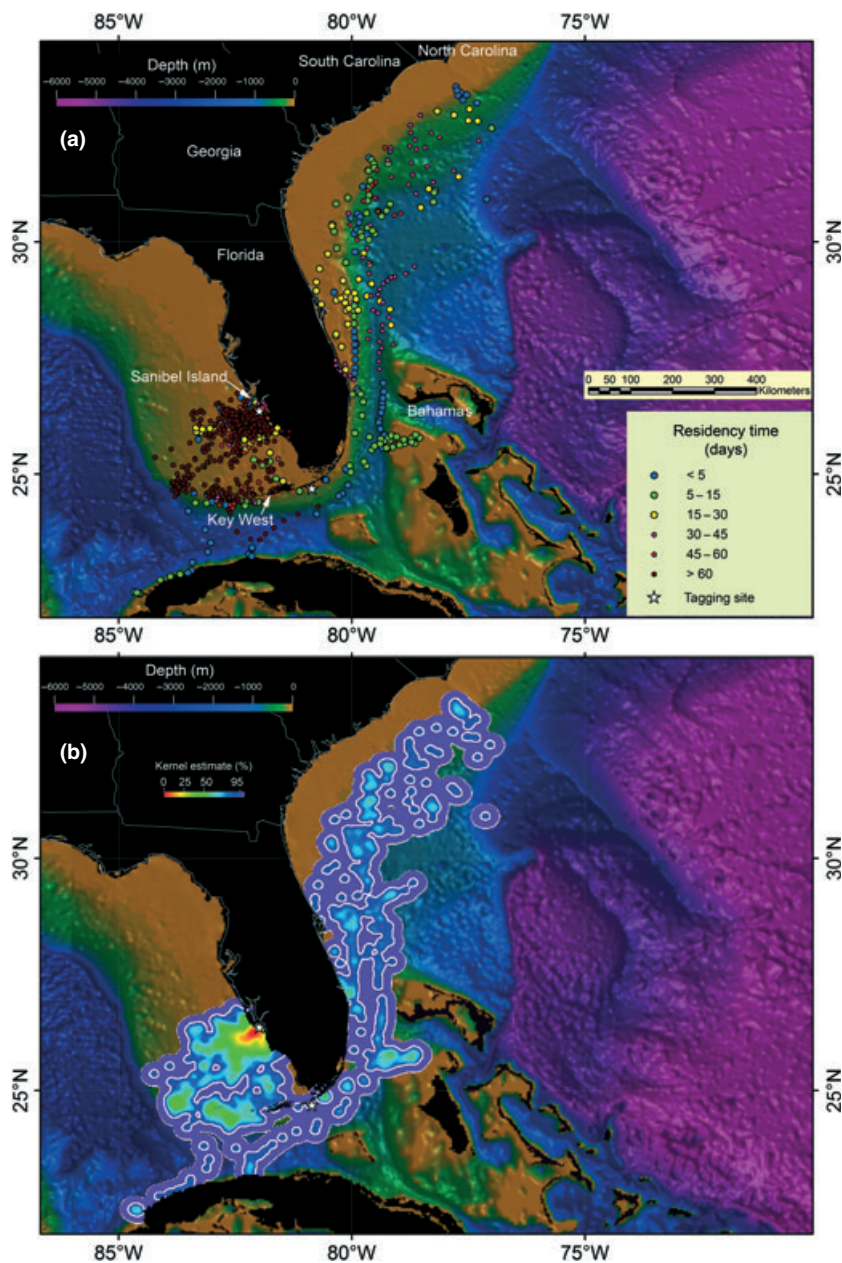


Fig. 1. Spatial distribution of 11 (nine female, two male) tiger sharks (*Galeocerdo cuvier*) satellite-tagged off Florida. (a) Residency times (number of tracking days within 100 km radius of each location) are indicated by colour-coded dots; (b) Kernel density area contours are represented by the rainbow colour scales from highest (red) to lowest density (purple). White stars indicate tagging locations.

