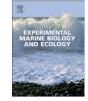
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Algal cover in mangroves affects distribution and predation rates by carnivorous fishes

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ABSTRACT

Distribution and survival of fish are influenced by benthic habitat and complexity. While many studies have investigated the effects of algal cover on fishes in reef habitats, comparatively less is known regarding this relationship in mangrove habitats. Possible links between substrate macro-algal cover and fish distribution were studied in a Caribbean mangrove lagoon via visual surveys and algal removal experiments. In addition, the effects of algae on relative predation were tested by calculating survival of tethered brachyuran prey, whose predators are known to include larger lutjanid (snapper) juveniles. Comparisons of algae and fish distributions show that percent cover of algae and juvenile lutjanid, *Lutjanus griseus* (gray snapper) abundances were significantly negatively correlated. Results from the algae removal experiment showed that algae had a negative effect on abundance of carnivorous fishes in two (out of three) locations in the lagoon. In addition, tethered prey had significantly higher proportional survival in plots with algae-present relative to plots with algae-absent. We present here experimental evidence that increased algal growth in mangroves may reduce predator encounter rates by prey. These observations are important, as the presence of carnivorous fishes is a key factor for the maintenance of high diversity in mangrove and on neighboring coral reefs. Furthermore, findings from this study imply that algal cover must be considered when protecting mangrove habitat.

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1. Introduction

Human influences in the tropics have often led to increased levels of algal cover (Granek and Ruttenberg, 2008; LaPointe et al., 2004; Mork et al., 2009; Sjoo et al., 2011). Many coral reefs are shifting from hard coral to algae dominant, resulting in a loss of species richness and abundance of fishes (Bellwood et al., 2004; Bruno et al., 2009; Szmant, 2001). The alternative stable state of algal dominant reefs is the result of a combination of over-fishing herbivorous fishes, pathogen-induced decline in herbivorous urchin populations, and increased nutrient levels (Scheffer et al., 2001).

In shallow habitats adjacent to reefs, increased algal cover may occur when mangroves are cleared, augmenting the amount of sunlight reaching the substrate (Granek and Ruttenberg, 2008). In addition, nutrients from sewage or land run-off may also increase algal growth in mangrove habitat (LaPointe et al., 2004). La Pointe's study in the Bahamas found that nutrient enrichment explained high biomass of macro-algae outside the entrance of a mangrove pond. Mangrove habitats are well recognized as providing important nursery habitat to juveniles of both coral-reef fishes and invertebrate species (Jaxion-Harm et al., in press; Nagelkerken et al., 2000a; Primavera, 1998). For many species, mangroves may disproportionately enhance

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numbers of juveniles that move into adult habitats, resulting in increased adult densities on neighboring coral reefs (Beck et al., 2001; Harm et al., 2008; Mumby et al., 2004). Increased algal cover on coral reefs has negative consequences (e.g. Bellwood et al., 2004; Bruno et al., 2009). Algal cover is also increasing in mangrove habitat (Granek and Ruttenberg, 2008; LaPointe et al., 2004), yet the effects of algal cover on fish distribution and prey detection in mangroves are poorly understood.

In most habitats, complex and heterogeneous structures provide refugia for small prey, and often result in an increase in their densities (Gratwicke and Speight, 2005; Hixon and Beets, 1993; Taylor and Freeberg, 1984). Algae may provide shelter for prey, and may deter predators from foraging in dense thickets (Gotceitas and Colgan, 1989). Indeed, many freshwater plant studies (Anderson, 1984; Diehl, 1993) and seagrass studies (Heck and Thoman, 1981; Hovel and Lipcius, 2001) have found that experimentally increasing vegetation complexity (e.g. macro-phytes and macro-algae) reduces foraging success of larger carnivorous fishes. Isaksson et al. (1994) studied the foraging efficiency of cod in Swedish waters suffering from eutrophication and increased algal cover. Survival of decapod prey was lowest in un-vegetated sites, increasing as vegetation was increased. Likewise, survival of tethered juvenile blue crabs in Chesapeake Bay, Virginia, increased as density of seagrass shoots increased (Hovel and Lipcius, 2001). To maximize foraging, predators must select habitats where prey encounter rates and capture success are optimal (Hugie and Dill, 1994).

