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Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral reef of Pacific Costa Rica

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ABSTRACT

Overfishing and nutrient enrichment are among the major local stressors to coral reefs worldwide, as they can alter the benthic reef community by promoting fast growing algae and bioeroders. The Northern coast of Pacific Costa Rica is strongly influenced by seasonal upwelling events that naturally increase nutrient concentrations between December and March. This study therefore investigated the combined effects of simulated overfishing and naturally increased nutrients on benthic community composition and succession on settlement tiles over a period of 24 weeks (October 2013 until March 2014) using exclusion cages deployed in a coral reef in the Gulf of Papagayo. Tile cover of functional groups and development of organic C and N on light-exposed and –shaded tile sites were assessed. Results revealed that the exclusion of fish significantly increased the development of organic C and N and decreased the C/N ratio on light-exposed tiles. Large filamentous algae (>2 mm), fleshy macroalgae and the colonial ascidian *Didemnum* sp. (Savigny 1816) (up to 80% tile coverage) were dominant on both tile sites. A significant peak of filamentous algae growth and associated organic matter C/N ratio occurred on light-exposed tiles throughout all treatments in February when nutrient concentrations were elevated. These results suggest that both herbivore exclusion and natural eutrophication have a strong influence on the benthic reef community composition and its early succession patterns. The presence of *Didemnum* sp. and turf algae could represent good early warning bioindicators for local overfishing and eutrophication and may therefore be included in management and monitoring strategies.

1. Introduction

Many coral reefs around the world suffer from combined effects of elevated nutrient concentrations and depleted fish stocks, which may result in pronounced changes in the benthic community composition (Burke et al., 2011). Recent studies have shown that not only filamentous turf- and fleshy macroalgae are major competitors to corals (Hughes, 1994), but also sponges, colonial ascidians and other sessile invertebrates successfully compete for space (reviewed in Chadwick and Morrow, 2011; Glynn and Enochs, 2011).

Herbivorous fish play a crucial role in preconditioning coral reefs to allow for a successful coral recruitment and recovery (Bellwood et al., 2004). Their grazing activities limit turf- and macroalgae growth and therefore not only decrease coral-algae interactions but also opens space for crustose coralline algae (CCA) (Mumby, 2009). The latter can facilitate the settlement of coral larvae by chemical cues (Harrington et al., 2004; Heyward and Negri, 1999; Ritson-Williams et al., 2010). Additionally, a loss of herbivores attributable to fishing activities may result in increased growth of fleshy algae and therefore a loss of hard coral cover due to competition (e.g. Burkepile and Hay, 2009; McCook et al., 2001; Smith et al., 2010). Subsequently, coral reefs may face a reduction of habitat with a structural complexity (reviewed in McCook et al., 2001), which provides refuge also for invertebrate predators such as Balistidae, Labridae and Haemulidae (McClanahan et al., 1999). Bioeroders like sponges and ascidians generally comprise only a minor part of the benthic reef community (Glynn and Enochs, 2011); nevertheless, they can compete successfully with scleractinian corals due to their fast growth and high reproduction rates, or the use of allelochemicals (Bak et al., 1981; Loh et al., 2015; López-Victoria et al., 2006; Sawada et al., 2001). The proliferation of benthic invertebrates or bioeroders is often triggered by changes in environmental conditions (e.g. decreased predation pressure or increased food availability) (Chadwick and Morrow, 2011).

A second local stressor is the over-enrichment with nutrients in coastal waters. Scleractinian corals are adapted to oligotrophic coastal

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waters (Muscatine and Porter, 1977). Some of the direct negative effects of high nutrient concentrations include a reduction in calcification rates (Ferrier-Pages et al., 2000), combined with limited coral growth (Fabricius et al., 2013) and a decrease in the reproduction activity (Loya et al., 2004). Eutrophication may also be tightly linked to the deleterious effects of coral bleaching (Wiedenmann et al., 2012) and an increased susceptibility to coral diseases (Vega Thurber et al., 2014). Furthermore, elevated levels of nitrate and phosphate may promote the growth of benthic as well as planktonic algae (McClanahan et al., 2007). As a source of food, the increased availability of organic matter in the water column can additionally favor filter feeders, which are not physiologically inhibited by higher concentrations of nutrients (Bak et al., 1996; Ward-Paige et al., 2005).

Coral reefs at the northern coast of Pacific Costa Rica are exposed to highly dynamic environmental conditions. Seasonally elevated nutrient concentrations due to coastal upwelling (Clarke, 1988; Stumpf and Legeckis, 1977) and a highly developed fishing industry challenge the present reefs (Mathiesen, 2012). Strong wind jets channeled through a mountain gap in the Central American cordillera between December and April (McCreary et al., 1989; Romero-Centeno et al., 2007) displace surface water masses away from the coast, which are then replaced by colder and denser water from the depth (Bakun, 1990). Primary productivity is high during upwelling season when nutrient rich water masses are welled up to the surface (Small and Menzies, 1981). Furthermore, marine ecosystems in this area have to cope with strong impacts by local fisheries. Almost 80% of the landings derive from artisanal fisheries, which target for reef and coastal fish species (Wehrtmann and Nielsen-Muñoz, 2009) to meet the high demand of fish products for the tourism sector (Salas et al., 2011).

