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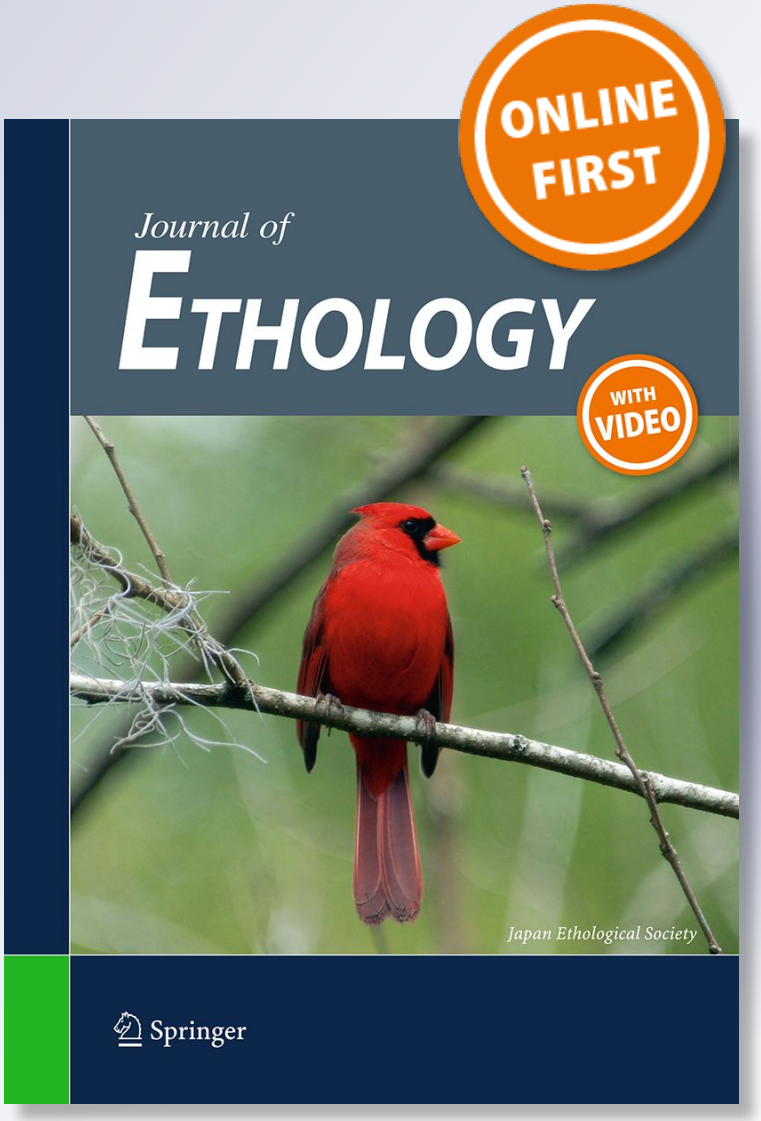

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SHORT COMMUNICATION

Apex predatory sharks and crocodiles simultaneously scavenge a whale carcass

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Abstract
Scavenging is an important component to the overall ecology of consumers in virtually all ecosystems on Earth. Given the energetic benefits of foraging on these resource subsidies, opportunistic predators will adjust their behaviors accordingly to maximize access. One of the many consequences of large-scale scavenging opportunities is species interactions that are rarely observed in nature. Here we describe the first published record of predatory sharks (tiger sharks, *Galeocerdo cuvier*) and saltwater crocodiles (*Crocodylus porosus*) foraging together in space and time, as documented on a large whale carcass off Western Australia. We report on and discuss the behaviors of the sharks and crocodiles in the hope of shedding new light on the interactions between apex predators that are rarely seen together, but may overlap under specific contexts.

