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Juvenile *Gobius niger* avoids seagrass in the presence and uncertain absence of seagrass-inhabiting predators

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ABSTRACT

We performed a series of laboratory tank experiments designed to identify possible mechanisms for the strict seagrass avoidance of juvenile *Gobius niger* previously observed in their natural habitat, the Novigrad Sea, northern Adriatic. Overall our results suggest that juvenile *G. niger* strongly prefers seagrass when predator absence is certain, avoids seagrass in the presence of predators, and chooses habitat based on both predator identity and on the degree of certainty of predator presence or absence. In the presence of predators, juvenile *G. niger* occupies the same habitat as adult size *G. niger* but avoids the habitat chosen by *Zosterisessor ophiocephalus*. Juvenile *G. niger* is most likely to switch habitat in response to addition or removal of *Z. ophiocephalus*, the predator with the stronger seagrass preference. A significantly lower likelihood of selecting seagrass was exhibited when predator absence was uncertain than when predator absence was certain. Our results suggest that juvenile *G. niger* identifies predators by species and responds differentially to perceived risk posed by each predator through differential habitat selection, which also depends on the certainty of predator absence. These results are consistent with the hypothesis that the importance of structured refuge habitats, such as seagrass, is relative: it depends on both the prey's perception of the relative predation risk posed by multiple predators in alternative habitats, and on the prey's specific antipredator response strategies. These responses could explain the avoidance of seagrass by *G. niger* in the Novigrad Sea.

1. Introduction

Predator–prey interactions can be the dominant process structuring communities and the distribution of community-level properties across habitat space. In shallow benthic habitats, three dimensional structure is thought to play an important role in mediating these interactions, and one key provider of such structure is the seagrass meadow. The seagrass superiority hypothesis (SSH) proposes that seagrass habitats are an unconditionally superior refuge for potential prey, because their structural complexity prevents detection and slows the predator's chase (Heck and Orth, 1980). In contrast, the predation-mode hypothesis (PMH) predicts that the value of seagrass as predator refuge is conditioned on the relative abundance of predation modes within and without the seagrass sward (Schultz et al., 2009). If chase predators that hunt transiently in seagrass pose the highest risk of predatory mortality, as postulated by the SSH, prey is expected to minimize that risk by concealing itself in seagrass. In contrast, the PMH predicts that if ambush predators are resident in seagrass, then its value as a refuge is reduced or eliminated completely (Schultz et al., 2009). Prey responses to the predator community may differ depending on the degree of perceptive certainty of predator presence or absence. Strategies that are specific to the predator's identity, risk, and habitat allow prey to be flexible in choosing optimal habitat in environments that change over space and time, and to avoid net negative outcomes in the ceaseless tradeoff between resource use and predation risk (Magnhagen, 1988, 1990).

Both consumptive and non-consumptive predator–prey interactions shape ecosystem level interactions and dynamics, and may influence a preference for habitat structure. Non-consumptive interactions involve alteration of any prey trait in response to the predation. Most obvious are behavioral alterations, and behavioral choices made by prey under differential predation risks have long been studied and interpreted adaptively (Lima and Dill, 1990). A common behavioral alteration observed in prey is the switching of habitats from high to low predation risk, in the presence of appropriate stimuli. Lima (1998) reviews over 90 studies of such habitat shifts. Much research has addressed the ability of prey to match their antipredator behavior to the perceived predation risk (Ferrari and Chivers, 2006; Lima and Bednekoff, 1999; Vainikka et al., 2005) and now much evidence indicates that the intensity and type of antipredator behavior varies according to the magnitude of the perceived risk (Helfman and Winkelmann, 1997). A prey's risk perception may depend on the predator's size (Bishop and Brown, 1992), behavior (Helfman and Winkelmann, 1997), or may depend on information from nearby conspecifics (Brown et al., 2006; Helfman and Winkelmann, 1997).

The prey's habitat choice and activity level may respond to details of a predator's mode of search and frequency of habitat occupancy. A long

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standing paradigm in fish ecology, and the primary assumption of the SSH, is that prey fish seek highly structured habitats in response to visual and highly mobile predators. Such move-and-chase predators are assumed to lack habitat preference and to frequent all available habitats transiently in search for and pursuit of prey. As a result, they are difficult to detect and monitor, and the best antipredator response may then be hiding passively in complex, three-dimensional structure (Horinouchi et al., 2009). The situation differs when predators are resident in the prey's habitats. Schmitz et al. (2004) hypothesized that prey should respond with activity level adjustments if a co-resident predator actively pursues them, through relocation upon detection. In contrast, negative habitat choice and habitat switching are predicted as the best response to ambush predation by a co-resident predator. In a review of a large number of experiments on fish predator–prey interactions Werner and Peacor (2003) concluded that effects of anti-predator behavior become more important relative to consumptive predator–prey effects with increased familiarity between prey and predator, as when both reside in the same locale.

Prey behavior that adaptively changes in response to predator species requires that prey not only can detect and identify predators, but also evaluate the relative predation risk posed by each predator across alternative habitats. Numerous studies indicate that prey do respond to such detailed information from a variety of cues, including visual, acoustic, and chemical. Visual cues for example can reveal predator size and distinguish behaviors indicating differential threat magnitude (Chivers et al., 2001; Helfman, 1989). Chemical predator cues also offer information beyond identification; e.g., cue concentration can indicate predator proximity and approximate location (Ferrari et al., 2010b; Kusch et al., 2004). A wide diversity of aquatic prey organisms releases and responds to chemical alarm cues produced during predation threat that signal degree of danger to conspecifics (reviewed in Chivers and Smith, 1998; Mirza and Chivers, 2002; Summey and Mathis, 1998). Predation risk assessment by prey has two components, an estimate of the current risk and of the degree of certainty of the risk (Lima and Steury, 2005). Studies investigating how level of certainty may affect decision-making found that unreliable predator information can still trigger antipredator responses and that prior experiences affect a prey's certainty about a currently perceived risk (Ferrari et al., 2010a; Fraker, 2009; Lima and Steury, 2005; Sih, 1992).

