Alarm call production and temporal variation in predator encounter rates for a facultative teleost grazer in a relatively pristine seagrass ecosystem

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A B S T R A C T

Predation risk can structure the spatial and temporal patterns and strength of grazer impacts on primary producer communities. Although teleost grazers have the potential to exert strong top-down effects on seagrass communities, relatively little is known about how risk might structure these effects. Here, we used tethering trials to identify potential predators of an abundant facultative teleost grazer, the western striped trumpeter (*Pelates octolineatus*, Jenyns 1840), and investigate patterns of predator encounter rates in a relatively pristine seagrass ecosystem. Pied cormorants (*Phalacrocorax varius*) were identified as the most common predator during 116 tethering trials that were video-recorded. Trumpeters also were preyed upon by giant shovelnose rays (*Glaucostegus typus*), nervous sharks (*Carcharhinus cautus*), and blue swimmer crabs (*Portunus pelagicus*). Predation events on tethered fish were higher during trials conducted during a warm period than a colder period, which corresponded to variation in cormorant densities observed along standardized transects. Activity rates of fish that survived the tether trials were similar to those that were preyed upon. Fish vocalization rates were low throughout the majority of tethering trials, but high immediately preceding and during predatory attacks suggesting that trumpeters may produce alarm calls. Although further studies are needed, our data suggest that seasonal variation in predation risk could be an important factor in structuring the behavior and foraging impacts of an abundant facultative teleost grazer in a relatively pristine seagrass ecosystem.

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1. Introduction

Predation is an important driver of habitat use, abundance, and foraging behavior in diverse taxa and can limit prey population sizes (e.g. Brown and Kotler, 2004; Lima and Dill, 1990; Ritchie and Johnson, 2009). Thus, predators may indirectly influence plant communities by altering spatial and temporal patterns and overall intensity of herbivory (e.g. Estes et al., 2011; Hairston et al., 1960; Schmitz et al., 2004 for reviews). Recent studies suggest that non-consumptive effects (or "risk effects"), including behaviorally-mediated indirect interactions (BMII) such as reduced activity and altered habitat use, may be equally or more important than indirect effects initiated by direct consumption of prey because of their tendency to affect large portions of prey populations (Creel and Christianson, 2008; Dill et al., 2003; Heithaus et al., 2008a; Preisser et al., 2005; Schmitz et al., 2004).

Despite their central role in the dynamics of many systems (e.g. Estes et al., 2011), top-down effects in seagrass ecosystems have only received attention relatively recently (Heithaus et al., 2009; Moksnes et al., 2008; Pages et al., 2012; Poore et al., 2009; Valentine et al., 2007). Previously, it was thought that direct herbivory had little impact on seagrass communities and the possibility that predators could affect seagrasses through direct predation or risk effects on herbivores – especially highly mobile species – was largely overlooked (reviewed in Heck and Valentine, 2006). Recently, however, it has become apparent that the intensity of herbivory can vary widely both temporally and spatially in seagrass systems, and may be at least partially driven by predators (Heck and Valentine, 2006; Heithaus et al., 2008b, 2009; Lewis and Anderson, 2012; Moksnes et al., 2008; Valentine et al., 2007). For example, fish can limit the abundance of low-mobility herbivores (Duffy and Hay, 2000), and invertebrate mesograzer abundances increase in the absence of predators, resulting in low biomass of algae on seagrass leaves (Eriksson et al., 2009; Moksnes et al., 2008). Also, top predators can modify foraging patterns of megaherbivores, including dugongs (*Dugong dugon*; Wirsing et al., 2007) and green turtles (*Chelonia mydas*; Heithaus et al., 2007). The potential indirect effects of predators on primary producers mediated through herbivorous fish are less known, but are likely (see Armitage and Fourqurean, 2006). Indeed, fish can remove substantial amounts of primary production and are at risk from a diversity of piscivores in many locations, making predation risk to teleost grazers in seagrass ecosystems of particular interest (Armitage and Fourqurean, 2006; Kirsch et al., 2002; Tomas et al., 2005).

Predation risk is a product of the encounter rate between predator and prey and the probability of death given an encounter (Lima and Dill, 1990). Measuring predation risk in relatively large-bodied and mobile species, like many teleosts, can be difficult. Restraining prey (or tethering) can provide insights into predator encounter rates and

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the ability to compare these encounter rates across space and through time, but the limitations of this technique must be considered (Aronson and Heck, 1995; Aronson et al., 2001; Lank and Ydenberg, 2003; Peterson and Black, 1994). For example, although tethering removes observer bias, it impedes escape behavior (i.e. increases the probability of death in an encounter situation) and may increase attack rates (i.e. increases estimates of encounter rates) if predators are attracted to tethered individuals. Continuous video recording of tethering trials, however, offers the potential for a more complete retrospective evaluation of the degree to which biases of tethering may differ between treatments (Peterson and Black, 1994). It also has the potential to provide insights into anti-predator behaviors, such as the use of alarm calls.

Shark Bay, Western Australia, has been used as a model system for investigations of top-down processes, particularly risk effects, in a relatively pristine seagrass ecosystem (Heithaus et al., 2009). Although predation sensitive foraging of large-bodied herbivores (dugongs and green turtles) (Heithaus et al., 2007; Wirsing et al., 2007), and their resulting impacts on seagrass (Burkholder et al., 2012, in press; Heithaus et al., 2007), has been studied in Shark Bay, less attention has been given to the potential for risk-sensitive foraging behavior of fish grazers and how this may impact seagrass ecosystem dynamics. The teleost *Pelates octolineatus* (western striped trumpeter; Terapontidae) is the most abundant mid-sized teleost (maximum length of 28 cm) in the long-term Shark Bay study site (Heithaus, 2004) and has been observed consuming substantial proportions of primary producers (Burkholder et al., 2012; Davis et al., 2012, Bessey unpublished data). Therefore, western striped trumpeters could impact seagrass and algal communities (Burkholder et al., 2012). Little is known, however, about the specific predators of *P. octolineatus* and how encounter rates with predators might vary in space and time. Likewise, little is known about the use of anti-predator behaviors, such as alarm calls, by these soniferous fish. Here, we used tethering trials with continuous video surveillance to identify potential predators of western striped trumpeters, investigate patterns of predator encounter rates, and determine whether fish might use alarm calls when threatened by predators.