Distribution of Bahamas sharks extended over a comparatively larger area that included the northern Bahamas archipelago, Gulf of Mexico coastal waters of Florida, the US eastern seaboard from Key West to New England and as far east as *c.* 40°W longitude. Residency times of Bahamas sharks were highest (i.e. > 60 days), mostly within 350 km of tagging site (white star in Fig. 2a), but also extended from the West End of the Bahamas to coastal waters off North Carolina (900 km). Bahamas sharks exhibited several core areas of occupancy (25% kernel), primarily centred near the Bahamas tagging site, but also coastal waters of North Carolina and the shelf edge off New Jersey (Fig. 2b). The calculated activity space was 8549 km².

Florida sharks only moved up to 1000 km from their tagging locations; however, 19% of the Bahamas sharks moved

> 1000 km and as far as 3500 km (Fig. 3). Florida sharks spent 54% of their time within 100 km of their tagging location, while Bahamas sharks spent about 27% of their time within this distance. Record distance appeared to increase as a function of time at liberty for both Florida and Bahamas sharks (Fig. 4). Within the first 40 days at liberty, Florida sharks seemed to have the greatest record distances; but, Bahamas sharks had much longer record distances over the course of this study. Put in another perspective, Florida sharks seemed to exhibit two modes of dispersion: one between days 1 and 35 with variable rates from 1 to 50 km day⁻¹ and another between days 36 and 175 with small rates about 2–3 km day⁻¹ (Fig. 5). Bahamas sharks averaged about 5 km day⁻¹ at day 1, to about 15 km day⁻¹ at day 175, except for a few high rates between days 1 and 5.