All the above cues, perceived over time by an individual prey organism, can result in learned evaluations of predator identity and predation risk (Holmes and McCormick, 2010). Such learning may even include associating a habitat with the presence of a particular predator species (Chivers and Smith, 1998; Ferrari et al., 2007; Mathis et al., 1996; Smith, 1999). If associations of predators with habitat are stable and predictable, then these learned associations may result in a stable habitat preference by prey individuals, and these may include negative preferences for complex three-dimensional structure such as seagrass meadows.

Extensive visual census field studies in the Novigrad Sea, an estuarine lagoon in the central Croatian Adriatic, revealed strong avoidance of seagrass and preference for unconsolidated sediments in juvenile black gobies, *Gobius niger* (Linnaeus), one of the commonest fish species (Schultz et al., 2009). While transient predators were observed to be relatively rare, two resident benthic predators, adult *G. niger*, preferring unconsolidated sediment, and grass gobies, *Zosterisessor ophiocephalus* (Pallas), preferring seagrass, were numerically dominant fish in their respective habitats. Both predator species are capable of piscivory (Costa, 1988; Miller, 1986) but they differ in their predation mode. *G. niger* is a wait-and-chase predator and, in Novigrad Sea, awaits potential prey from a motionless position either from within sediment patches or from the edges of rock or seagrass patches bordering bare sediment. Upon detection of prey, including smaller individuals of its own species, *G. niger* follows it across the sediment in a chase-like manner that can last several minutes and result in repeated prey attacks (Kruschel and Schultz, 2010; Schultz and Kruschel, 2010). In contrast, *Z. ophiocephalus* is an ambush predator that awaits potential prey by suspending itself motionless in the seagrass (Ota et al., 1999). Immediately upon detection of potential prey, *Z. ophiocephalus* bursts toward the prey in one rapid movement and almost never follows up with a second attack (Kruschel and Schultz, 2010; Schultz and Kruschel, 2010). In tank and *in-situ* experiments *Z. ophiocephalus* posed a greater predation risk for small gobiids (*Pomatoschistus* spp.) than *G. niger*, and gut content analysis of wild caught predators revealed that *Z. ophiocephalus* consumed larger prey than *G. niger* (Schultz and Kruschel, 2010).

This study was designed to investigate possible mechanisms that could explain why juvenile *G. niger* shows strong avoidance of seagrass and preference for bare sediment in the Novigrad Sea (Schultz et al., 2009), while showing reverse preference in other locations, including the Venice lagoon in the western Adriatic, a Portuguese Mediterranean Sea lagoon, as well as shallow bays in northern Europe (Franco et al., 2006; Gordo and Cabral, 2001; Magnhagen, 1988; Malavasi et al., 2005; Wiederholm, 1987). We hypothesized that the prey's choice is the outcome of avoidance strategies that may be sensitive to predator identity. In detail we asked the following questions: (1) Do juvenile *G. niger* in the absence of predators occupy the two available habitats as expected by chance? (2) Do predators exhibit species-specific habitat preference? (3) Does *G. niger* habitat choice depend on predator species? (4) Does prey keep a larger distance from the seagrass during predator presence and is the distance prey keeps from the predator dependent on identity and size of the predator? (5) Do juvenile *G. niger* switch habitat in response to predator addition and removal, and if so, is this response dependent on predator identity and size, and the time of day? (6) How does the certainty of predator absence affect habitat choice by juvenile *G. niger*?

2. Materials and methods

2.1. Fish acquisition

Prey fish, juvenile *G. niger*, 3–5 cm long, were caught by a sink net, (Mosella Köderfisch Senke 100 × 100 cm Senknetz Köfis). Juvenile *G. niger* were chosen as prey because they are the most common juvenile fish in their source location within Novigrad Sea, and because there is sufficient field observational and experimental evidence that this species avoids seagrass at this location (see Introduction) and that it is a potential prey of either predator when brought together experimentally (Kruschel, unpublished data). Also, *G. niger* is known to prefer seagrass habitat in various other similarly shallow and protected bays. Adult *G. niger* (mean length 10.1 cm, standard deviation 0.95 cm) and *Z. ophiocephalus* (mean length 14.4 cm, standard deviation 3.2 cm) were caught by a simple hooked and weighted line (the locally produced “tunja”). The hook was baited with freshly caught but dead *Pomatoschistus marmoratus* (Risso). Caught predator specimens were rejected for further use in experiments if the hook damaged any other part but the skin around the mouth. Accepted specimens were held in closed, opaque insulated containers 28 (L) × 20 (W) × 22 (H) cm, filled with ambient water sampled at the same time and location as the fish were caught. Fish were held in three holding tanks, each aerated by a single bubble stone, one for the prey specimens and one for each of the two predator specimens. Holding tanks were kept in a quiet location and not opened prior to the experiment. Minimum time spent in the holding tank was 24 h, maximum of 48 h, and specimens were evaluated for their vitality prior to their being used in the experiment. Specimens showing signs of bleeding, physical damage, or behavioral abnormalities (e.g. very fast or very slow breathing or unbalanced body positioning) were excluded. Prey or predator specimens were never used more than once in experiments and never later than 48 h following capture. All specimens were returned to a location near the location of capture after the completion of an experiment.

2.2. Tank design

The bottoms of four clear white plastic experimental tanks, each 70 (L) × 50 (W) × 18 (H) cm, were covered with a 5 cm thick layer of