2. Materials and methods

2.1. Study site

Our study occurred in the Eastern Gulf of Shark Bay offshore of the Monkey Mia Dolphin Resort. Shark Bay (25°45′S, 113°44′E) is a ca. 13,000 km^2 subtropical embayment in Western Australia with approximately one-third of its area (~4000 km^2) covered by seagrass meadows (Walker et al., 1988). Water temperatures are generally high (>20 °C) during September to May (warm season) and drop to as low as 12 °C during June to August (cold season) (Heithaus and Dill, 2002, 2006).

The study site is made up of a series of shallow offshore banks (<4.5 m depth) surrounded by deeper waters of 6–12 m depth. Shallow banks are largely covered by seagrass, although the community composition varies with depth, while deep waters are largely unvegetated (Burkholder et al., 2013). Western striped trumpeters are largely confined to shallow habitats and are concentrated in vegetated areas (Heithaus, 2004).

2.2. Tethering trials

We tethered individual western striped trumpeters at least 100 m apart within shallower (mean water depth ± sd = 2.1 ± 0.4 m) and deeper (mean water depth ± sd = 4.4 ± 0.5 m) portions of three separate seagrass banks in our study site. We chose 100 m as a conservative distance that would exceed the visual (Strod et al., 2008), electrosensory (Haine et al., 2001), and echolocation range (Wilson et al., 2013) of potential predators foraging in a seagrass meadow (e.g. small sharks,

large teleosts, dolphins, marine birds); thereby minimizing the likelihood of multiple predation events by a single individual predator. We used continuous video surveillance to determine time to attack of tethered fish, predator identity, as well as to make post-hoc comparisons of tethered fish behavior. A total of 116 tethered fish were deployed over nine days during the warm period (April 3–May 8, 2012; mean water temperature ± sd = 22.8 ± 0.7 °C; n = 30 in deeper and n = 31 in shallower microhabitats), and eight days in the cold period (June 30–August 4, 2012; mean water temperature ± sd = 15.5 ± 0.6 °C; n = 27 in deeper and n = 28 in shallower microhabitats). It was necessary to place tethered fish in patches of sand or sparse seagrass within each microhabitat to prevent tethered fish from becoming entangled in seagrass shoots. Although this method likely increases the rate of predation on tethered fish above that which would occur were fish able to hide in dense seagrass, western striped trumpeters do occur in sparse seagrass habitats and our method facilitates identification of potential predators while providing an index of relative encounter rates through time.

Tethered fish were obtained on the day of trials using squid-baited fish traps (34 × 24 × 21 cm; 12 × 13 mm mesh) and measured for fork length (mean ± sd = 16.7 ± 1.9 cm). Individual fish were tethered to a swivel on the end of a stake using a 30 cm long leash of monofilament fishing line tied through the membrane behind the lower jaw of the fish and out the mouth. The 30 cm leash allowed for natural swimming behavior of fish (representative video provided below) while limiting the range of movement to within the field of view of the camera. The length of leash also minimized entanglement of tethered fish with structure in the immediate vicinity. The stake was positioned 80 cm in front of an 8 kg I-beam that was mounted with a GoPro Hero (Woodman Labs, http://gopro.com, Nov. 20, 2012) underwater camera. Fish were tethered between 9 am and 2:30 pm because grazers typically display diurnal feeding patterns (Helfman, 1986). Continuous video footage of each trial was obtained for the duration of the trial (mean ± sd = 186 ± 26 min). All equipment was collected at the end of each day and all remaining fish were released. All fish that were not preyed upon survived the tether trials and were in apparent good health and readily swam away. Video footage was used to determine the identity of attacking predators. In addition, the video footage from 40 trials where tethered fish survived was reviewed to determine if a potential predator was observed within the field of view (n = 40; 10 from each microhabitat and each period).

Tethering fish allowed us to limit escape and anti-predator behavior as interacting determinants of mortality. However, to investigate behavioral differences in tethered fish that might lead to increase attraction of predators, we determined activity rates and vocalizations using video footage of trials. The activity rate of a fish was measured as the average number of seconds spent swimming (caudal fin movement) versus stationary (no caudal fin movement) during five different randomly assigned 1-min segments of a trial. We determined the activity rate of 88 different fish; 60 fish that survived (30 from the warm period and 30 from the cold period), and 28 fish that were preyed upon. In addition, we recorded whether each fish was heard vocalizing at any time during the analyzed footage. Vocalization was also determined for the minute immediately prior to the predation event for preyed upon fish.

A representative video of tethered fish behavior, as well as, behavior of conspecific fishes near the tethered individual are provided as Supplemental material (TetherTrialMovie_BesseyHeithaus.wmv).

2.3. Belt transects

To compare attack rates on tethered fish to abundances of pied cormorants, the most abundant air-breathing predator in the study area (Heithaus, 2005), we conducted visual surveys of cormorant abundance along pre-established belt transects (~3.2 km long) over the seagrass banks where tether trials were conducted. We completed eight passes over seagrass banks during five different days in the warm period and