Journal of Experimental Marine Biology and Ecology 506 (2018) 155–162

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs

Jacob G. Eurich[1,*], Simone M. Shomaker[1], Mark I. McCormick, Geoffrey P. Jones

ARC Centre of Excellence for Coral Reef Studies, Department of Marine Biology and Aquaculture, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

ARTICLE INFO

Keywords:
Surgeonfish
Parrotfish
Rabbitfish
Removal experiment
Competition
Sediment dynamics

ABSTRACT

Roving herbivorous fishes play an important role in coral reef communities by removing turf-algae, which can facilitate the settlement of coral larvae. Territorial damselfishes can influence the foraging patterns of roving herbivores by excluding them from their territories, altering the benthic assemblage. However, the impacts depend on the intensity of aggression and which taxonomic groups of roving herbivores are being excluded. Here we document the foraging activity of roving herbivores (Acanthuridae, Scaridae, Siganidae) and the extent to which they are subject to aggression by *Pomacentrus adelus*, the most abundant territorial damselfish in Kimbe Bay, Papua New Guinea. We then conducted experimental removals (220 m^2 plots on the reef flat) of *P. adelus* to examine its impact on roving herbivores and the benthic community structure. We hypothesized that the removal of *P. adelus* would lead to an increase in roving herbivore abundance and foraging activity and a decline in algal cover. The relative abundance (MaxN) and foraging activity (bite rate) of each taxa were examined pre and post-removal using video quadrats. The overall relative abundance of roving herbivores was not influenced by the removal of *P. adelus*. No changes in foraging patterns were observed for parrotfish, the family that received the highest rate of agonistic interactions, and rabbitfish. The removal of *P. adelus* resulted in a significant decrease in surgeonfish feeding, suggesting *P. adelus* alters foraging patterns indirectly through territorial maintenance and not aggression. The only measurable benthic impact of the *P. adelus* removal was an increase in sediment, while all other substratum types remained constant. These results indicate that *P. adelus* does not have a negative impact on all roving herbivores and instead may contribute to surgeonfish foraging indirectly through the removal of sediment. The generalisation that territorial damselfish reduce foraging rates of roving herbivores may not be applicable in all systems or for all species.

1. Introduction

Roving herbivorous fishes play an important role on coral reefs in reducing algal biomass and preventing alternative algal dominated stable states (Francini-Filho et al., 2010; Mumby et al., 2006; Hughes et al., 2007). Hence, they are considered important in maintaining healthy coral cover and promoting ecosystem resilience (Burkepile and Hay, 2008; Hamilton et al., 2014; O'Leary and McClanahan, 2016). The most important roving herbivores, in a broad use of the term, appear to be surgeonfish (Acanthuridae), parrotfish (Labridae: Scarini), and rabbitfish (Siganidae) in terms of algal biomass consumption or removal (Francini-Filho et al., 2010; Lewis and Wainwright, 1985). However, these taxa do not have exclusive access to algal covered reef habitat. Territorial farming damselfish often influence the structure of algal communities though the deterrence of larger roving herbivores (reviewed by Hata and Ceccarelli, 2016). The aggressive territorial defence may lead to an increase in turf algae, a desired food source of roving herbivores (Ceccarelli et al., 2005a; Hixon and Brostoff, 1983; Hixon, 1996; Russ, 1987). Studies that combine the foraging patterns of roving herbivores and agonistic interactions within a healthy community can together help define the mechanistic drivers that underlie reef habitat structure and resilience.

Surgeonfish, parrotfish, and rabbitfishes cohabit the most productive coral reef zones where they may forage in mixed species groups and partition resources (Williams, 1991). The difference in resource utilization among families is strongly related to morphology, with the recognition of three main functional groups: browsers, scrapers, and excavators (Ross, 1986; Bellwood and Choat, 1990; Francini-Filho et al., 2008; Streelman et al., 2002). Surgeonfish, typically categorized as browsers, largely feed on the epilithic algal matrix (Goatley and

* Corresponding author.
E-mail address: jacob.eurich@my.jcu.edu.au (J.G. Eurich).
[1] These authors contributed equally to this manuscript.

https://doi.org/10.1016/j.jembe.2018.06.009
Received 1 March 2018; Received in revised form 15 June 2018; Accepted 21 June 2018

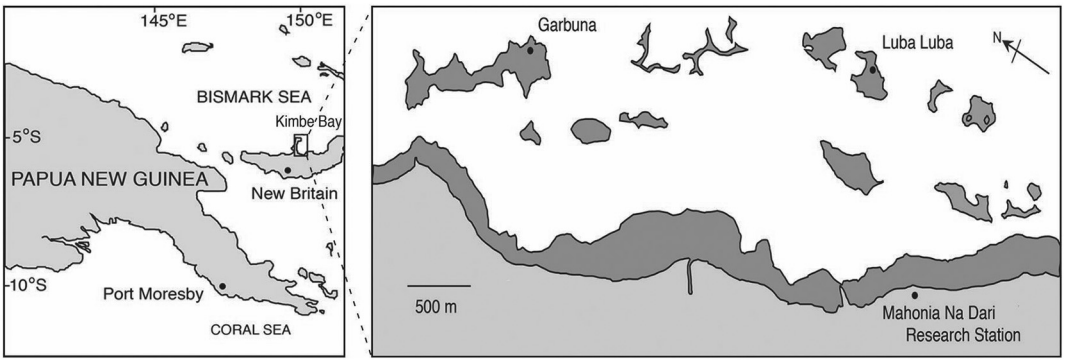

Fig. 1. Location of Kimbe Bay, West New Britain, Papua New Guinea, and the 2 reef sites (Garbuna and Luba Luba).