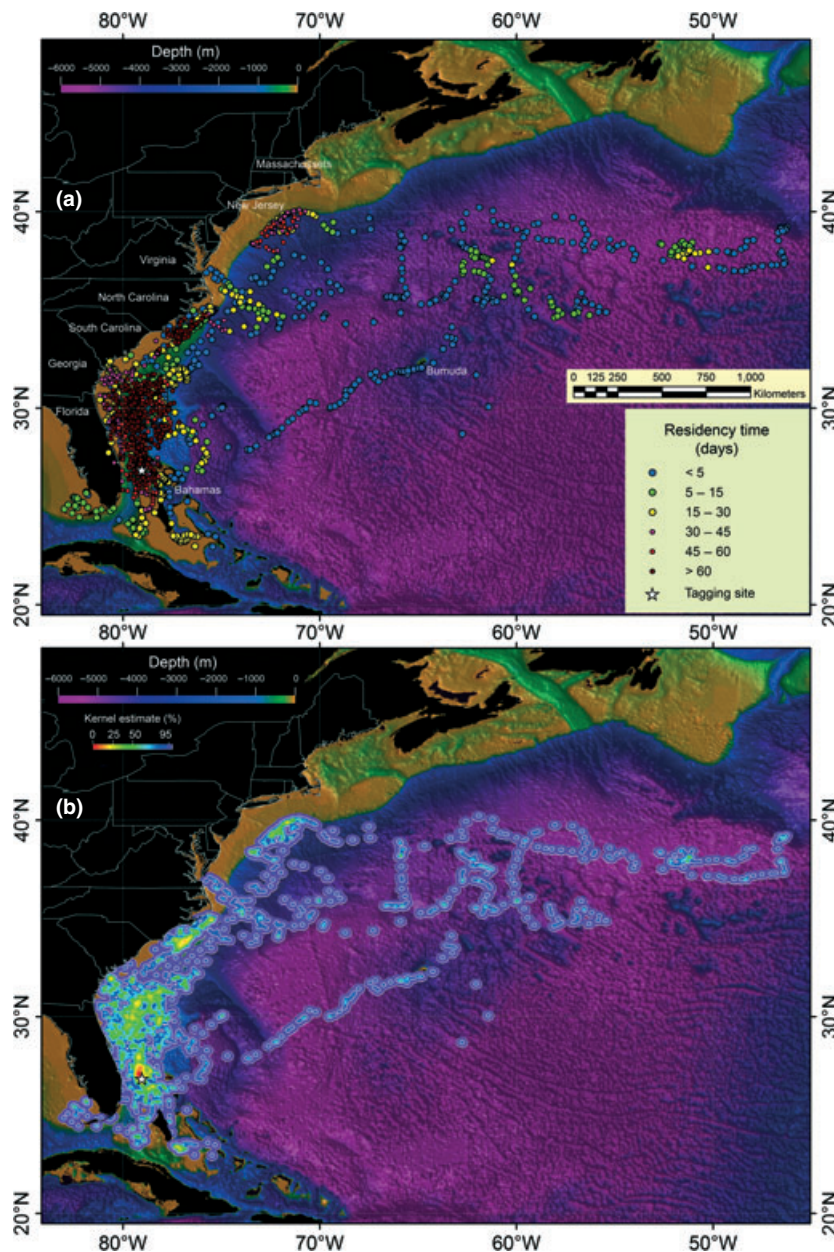


Fig. 2. Spatial distribution of 14 female tiger sharks (*Galeocerdo cuvier*) satellite tagged at the Bahamas provisioning ecotourism site (Tiger Beach). (a) Residency times (number of tracking days within 100 km radius of each location) are indicated by colour-coded dots; (b) Kernel density area contours are represented by the rainbow colour scales from highest (red) to lowest density (purple). White stars indicate tagging locations.

Discussion

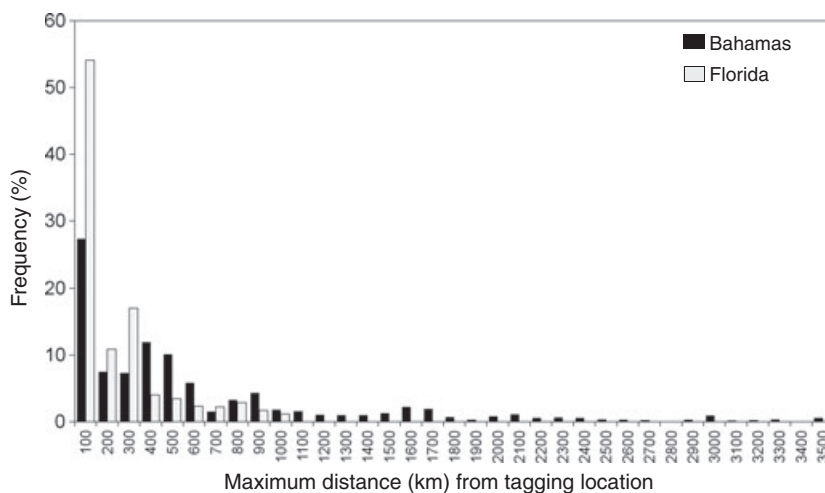
Our satellite-tagging study did not support the hypothesis that *G. cuvier* tagged at the Bahamas provisioning site show restricted activity space and low site fidelity as compared to Florida sharks. In fact, Bahamas *G. cuvier* tended to exhibit relatively larger activity spaces, broader movement patterns and lower residency patterns near tagging sites as compared to Florida conspecifics. Two provisional hypotheses related to reproductive and foraging strategies, although not mutually exclusive, can be posed to explain the observed shark habitat use patterns.

If *G. cuvier* movements at the provisioning site were influenced by un-natural feeding, then Tiger Beach should have also been frequented by males. However, over the past 10 years, there have been thousands of tiger shark-diver

interactions at Tiger Beach, yet only seven documented encounters with male sharks (Jim Abernethy's Scuba Adventures, pers. comm.). Sex segregation is a common and well-documented phenomenon in sharks; however, one would not expect segregation to persist if provisioning were concentrating and nourishing animals. Moreover, the majority of females found year-round at Tiger Beach are at, or above, the size at sexual maturity (≥ 300 cm, Whitney & Crow 2007) including all those tagged in this study (i.e. 329 cm TL \pm 32 cm). Observations of late-stage gravid sharks (i.e. distended stomachs and abnormal ventral girths) with healing and/or healed physical trauma (i.e. fin and outer-gill lacerations and bite-marks) resulting from mating behaviour are common place at Tiger Beach, including our multiple sightings of the same gravid individuals over multiple years (N. Hammerschlag & A.J. Gallagher, unpublished data).