Keywords Behavior · Carcass · Saltwater crocodile · Predator · Tiger shark · Whale

Introduction

Food pulses create resource subsidies that organisms can exploit over discrete spatial and temporal scales. Scavenging, the opportunistic feeding on dead organic material by heterotrophic species, is a fundamental but poorly understood ecological process. Studies have suggested that scavenging can exert important top-down ecological effects that influence food web dynamics, while imparting that it is likely more common than previously thought (DeVault et al. 2003; Wilson and Wolkovich 2011). Carrion attracts a wide variety of consumers; however, the ecology of scavenging among top predators is becoming an area of focus (Wilson and Wolkovich 2011), particularly in fragmented habitats affected by human activities (Gomo et al. 2017). Moreover, the advent of portable, high quality video recording devices has made the observation of predators scavenging in the wild more common, thereby fostering new questions and perspectives on their foraging and social interactions (Moleón and Sánchez-Zapata 2015). The benefits of opportunistically utilizing random food pulses are arguably greatest for predatory animals who otherwise must burn significant energy to encounter and subjugate agile prey (Krofel et al. 2012). Knowledge of scavenging by predators may help us better understand their trophic dynamics and the drivers that govern their physiological and metabolic processes (Bouveroux et al. 2014; Hammerschlag et al. 2016). Scavenging studies also provide a unique window into the social behaviors of species which otherwise remain cryptic or poorly understood, thus overcoming the challenges of observing both feeding events (which are stochastic) and the rarity of finding multiple predators within close proximity (Fallows et al. 2013).

Sharks and crocodilians overlap in some coastal environments where they act as reciprocal intra-guild predators (Nifong and Lowers 2017). The majority of these documented interactions are between adults of one species and juveniles of another. Even less is known about competitive interactions between adult crocodilians and larger shark species. Here we present the first published record of predatory

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sharks and crocodiles foraging together in space and time, as documented on a large whale carcass off Western Australia.

Methods and results

On September 24, 2017, an approximately 15-m male humpback whale (*Megaptera novaeangliae*) was found dead and floating upside down just north of Montgomery Reef, Kimberley, Western Australia (− 15.99S, 124.239722E), about 1 km from shore at 0815 h by a dive charter company. Based on the odor and rotted appearance of the whale carcass, the charter staff estimated the whale had been dead for over 1 week (there were also hundreds of bite marks from sharks on the ventral side of the whale). Upon closer inspection, four tiger sharks (*Galeocerdo cuvier*) and one saltwater crocodile (*Crocodylus porosus*) were seen feeding on the carcass. An aerial drone (DJI Phantom 4) was launched at 0847 h to capture photographs and videos of the event.

A total of 5 min and 48 s of 4 K footage from the carcass were obtained. Two tiger sharks, estimated to be ~ 300 cm total length (adults), were recorded feeding on the carcass throughout the footage. Only one shark was ever observed feeding at any given time. Tiger sharks showed a preference for the pectoral fins of the carcass (Fig. 1a), and after a feeding event would sink beneath the surface and slowly swim away from the carcass. Sharks would then approach from depth to the surface for subsequent feeding passes, which included large half-moon bites that pulled flesh from the whale. Throughout the footage, all tiger sharks appeared to be in a state of post-feeding torpor, as seen in other sharks when gorging themselves on whale carcasses (Fallows et al. 2013), suggesting they had been foraging for some time. The saltwater crocodile estimated to be 400 cm in length (adult) was observed from the beginning and throughout the footage (Fig. 1b). The crocodile fed at various locations on the carcass, including the rostrum and fluke, with a preference for the pectoral fins (Bornatowski et al. 2012). Unlike the half-moon bite marks left by the tiger sharks, the crocodile appeared to pull and tear smaller pieces of flesh from the carcass with a ripping motion (ESM1). There were no major apparent bite marks left like those seen from tiger sharks. Crocodile feeding behaviors were characterized into two categories: (1) horizontal bites where the crocodile floated on the surface of the water, which were common on pectoral fins and the fluke (Fig. 2a); and (2) vertical body positioning which included tearing and ripping, with use of the tail to generate pull and maintain body position, which focused on the fleshy rorquals of the whale (Fig. 2b). Behavior (2) on the rorquals occurred once, and during this event a tiger shark made brief contact with the crocodile, appearing to splash the water with its tail, likely in an effort to deter the crocodile from the region (ESM1, 0:28 s). After this interaction, the shark quickly abandoned the region, after which the crocodile buried its head into the cavity of the whale, presumably in an effort to find more desirable pieces of flesh (ESM1). Afterwards, the crocodile used its front legs to climb on to the pectoral fin where it remained for ~ 1 min to either rest or avoid detection by tiger sharks (Fig. 2c).