Bellwood, 2010) with some species targeting detritus aggregates within algal turfs (Marshell and Mumby, 2012; Tebbett et al., 2017a, 2017b). Unlike surgeonfish, parrotfish alter the substratum by scraping or excavating the surface leaving distinct scars on the benthos (Bellwood and Choat, 1990; Bellwood, 1995, 1996). Despite recent work suggesting that parrotfish may be targeting endolithic microbes and detritus (Clements et al., 2017), the removal of microalgae in the process of foraging remains functionally important when considering the biotic composition of reef benthos (Morgan and Kench, 2016). In contrast, rabbitfish feed significantly more in reef crevices than the other two families due to differences in morphology and dentition (Brandl and Bellwood, 2014; Fox and Bellwood, 2013). While the majority of rabbitfish species target macroalgae by browsing or cropping, the family also contains a distinct group of mixed feeders, which target microalgal material, cyanobacteria, and sediment (Hoey et al., 2013). The diversity of foraging methods, and their implications for impacts on benthic habitat structure, indicates that our understanding of how species interact with the surrounding community must be species and family specific (Choat and Clements, 1993; Fox and Bellwood, 2007; Ong and Holland, 2010; Polunin et al., 1995). Therefore, it is important to assess the grazing ability of species individually as grazing rates can vary due to differences in community structure and species encountered.

Territorial damselfish (Pomacentridae) are highly abundant small-bodied consumers that often occupy the reef crest and reef flat habitats (Ceccarelli et al., 2001; Ceccarelli, 2007; Eurich et al., 2018). The modification of algae through farming behaviour and territorial defence is thought to play an important role on the benthic community structure (Barneche et al., 2009; Ceccarelli et al., 2005a; Ceccarelli, 2007; Hixon and Brostoff, 1983; Wellington, 1982). Thus, territorial damselfishes influence on coral recruitment (Ceccarelli et al., 2005a; Sammarco and Carleton, 1981; Wellington, 1982), and the abundance and composition of algae within the territorial boundaries (Ceccarelli et al., 2005b; Hixon, 1996), have been well documented. Territorial damselfish have been predominantly categorized into three guilds based off the species' effect on benthic assemblage structure and aggression: intensive farmers, extensive farmers, and an intermediate group (Ceccarelli, 2007; Hata and Ceccarelli, 2016; Hata and Kato, 2004). Where, intensive farmers weed low diversity algal turfs intensively with aggressive defence, extensive farmers weed and defend larger territories to a lesser degree, and an intermediate group that maintains discrete, but significantly different to the surrounding environment, territories of algal turf (Emslie et al., 2012; Pratchett et al., 2016). Several experimental studies have shown that the aggressive exclusion of roving herbivores by extensive or intensive farming species effects the benthic assemblage structure (Ceccarelli et al., 2005a; Hixon and Brostoff, 1983; Hixon, 1996; Russ, 1987). However, there is conflicting evidence that all territorial damselfish, especially intermediate farming species - the most abundant guild (Pratchett et al., 2016), hinder the foraging patterns of roving herbivores through agonistic interactions. Some studies have shown that roving herbivores will actively avoid the territories of territorial damselfish to feed on desirable algae without harassment (Hamilton and Dill, 2003; Robertson et al., 1976). Additionally, surgeonfish and parrotfish periodically may use schooling behaviours to overwhelm territorial damselfish and gain access (Robertson et al., 1976; Foster, 1985a). However, Ceccarelli et al. (2005b) found that extensive and intermediate territorial damselfish were fairly inefficient at excluding roving herbivores from their territories and roving herbivores had a significant impact on benthic habitat, both with and without the presence of territorial damselfish.

While both roving herbivores and territorial damselfish can exert a strong influence on the structure of the benthic community, the extent to which the general paradigm holds true for intermediate territorial damselfish remains unclear. In this study we document the natural foraging activity of roving herbivores and the extent to which this was affected by an intermediate farming territorial damselfish in Kimbe Bay, West New Britain, Papua New Guinea. We then undertook a large-scale removal of the most abundant territorial damselfish, *Pomacentrus adelus*, to evaluate how the abundances and foraging activity of roving herbivores would change following an agonistic release. Lastly, we determined whether the benthic community structure was altered in the absence of *P. adelus*. Specifically, we tested the following three predictions: (1) the local abundance of roving herbivores should increase in abundance following the removal of *P. adelus*; (2) the feeding activity of roving herbivores should increase after the removal of *P. adelus* as benthic resources are undefended; (3) the benthic habitat may be altered due to changes in herbivore foraging and the elimination of *P. adelus* farming and territorial behaviour.

2. Materials and methods

2.1. Study location and species

This study was conducted in Kimbe Bay, West New Britain, Papua New Guinea (Fig. 1; 5°30′ S, 150°05′ E). Kimbe Bay lies within Oceania and is a region of West New Britain recognized for high coral reef biodiversity and large platform reefs (Roberts et al., 2002). Two inshore reefs, Garbuna and Luba Luba, were selected as the study locations due to similarities in species composition and reef aspect. Both reefs are nearshore (< 1 km from land), and have a similar reef structure: a shallow reef flat (exposed during extreme low tides), a reef crest, and a gentle reef slope ending in a sandy bottom at 30–50 m. Coral reefs in Kimbe Bay have a high diversity of both coral and fishes despite several regional coral mortality events (Boström-Einarsson et al., 2014; Jones et al., 2004). At least 20 families of reef fishes are found in Kimbe Bay (Jones et al., 2004), including many species belonging to families loosely described as herbivores, namely Acanthuridae, Labridae (Scarini tribe), and Siganidae. For the purposes of this study, only roving herbivores that occupied the zones where *P. adelus* occurred were analysed.

The most abundant damselfish, *Pomacentrus adelus*