Table 1. Summary data for: (A) 11 *Galeocerdo cuvier* satellite tagged in Florida coastal waters; and (B) 14 *G. cuvier* satellite tagged at the Bahamas provisioning site (Tiger Beach)

| Shark ID | Date | Latitude | Longitude | TL (cm) | Sex | Days at liberty |
|--------------------|------------------|----------|-----------|---------|-----|-----------------|
| (A) Florida | | | | | | |
| 68477 | 29 October 2010 | 26:37 | -81:98 | 200 | M | 131 |
| 33992 | 26 May 2010 | 26:37 | -81:98 | 203 | F | 297 |
| 34021 | 26 May 2010 | 26:37 | -81:98 | 249 | F | 75 |
| 55494 | 10 June 2010 | 26:37 | -81:98 | 250 | F | 113 |
| 34029 | 26 May 2010 | 26:37 | -81:98 | 255 | F | 209 |
| 34107 | 25 May 2010 | 26:37 | -81:98 | 255 | F | 278 |
| 34020 | 26 May 2010 | 26:37 | -81:98 | 263 | M | 40 |
| 55495 | 9 June 2010 | 26:37 | -81:98 | 295 | F | 137 |
| 98332 | 12 November 2010 | 24:70 | -80:85 | 184 | F | 82 |
| 68471 | 29 January 2011 | 24:70 | -80:85 | 245 | F | 26 |
| 34203 | 13 November 2010 | 24:70 | -80:85 | 255 | F | 46 |
| (B) Bahamas | | | | | | |
| 68496 | 20 February 2011 | 26:86 | -79:04 | 280 | F | 178 |
| 68555 | 20 February 2011 | 26:86 | -79:04 | 286 | F | 168 |
| 68488 | 20 February 2011 | 26:86 | -79:04 | 295 | F | 178 |
| 105600 | 20 February 2011 | 26:86 | -79:04 | 310 | F | NA |
| 68486 | 20 February 2011 | 26:86 | -79:04 | 320 | F | 165 |
| 68556 | 20 February 2011 | 26:86 | -79:04 | 322 | F | 181 |
| 68495 | 20 February 2011 | 26:86 | -79:04 | 325 | F | 177 |
| 68529 | 19 February 2011 | 26:86 | -79:04 | 325 | F | 182 |
| 105595 | 22 February 2011 | 26:86 | -79:04 | 325 | F | NA |
| 68485 | 19 February 2011 | 26:86 | -79:04 | 335 | F | 95 |
| 105599 | 20 February 2011 | 26:86 | -79:04 | 340 | F | 40 |
| 68494 | 19 February 2011 | 26:86 | -79:04 | 365 | F | 181 |
| 105594 | 22 February 2011 | 26:86 | -79:04 | 375 | F | NA |
| 68554 | 19 February 2011 | 26:86 | -79:04 | 403 | F | 181 |

**Fig. 3.** Frequency distribution of tiger shark (*Galeocerdo cuvier*) migration distances between filtered position locations and tagging sites in Florida (light bars) and Bahamas (black bars).

Accordingly, we speculate that the site may be related to gestation or puration, an aspect of this species (and most sharks') life history that remains unknown. Future research at the study site is needed to evaluate this assertion using non-lethal methods for measuring reproductive status such as blood hormone analysis and ultrasound imaging (Hammerschlag & Sulikowski 2011).

A second hypothesis relates to feeding strategy. *G. cuvier* are effective generalist predators that forage on a diverse range of prey, which must meet the stringent metabolic demands of an active predator (Springer 1961; Lowe *et al.* 1996; Carlson, Grace & Laco 2002; Gallagher, Jackson &

Hammerschlag 2011). No previously published studies have quantified this aspect of tiger shark food-consumptive needs (e.g. daily ration). Using simple bioenergetic models developed for *Negaprion brevirostris* (lemon sharks) and *Carcharhinus leucas* (bull sharks) (Cortes 1987; Froese & Pauly 2011) as a proxy for *G. cuvier*, we estimated that our large (c. 210 kg; Branstetter, Musick & Colvocoresses 1987) Bahamian *G. cuvier* must consume approximately 3.7% of their body weight per day (almost 8 kg per day). The large metabolic needs of *G. cuvier* would likely not be met by the amount and quality of energy-poor carcasses presented by dive boats at Tiger Beach. In contrast, we speculate that the long-distance

Fig. 4. Distances to tagging locations by individual tiger sharks (*Galeocerdo cuvier*) during times at liberty. Grey dots denote distance to tagging location calculated every 12 h for each Bahamas shark. Red dots denote the first record of maximum observed distance for each Bahamas shark. Open squares denote distance to tagging location calculated every 12 h for each Florida shark. Blue squares denote the first record of maximum observed distance for each Florida shark.

