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You are what you eat: Examining the effects of provisioning tourism on shark diets

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ABSTRACT

Wildlife tourism is a growing industry, with significant conservation and socio-economic benefits. Concerns have however been raised about the possible impacts of this industry on the long-term behaviour, health and fitness of the animal species tourists come to see (the target species), particularly when those species are regularly fed to improve the tourism experience. Information on the contribution of food rewards to the diet of the target species at feeding sites is critical to assess the dependency on handouts and to identify possible health/fitness problems that might be associated, if handouts become the main part of animals' diets. Here, we use stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to evaluate the importance of handouts for a marine predator, the bull shark (*Carcharhinus leucas*), at a feeding site (Fiji) where shark feeds occur 5 days/week and sharks (up to 75 individuals/dive) are fed ~200 kg of tuna heads/day. There was no evidence of incorporation of food provided, even for individuals that regularly consume food rewards. Results, when combined with those from previous studies on bull shark movements and feeding rates at our study site, show that current levels of provisioning likely have no long-term impacts on bull shark diet or behaviour. This study also demonstrates the applicability of stable isotope analysis to assess and monitor the contribution of food rewards to wildlife, and highlights the benefits of using multi-sources of information to gain a holistic understanding of the effects of provisioning predators.

1. Introduction

Wildlife tourism is a growing industry that often involves feeding (provisioning) wildlife to increase the chances of viewing animals up close. Despite that provisioning tourism can have significant conservation, economic and social benefits (Cisneros-Montemayor et al., 2013; Gallagher and Hammerschlag, 2011), concerns are being raised about the impacts this expanding industry might have on the long-term behaviour, health (i.e. functional and metabolic efficiency) and fitness (i.e. reproductive success) of the target animals, with several studies asking if the negative impacts might outweigh the positive (e.g. Burgin and Hardiman, 2015; Shannon et al., 2017; Trave et al., 2017). Although tourism-related behavioural changes have been documented for many species (e.g. of the 48 provisioning studies in the marine environment reviewed by Trave et al. (2017), behavioural changes were evident in 89.5% of the cases), little information is available on tourism effects on health and fitness. This issue has been repeatedly pointed out in recent wildlife tourism reviews for both the terrestrial (e.g. Newsome et al., 2015; Penteriani et al., 2017) and aquatic (e.g. Brena et al., 2015; Burgin and Hardiman, 2015; Trave et al., 2017) environments.

To better understand if wildlife provisioning might have a negative impact on the animal species tourists come to see (i.e. the target species), information on the basic factors that may affect the health and fitness of those animals is crucial. This includes information on parameters such as individual consumption rates at feeding events, energy content of provisions, daily energetic requirements, and the contribution of these food rewards to the overall diet of the target species. This information is critical to assess the level of dependency on food handouts and any possible problems that might be associated, if food rewards become the main part of the animal's diets.

Predators regulate ecological communities by controlling prey populations through both direct predation and by influencing prey behaviour (risk effects) (Beschta and Ripple, 2009; Estes et al., 2011; Wirsing and Ripple, 2011). Artificially providing food can lead to direct effects such as altered predator abundance, diet, life-history, social behaviour and spatial use, as well as to indirect effects such as increasing competition between co-occurring species, increased predation pressure on native prey, and prey switching (see Newsome et al. (2015) and Burgin and Hardiman (2015) for examples). Food provisioning therefore has the potential to alter trophic structure and dynamics of

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both aquatic and terrestrial systems (Brena et al., 2015; Burgin and Hardiman, 2015; Newsome et al., 2015). However, its effects greatly vary depending on species- and case-specific settings (Brena et al., 2015; Newsome et al., 2015; Penteriani et al., 2017).

Diving with sharks is becoming increasingly attractive to recreational divers worldwide. Many dive operators regularly feed sharks to ensure that animals attend the dive sites, so that shark-tourist interactions can be guaranteed. Although some studies have detected effects of feeds/attracts on shark community composition (e.g. Brunnschweiler et al., 2014; Clarke et al., 2013; Meyer et al., 2009), shark behaviour (e.g. Clua et al., 2010; Fitzpatrick et al., 2011) and metabolic rate (Barnett et al., 2016), it is still not known if those changes have any negative long-term consequences for the sharks' health and fitness (Brena et al., 2015; Burgin and Hardiman, 2015; Gallagher et al., 2015).

In the present study, stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are used to evaluate the importance of food subsidies for a marine predator, the bull shark (*Carcharhinus leucas*, Carcharhinidae), the main species at the Shark Reef Marine Reserve, a tourism feeding site in Fiji (Brunnschweiler et al., 2014). According to a recent study, the consumption of 2.3 tuna heads per week can meet the energetic requirements of a ~2.8 m bull shark individual, suggesting that bull sharks could meet their energy requirements exclusively from provisioning (Brunnschweiler et al., 2017). This stresses the importance of determining the contribution of bait for these animals' diets, so that potential impacts on their health and fitness and on the overall food web can be assessed. Such information can be used to inform the tourism operators of “safe” feeding levels, therefore contributing to setting best practices for the appropriate management of the industry. Whitetip reef sharks (*Triaenodon obesus*, Carcharhinidae) were also sampled as this species has relatively small home ranges and, unlike bull sharks which move in and out of the study area (Brunnschweiler and Barnett, 2013), whitetip reef sharks are typically resident in the reefs where they occur (Barnett et al., 2012; Speed et al., 2012). Since whitetip reef sharks are also an important part of the shark dive in Fiji (Brunnschweiler et al., 2014), it is likely that this species would more easily reflect any significant incorporation of bait provided.