At 1251 h the drone stopped recording and the main ship departed north towards the Prince Regent River. On the return trip 7 days later, the carcass had washed ashore and up to 12 saltwater crocodiles were seen foraging on and remaining around the carcass (although no footage was obtained).

Discussion

Scavenging by sharks is relatively common, and likely an important component of their feeding ecology (Barnett et al. 2012; Fallows et al. 2013; Hammerschlag et al. 2016). A number of whale carcass scavenging events by sharks, mainly white (*Carcharodon carcharias*) and tiger sharks, have been documented (e.g., Long and Jones 1996; Dudley et al. 2000; Dicken 2008; Clua et al. 2013; Fallows et al. 2013). Apart from highlighting the importance of whale

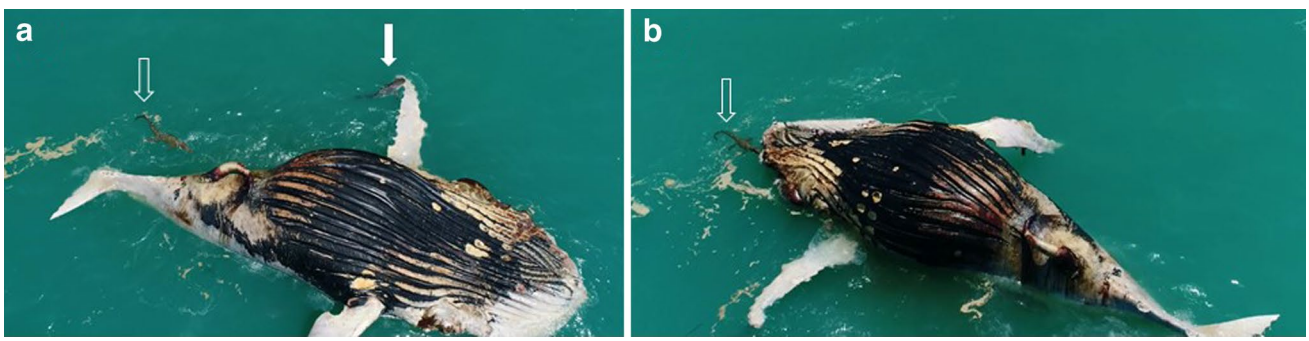

Fig. 1 **a** Tiger shark (*white filled arrow*) scavenging on pectoral fin of humpback whale (*top-center of image*), note the half-moon bite marks indicative of shark scavenging throughout. **b** A solitary saltwater crocodile (*white open arrow*) scavenging on the front of the whale carcass (*top-left of image*)