Even though studies have analyzed the combined effects of human induced eutrophication and overfishing on benthic algae growth, these investigations have almost exclusively been carried out in the Caribbean and the Red Sea (e.g. Burkepile et al., 2013; Jessen et al., 2013; Rasher et al., 2012; Smith et al., 2010). Additionally, most studies have only considered the impacts on the algal community, but little is known about the influences on invertebrate recruitment in this context (e.g. Abelson et al., 2005; Jessen et al., 2014). Furthermore, there are no studies available, how natural enhanced nutrient concentrations due to coastal upwelling may influence the benthic community composition and succession on tropical coral reefs. However, in order to sustain coral reef systems worldwide and to implement protecting management strategies, it is necessary to get a detailed understanding of the respective ecosystem (Daily et al., 2009; Hoegh-Guldberg et al., 2007). This study thus for the first time investigated the combined effects of simulated overfishing and natural seasonal eutrophication on the composition and succession of benthic algae and sessile invertebrate communities in a Pacific coral reef along the American continent. Fish exclusion cages with settlement tiles and the natural effects of coastal upwelling were used to: (1) assess the impact of simulated overfishing on *in-situ* succession of benthic algae and invertebrates and (2) determine the effects of changing nutrient concentrations due to coastal upwelling on settling succession and composition of benthic algae along with invertebrates on a temporal scale.

2. Material and methods

2.1. Study site

The study was carried out from October 2013 until March 2014 (duration = 24 weeks) in a patch reef located in the Gulf of Papagayo at the Northern Pacific coast of Costa Rica (N10°32′18.6″ , W85°45′ 54.4″) (Fig. 1). Matapalo Reef is located southwest of the well-studied bay Bahía Culebra (reviews by Cortés, 2012a,b). The reef is situated in close distance to the shore (approximately 20–30 m), in water depth of 5–7 m, depending on the tide. It is dominated by the branching hard coral *Pocillopora* sp.. The Gulf of Papagayo experiences seasonal coastal upwelling that usually takes place between December and March (Jiménez, 2001).

2.2. Nutrient concentration measurements

Water samples were taken in triplicates directly from above the reef over the total study period of 24 weeks in a biweekly resolution. Concentrations of ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}) were determined. Samples were filtered through syringe pre-filters and analyzed directly for concentrations of NH_4^+ and PO_4^{3-} using a Trilogy® Laboratory Fluorometer (Turner Designs) for fluorometric analysis of ammonia and spectrophotometric determination of phosphate according to Murphy and Rley (1962). A part of the samples was frozen for determination of nitrite and nitrate using a method with the reduction of nitrate by vanadium(III) and a Photometer *Thermo Scientific UV Evolution 201*®. Chlorophyll a (Chl a) concentrations were measured by filtering 3 L of seawater on pre-combusted filters (particle retention 1.6 μm), which were then incubated in 10 mL 90% Acetone for 24 h at 4 °C before analyzed with a spectrophotometer.

2.3. Enumeration of fishes

Visual surveys of fish were carried out using underwater fish census methods described by Green et al. (2009) Five transects with a length of 10 m each (n = 3 long-swims/replicates) were observed monthly from November 2013 to March 2014 investigating abundance, biomass and size classes of the fish community. The surveys were conducted between 9 am and 12 pm, 2.5 m left and right of the transect lines, surveying a total area of 250 m^2. All individuals ≥ 5 cm were counted and grouped in one of 6 size classes (5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, 25–30 cm and 30–40 cm). Cryptic species were not included in the surveys. Biomass estimations were calculated using known length-weight relationships (LWR) for fishes: The weight in grams (W) of a fish can be predicted by its fork length in cm (L) by using the formulae $W = aL^b$ (Froese et al., 2014). Parameters a and b are compiled at FishBase (Froese and Pauly, 2009) for most species. If parameters were not available for single species, a higher taxonomic rank (e.g. family) was chosen. The mid value of each size category was used for the biomass estimation (e.g. 17.5 cm for size category 15–20 cm). Fish diversity was calculated for each sampling using the Shannon-Wiener index (Shannon, 2001). Fishes were categorized as carnivore or herbivore, according to their ability to remove benthic algae (information taken from Froese and Pauly, 2009). Due to their potential positive effect on algae growth through gardening and / or their territorial behavior (Hoey and Bellwood, 2010), damselfish were not classified as herbivores in this study.

2.4. Experimental cage set-up

Twelve anodized aluminum frames (50 x 50 cm) were deployed in the reef with at least 1.5 m distance to each other. Three different treatments were applied to the frames (each with n = 4 replicates): (1) open cage / control (only the frame structure); (2) closed cage (frame structure surrounded with plastic net with a mesh size of 2 cm to exclude larger fishes and invertebrate grazers like sea urchins); (3) semi-closed cage (frame with closed sides but open top to only exclude large invertebrate grazers like sea urchins, but not fishes). Previous experiments have shown that exclusion nets have no significant effects on response parameters on settlement tiles (Miller et al., 1999; Smith et al., 2001). Each frame was equipped with 24 terracotta tiles, each with an average surface area of 168.8 ± 0.8 cm^2. Rough terracotta tiles were used, as their heterogeneous surface simulates coral rock and enhances species richness and biomass compared to other artificial substrates (Brock, 1979; Fitzhardinge and Bailey-Brock, 1989). Tiles were arranged pairwise on top of each other with plastic