Stable isotope analysis is useful for this study because $\delta^{13}C$ and $\delta^{15}N$ can differ among primary sources of nutrition, and because $\delta^{13}C$ and $\delta^{15}N$ change in a predictable way as they are passed on from food source to consumer. $\delta^{13}C$ is particularly useful as a source indicator in coastal systems as different primary producers (e.g. plankton, algae, seagrass) typically have different $\delta^{13}C$ values, and because $\delta^{13}C$ values change little as material is passed on from food to consumer (0–1‰; DeNiro and Epstein, 1978; McCutchan et al., 2003). $\delta^{15}N$ is generally used as a trophic level indicator (Post, 2002) because of the higher $\delta^{15}N$ trophic fractionation (2–3‰; McCutchan et al., 2003; Minagawa and Wada, 1984). $\delta^{15}N$ will be particularly important in the present study because sharks at our study site are fed tuna heads/frames. Since tunas are typically high trophic level pelagic species (Olson et al., 2010), they have $\delta^{13}C$ values in the lower part of the marine $\delta^{13}C$ spectrum, and $\delta^{15}N$ values much higher than those of local reef prey, meaning that it will be possible to identify and quantify any contribution of tuna provided to shark nutrition. Given that tuna heads provided can fuel the energetic needs of bull sharks (Brunnschweiler et al., 2017), we expect that tuna will make up a significant component of the diet of at least some bull sharks individuals. Note however that the study from Brunnschweiler et al. (2017) was conducted in 2008, and that the number of sharks attending the dive site in 2008 was lower than in 2015, when the present study was done (see Fig. 1). This means that in 2008 bait was shared among a smaller number of bull shark individuals and therefore that bait contribution could have been higher than in 2015, the year the present study was conducted.

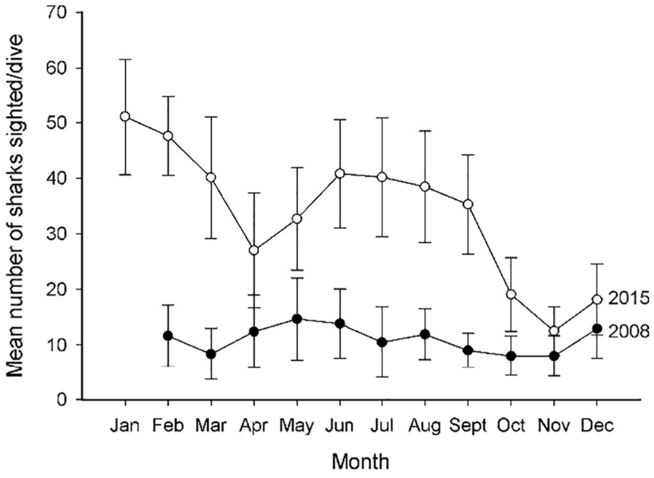

Fig. 1. Monthly mean (± SD) number of bull sharks sighted per dive for 2008 (when feeding rate data used in Brunnschweiler et al. (2017) was collected) and 2015 (when stable isotope data from the present study was collected).

2. Methods

2.1. *Study site and study species*

This study was conducted at the Shark Reef Marine Reserve, a multi-species shark diving site on the southern coast of Viti Levu, Fiji (Brunnschweiler et al., 2010). For a detailed description of the dive protocol and for information on species composition and relative abundances of sharks at this provisioning site, see Brunnschweiler and Baensch (2011) and Brunnschweiler et al. (2014). Currently, shark feeds occur 5 days/week in two feeding dives/day, where ~100 kg of tuna (*Thunnus* spp. (Scombridae)) heads (each ~2.4 ± 0.9 kg (± SD)) are fed on the first and again on second dive of the day. Several shark species are attracted to the dive site but the bull shark is the most abundant species and the main attraction of this shark dive (Brunnschweiler et al., 2014). In 2015 (when stable isotope samples for the present study were collected), up to 75 individual bull sharks could be seen in each dive.

Bull sharks inhabit coastal and tropical reef habitats (Brunnschweiler et al., 2010; Carlson et al., 2010; Daly et al., 2014; Espinoza et al., 2016), and feed mostly on fish including teleosts and also on elasmobranchs such as batoids and smaller sharks (Cliff and Dudley, 1991; Olin et al., 2013; Trystram et al., 2016). The bull sharks of the Shark Reef Marine Reserve range in size from ~1.8 m to ~3.5 m (subadults and adults; average size ~2.8 m) and include both males and females. Although bull sharks can be seen throughout the year, there are seasonal cycles in abundance: more individuals are present between January and September (mean ± SD: 39.0 ± 11.5 individuals/dive; mode: 40 individuals/dive for 2015; unpubl. data) and less between October and December (~16.6 ± 6.5 individuals/dive, mode: 15 individuals/dive for 2015) (Fig. 1), as animals move out of the area for weeks to months at the end of the calendar year (likely for reproductive purposes), typically returning in the beginning of the following year (Brunnschweiler et al., 2014; Brunnschweiler and Baensch, 2011; Brunnschweiler and Barnett, 2013). Tracking studies show that different bull shark individuals have different degrees of site fidelity to the feeding site, with some individuals being present almost year round while others spend longer periods of time away (Brunnschweiler and Barnett, 2013). These regular movements out of the study area, coupled with the relative slow muscle turnover rate of large sharks (Logan and Lutcavage, 2010; MacNeil et al., 2006) can limit our ability to quantify a possible incorporation of bait based on stable isotope analysis. Therefore, the importance of bait for whitetip reef sharks, a resident shark species that is also an important focus of the shark dive at the