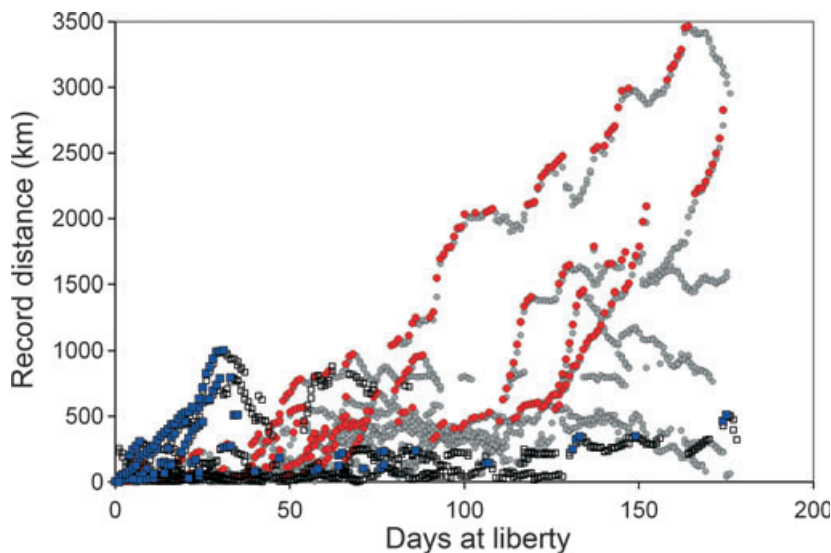
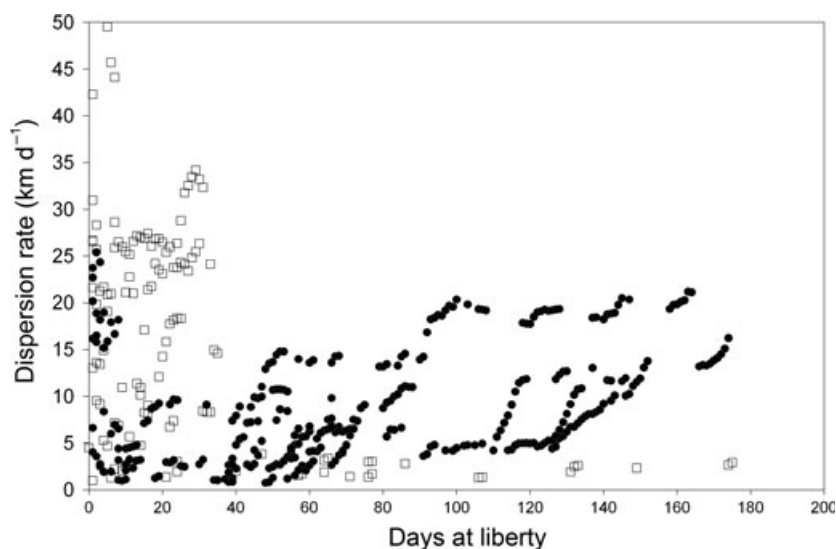


Fig. 5. Dispersion rates (km day^{-1}) for tiger sharks (*Galeocerdo cuvier*) tagged in Florida (open squares) and the Bahamas (closed black dots).



migration patterns observed in this study are linked to foraging forays.

Previous telemetry studies in the Indian and Pacific Oceans have described the tiger shark as a 'coastal species' which at times exhibits directed movements across pelagic ocean environments, likely linked to feeding (see Heithaus *et al.* 2007; Meyer, Papastamatiou & Holland 2010; Papastamatiou *et al.* 2011; Nakamura *et al.* 2011, and references therein). For example, *G. cuvier* tagging studies in north-western Hawaiian Islands have found that *G. cuvier* undertake long-distance movements to coincide with seasonal prey accessibility at neighbouring islands (i.e. fledging black-footed albatross, *Phoebastria nigripes*; Meyer, Papastamatiou & Holland 2010). In our study, both Bahamas and Florida groups moved significant distances away from their tagging locations out into the open waters of the Gulf Stream (Figs 6 and 7). The warm and tenacious currents of the Gulf Stream support great productivities of all trophic levels along its course (Stommel 1976; Deibel 1985; Nelson