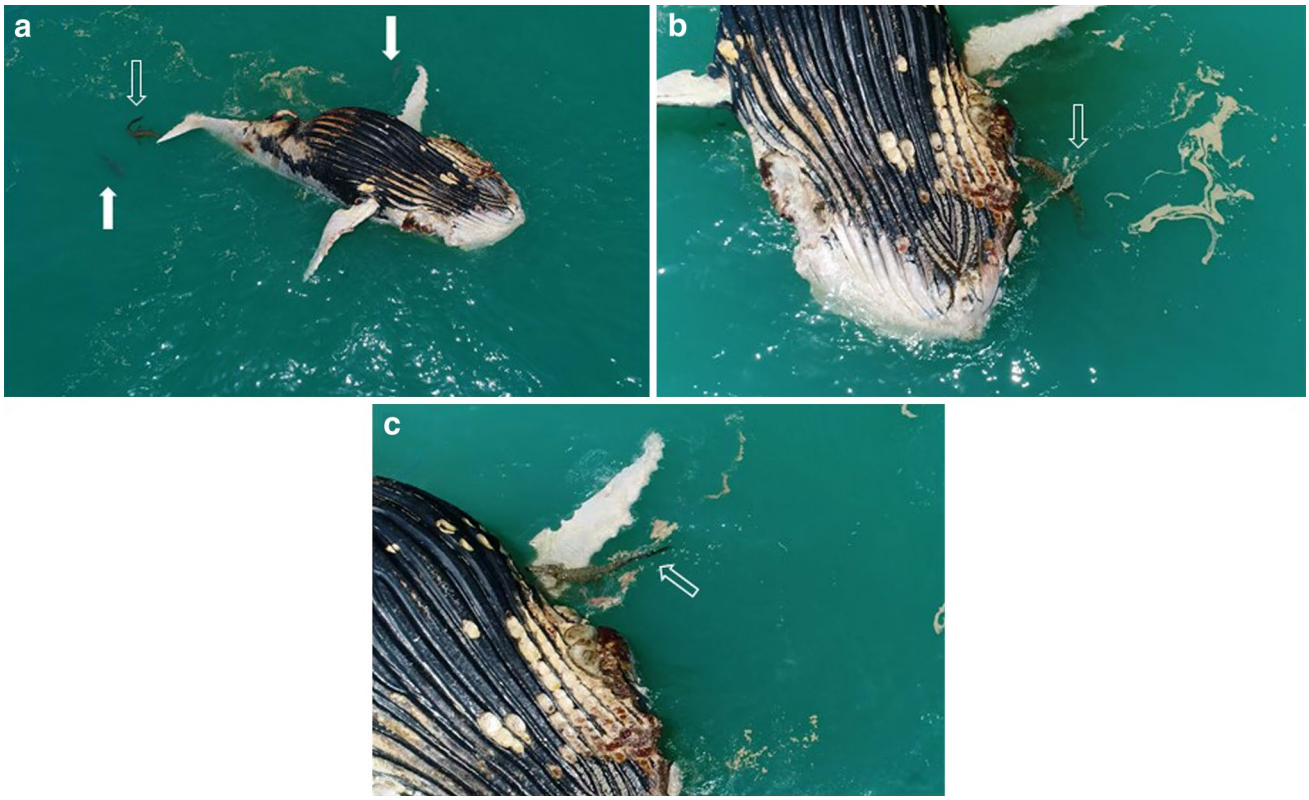

Fig. 2 Saltwater crocodile (*white open arrow*) exhibiting **a** horizontal biting behavior on the tail fluke of a humpback whale carcass, **b** vertical tearing on the whale's rorquals, and **c** resting on the pectoral fin in between foraging bouts

carcasses to shark diets, these opportunistic studies also revealed information on shark behavior. Dudley et al. (2000) observed both tiger and white sharks feeding concurrently on a whale carcass, with no competition or aggression observed between the two shark species or between tiger shark individuals; conversely, white sharks showed some intra-specific antagonistic behavior. Clua et al. (2013) identified at least 46 individual tiger sharks feeding on a blue whale (*Balaenoptera musculus*) carcass over 8 days. A size-based dominance hierarchy was observed, but with an increased tolerance toward smaller animals over time. Fallows et al. (2013) documented over 40 individual white sharks feeding on a whale carcass off South Africa, with no evidence of aggression despite a clear size-based pecking order.