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Predatory foraging is difficult to measure in the field; instead tethering methods are employed that measure the survival of prey (Aronson and Heck, 1995). In mangrove habitat, previous studies have compared survival of prey fish (small or juvenile) between habitats. These include contrasts of mangroves versus seagrass and coral reefs (e.g. Chittaro et al., 2005; Dorenbosch et al., 2009; Ellis and Bell, 2004), at different depths (Ellis and Bell, 2004; Rypel et al., 2007), and among seagrass locations with differing distance to mangrove forests (Hammerschlag et al., 2010). While previous mangrove literature has focused on relative predation on small prey fishes, information on predation by carnivorous fish in mangroves and algal beds is relatively scarce.

Harm et al. (2008) found that Caribbean mangroves in a lagoon semi-enclosed from ocean waters by barrier beaches housed many carnivorous fishes, including commercially important species of the lutjanid (snapper) family. Semi-enclosed lagoons often semi-isolate mangroves from neighboring habitats such as seagrass and coral reefs, which are usually found in open waters. Bottom substrate of the main mangrove lagoon on Utila was covered in foliose macroalgae and was lacking both seagrass beds and coral reefs. Semiisolated mangroves are often ignored in reef-associated literature. However, many regions in the Indo-Pacific and Caribbean house semi-isolated mangroves (e.g. Pittman et al., 2007; Tongnunui et al., 2002), and fish communities in these mangroves often differ from those in open, connected mangroves (Dorenbosch et al., 2007; Jaxion-Harm et al., in press; Pittman et al., 2007).

In the current study, we hypothesized that (1) fewer carnivorous fishes would be found in areas with high densities of algae and (2) algae would negatively affect predator encounter rates by prey.

To test this hypothesis, a series of experiments was conducted in a semi-isolated lagoon to answer the following questions: (1) Are fish densities in mangroves correlated with macro-algae covering the bottom substrate? (2) Are macro-crustacean prey abundances affected by algal cover? (3) Does the removal of algae from the bottom substrate affect fish abundance? (4) Do algae affect predation rates of piscivorous fishes on benthic crustacea?

2. Methods

2.1. Study sites

The current study was conducted in Oyster Bed Lagoon, Utila, which is one of the Bay Islands located 29 km off the Caribbean coast of Honduras (Fig. 1). Utila has very little tidal exchange (tidal range of approximately ± 20 cm) or freshwater influence during the dry, summer months; therefore the island is representative of many Caribbean islands (e.g. Aguilar-Perera and Appeldoorn, 2008; Dorenbosch et al., 2007; Gratwicke et al., 2006; Hauser et al., 2007; Nagelkerken et al., 2000a). Oyster Bed Lagoon houses mangrove forests that surround shallow, highly sedimentous bodies of water semi-separated from the open sea. Oyster Bed Lagoon consists of two large bodies of water separated by a small (110 m long) canal (Fig. 1). The opening of the lagoon measures 75 m across and allows for exchange of water with the sea. The lagoon is shallow with an average depth of 1.5 m, and maximum depth of 3 m. Small portions of the lower and upper lagoons have undergone mangrove loss from land reclamation. Two artificial canals have been cut and dredged to a water depth of 2-3 m on the West and Northwest

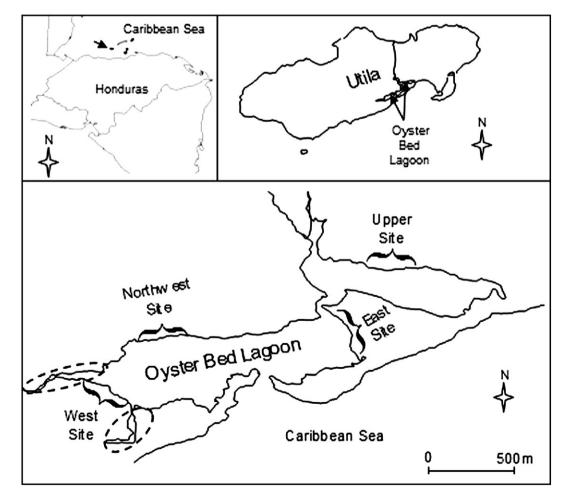


Fig. 1. Map of Oyster Bed Lagoon (N 16 06 25, W 86 54 75), Utila, Honduras, Central America and location of sites. Dashed circles drawn around man-made, dredged canals.

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