et al. 1985; Yoder *et al.* 1985; Nero *et al.* 1990; Lee, Yoder & Atkinson 1991; Flierl & Davis 1993; Govoni 1993; Sedberry, McGovern & Pashuk 2001). The US longline fishery data (Cramer 1996) showed that the Gulf Stream and its associated eddy systems are high-productivity areas of known prey for *G. cuvier*, including tunas and billfish, all having similar distribution patterns as tiger sharks in this study (Fig. 7). The observed pelagic migrations of both Florida and Bahamas sharks, overlapping with the distribution of their prey along the dynamic Gulf Stream current system, are indicative of an opportunistic foraging strategy that is not dependent on tourism-related provisioning at large spatial and long-term temporal scales (Figs 6 and 7). Furthermore, the documented long-distance, north-easterly movements and open-ocean habitat use patterns, persisting over the course of months, suggest Atlantic tiger sharks have a more extensive pelagic phase than previously assumed based on satellite-tagging data from individuals tagged in the Pacific and Indian Oceans.

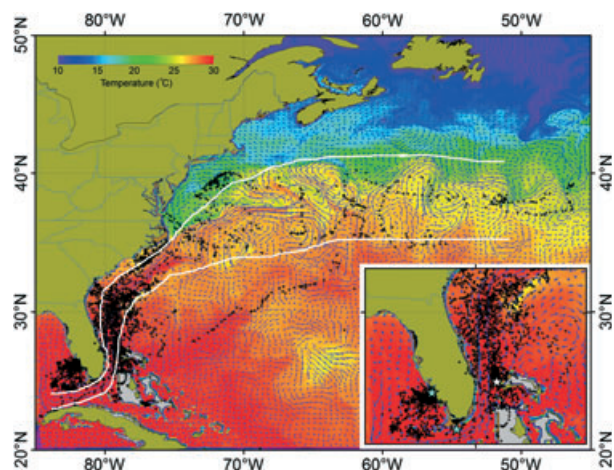


Fig. 6. Standardized Bézier-interpolated 12-h locations (black dots) for both Florida and Bahamas tiger sharks (*Galeocerdo cuvier*). Surface current vectors and sea surface temperatures from Hybrid Miami Isopycnal Ocean Model (HYCOM; <http://www.hycom.org>) outputs for September 30, 2011. White outlines show the boundary of the Gulf Stream extending from Florida to South Carolina, where two blue stars indicate Florida tagging locations, and the white star indicates Bahamas tagging location.

Although we did not find evidence of restricted movements by Bahamas sharks in relation to Tiger Beach, when *G. cuvier* are in the vicinity of diving tourism there, chumming activities will frequently draw sharks to the vessels; where sharks will

scavenge on fish carcasses offered (direct observation). However, the extent of this impact on the overall fitness of *G. cuvier* is unknown and beyond the scope of this article; but future work addressing the impact of provisioning on fine-scale movements and long-term fitness of tiger sharks is clearly warranted. Moreover, given the Bahamas provisioning site is encompassed within the observed migration patterns of our tagged *G. cuvier*, we cannot discount possible linkages between sharks habitat use and ecotourism activities.

Sharks generally increase their habitat range as they increase in size (Cortes & Gruber 1990; Morrissey & Gruber 1993). Thus, when interpreting our results, it is worth considering that the size range of Florida sharks tagged was smaller than that of the Bahamas sharks and, therefore, not directly comparable as experimental controls. Further, it is possible that Florida and Bahamas sharks represent the same group. Regardless, even without comparison against Florida sharks, the observed movement patterns of Bahamas sharks are not indicative of restricted patch use, nor do they support behaviourally modified effects of provisioning ecotourism over the relatively large spatial and temporal scales examined. Interpreted thusly, the large-scale migrations and apparently opportunistic foraging behaviour reported here indicate a relatively low level of sensitivity to ecotourism-related disturbance. We suspect that the preponderance of conflicting results on the impacts of ecotourism on shark behaviour in the literature is partially explained by differing species'