Tiger sharks are known generalist predators (Lowe et al. 1996; Dicken et al. 2017). They are also highly opportunistic and will respond quickly to and subsequently forage on novel prey items including fresh carcasses (Gallagher et al. 2011). Although saltwater crocodiles will eat dead animals (Taylor 1979), information on scavenging behavior by this species is lacking in the literature, and nothing is known about the prevalence of saltwater crocodile scavenging on whale carcasses. Indeed, limited quantitative data are available for the diets of large crocodiles in Australia, but consumption of prey such as cattle, kangaroos, dogs, buffalo, goats, horses, reptiles and fish has been observed (Taylor 1979; Whiting and Whiting 2011). Body size is believed to be a good predictor of diet of saltwater crocodiles, with larger individuals (> 188 cm total length) targeting larger prey, and potentially consuming prey from three distinct food webs, linking terrestrial, freshwater and saltwater ecosystems (Whiting and Whiting 2011; Hanson et al. 2015). Saltwater crocodiles from Northern Australia primarily feed on small marine fishes and benthic estuarine prey, although larger individuals are known to prey on terrestrial mammals and birds (Taylor 1979). Habitat use of saltwater crocodiles and tiger sharks is likely to show minimal overlap (e.g., coastal areas when crocodiles move out of river systems), largely separating these two apex predators. The saltwater crocodile's most pronounced dietary overlap with sharks could be sea turtles, as nesting turtles are important seasonal prey for both predatory species (Heithaus et al. 2008; Whiting and Whiting 2011; Hammerschlag et al. 2016). Given that saltwater crocodiles typically occur in riverine and coastal wetlands, the likelihood of feeding on whale carcasses is influenced by the carcass being close enough to shore (i.e., ~ 1 km or less) and in areas with higher saltwater crocodile densities,

as seen in our observations. This is further supported by our observation of up to 12 crocodiles scavenging on the whale carcass once it had washed ashore.

In addition to the sharks and crocodiles in this study appearing not to feed from the same location on the whale simultaneously, we also did not observe any repeated interspecific agonistic interactions or indications of dominance hierarchies from our limited sample (except for the one instance when the tiger shark splashed with its tail). Crocodiles have been observed killing smaller sharks (e.g., bull sharks, *Carcharhinus leucas*) in narrow estuaries and rivers where they may have the advantage, and there is even some evidence for juvenile sharks being chemically aware of crocodiles (Rasmussen and Schmidt, details within Nifong and Lowers 2017). Alternatively, there is some evidence of an adult crocodile having been killed by sharks (Nifong and Lowers 2017). Our observations suggest adult tiger sharks and saltwater crocodiles can scavenge the same food source simultaneously with few or no agonistic interactions. How often these situations arise is unknown, as is the response of crocodiles when the number of sharks on the carcass start to increase (there could be more sharks at discrete coastal sites with signigicant tidal flow, since oils and sensory cues from the carcass travel widely).

Through the opportunistic capture of drone footage, we present one of the first ethograms of large, apex predatory sharks and crocodiles simultaneously foraging together on a shared resource. Scavenging events attract a diversity of species, some of which may not be commonly encountered together. Upon closer examination, our footage suggests that sharks can detect and perceive the presence of a large crocodile, but whether crocodiles are perceived as a risk or threat to sharks remains unknown. We recognize that our report is only one small record of these species co-existing; however, it may provide a window into future studies interested in evaluating the trophic linkages and social interactions between aquatic apex predators. Recent studies suggest increased interest in scavenging research (Moleón and Sánchez-Zapata 2015), and the growing body of empirical work suggests that this process is crucial for understanding the biology, evolution, and the behavioral ecology of top predators (e.g., DeVault et al. 2003; Wilson and Wolkovich 2011). Furthermore, as ecosystems change and mobile, aquatic predators are pushed into new areas, these types of interactions could increase in certain coastal areas. As such, we believe the reporting of these types of events is valuable and ecologically important, especially for threatened species of top predators.

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