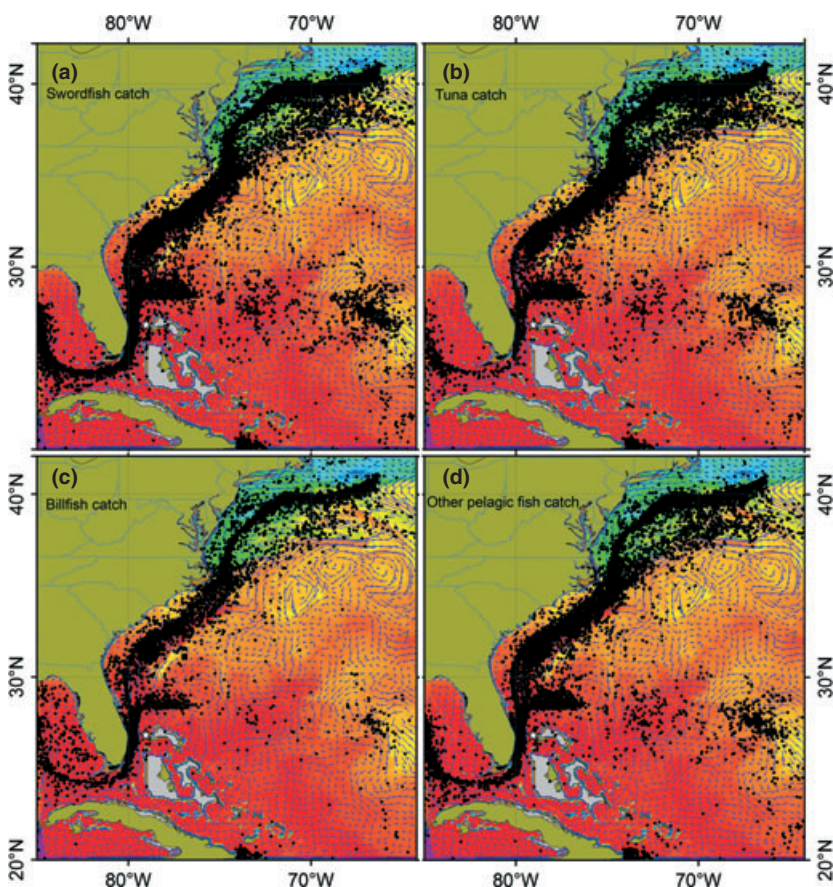


Fig. 7. Locations of positive longline catches by US fleet (black dots) during 1992–1995 for key prey species of tiger sharks: (a) swordfish (*Xiphias gladius*); (b) tunas (*Thunnus obesus*, *Thunnus thynnus*, *Thunnus albacores*, *Thunnus alalunga*, *Thunnus atlanticus*, other tunas); (c) billfishes (*Tetrapterus albidus*, *Tetrapterus pleuger*, *Makaira nigricans*, *Istiophorus albicans*); and (d) other pelagic fishes (*Coryphaena hippurus*, *Acanthocyium solandri*, *Scomberomorus cavalla*, *Lepidocybium flavobrunneum*, *Seriola dumerili*, *Katsuwonus pelamis*). Data obtained from the National Marine Fisheries Service (Cramer 1996).

sensitivities to such stimuli because of variation in foraging and life histories strategies. Thus, we are reticent to extend our results to other species and/or provisioning ecotourism locations around the world. We, therefore, suggest that behavioural impacts of ecotourism provisioning on sharks are likely scale, site and species specific.

Given recent emphasis on the need for ecosystem-based management plans in marine ecosystems (e.g. Pikitch *et al.* 2004; Halpern *et al.* 2012) and the pressing need for improved understanding of the functional ecology of apex predators relative to human disturbance, we recommend future work in this burgeoning field of study transition from asking whether tourism-related provisioning is impacting 'sharks', to a more synthetic view that questions why particular species have differential responses, and further, how ecotourism policy and practice might be structured to minimize ecological risks and maximize conservation efforts. Such a perspective is especially important in structuring 'best practice' ecotourism policy that may help to mitigate the negative consequences of cascading ecosystem impacts of apex-predator declines. Because shark-based ecotourism generates significant economic and conservation benefits (Topelko & Dearden 2005; Gallagher & Hammerschlag 2011), and further because of the apparently unfounded concerns of negative resource impacts of dive ecotourism in the Bahamas on *G. cuvier* habitat use over the large spatiotemporal scales we evaluated herein, we believe that managers should not be reactionary and 'bite the hand that feeds' until sufficient data were to demonstrate otherwise.

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