## ARTICLE IN PRESS

Marine Environmental Research xxx (xxxx) xxx-xxx



Contents lists available at ScienceDirect

### Marine Environmental Research



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

## Empirical data demonstrates risk-tradeoffs between landscapes for herbivorous fish may promote reef resilience

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#### ARTICLE INFO

Keywords: Coral reefs Risk effects Herbivorous fishes Community state Trade-offs

#### ABSTRACT

Herbivores balance resource requirements with predation risk, which can differ among landscapes; hence, landscape can shape these trade-offs, influencing herbivore distribution and behavior. While this paradigm has been well established on coral-dominated reefs, tropical reefs worldwide are shifting to algal dominance. If herbivores avoid algae due to higher risk and forage in coral, these algal states may be stabilized. However, if herbivores forage more in resource-rich algal states, this may promote coral recovery. We assessed the distribution and behavior of herbivorous fishes in Moorea, French Polynesia in coral and algal turf-dominated fringing reef sites. Acanthuridae were more abundant in coral states and Labridae, tribe Scarinae, in algal turf states, though total fish abundances were equivalent in the two states. Fish in both families spent more time feeding in algal states and hiding/swimming in coral states. Thus, behavior reflects the trade-off between resource acquisition and refuge in these two landscapes and may promote recovery to coral.

#### 1. Introduction

Herbivore behavior is driven by trade-offs between resource availability and predation risk, which can be influenced by the landscape (e.g. Randall, 1965; Madin et al., 2011; Catano et al., 2016). On coral reefs, this tradeoff was first proposed over 50 years ago (Randall, 1965), and since has become a paradigm of coral reef ecology (reviewed in Graham and Nash, 2013). Coral reefs are biogenic structures where the dominant benthic space-holders determine landscape characteristics; corals produce topographically-complex landscapes with many refuges but few resources for herbivores while, historically, resource-rich macro and turf algal communities usually occupy off-reef habitats with lower complexity and higher risk (for a review see Fong and Paul, 2011). An example of how this trade off shapes coral reef landscapes is the 'halo effect', where bare substrates created by intense grazing surround the relative safety of biogenic reef structure (Randall, 1965; Muthukrishnan et al., 2016). Topographic complexity may be the main driver of this landscape of fear (Randall, 1965; Madin et al., 2011; Graham and Nash, 2013). Thus, herbivorous reef fishes respond strongly to trade-offs presented by different habitats and structures and these behavioral differences strongly influence benthic community composition.

Generally, coral habitats are considered safe due to complexity and

algal habitats risky due to their off reef/flat topography; however, this may not be true following at least some types of disturbances. When reefs lose coral cover due to a crown-of-thorns outbreak or a bleaching event, the underlying structure created by the coral may be retained for several years (Sano et al., 1987; Garpe et al., 2006). Thus, following disturbances that leave reef structure intact, algal turf rapidly proliferates, is resource-rich, and covers structurally complex dead coral (Sano et al., 1987; Garpe et al., 2006; reviewed in Pratchett et al., 2008). While, without recovery to coral dominance, bioerosion will eventually reduce complexity and result in few hiding places from predators, initially the resource rich landscape offers some refuge (Sano et al., 1987; Garpe et al., 2006). Thus, while herbivorous fish must balance resource availability and predation risk in coral-versus algal turf-dominated states, the trade-offs presented by these transitional landscapes may not be the same as those found historically on undisturbed coral reefs (see Randall, 1965).

Understanding behavior and spatial distribution of herbivorous fishes on coral reefs in relation to landscape is important because herbivorous fishes exert strong top-down control that may confer resilience, or the ability of reefs to recover to coral after disturbance. For example, experimental exclusion of grazing fishes in the Caribbean rapidly shifted landscapes from coral-to macroalgal-dominance, and removal of exclusion cages resulted in rapid recovery via reduction of

https://doi.org/10.1016/j.marenvres.2017.11.001

Received 20 June 2017; Received in revised form 26 October 2017; Accepted 2 November 2017 0141-1136/ @ 2017 Elsevier Ltd. All rights reserved.

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accumulated macroalgae (Lewis, 1986). Similarly, phase shifts to macroalgae were experimentally induced in Australia by excluding herbivores and, when herbivore exclusion was removed, fishes rapidly reduced biomass reversing this phase shift (Hughes et al., 2007). Further, shifts to longer, sediment-laden turfs on Australian reefs have been associated with decreased fish foraging, resulting in a stabilized algal turf community state (Goatley et al., 2016). Recently, following a disturbance-mediated expansion of turf and macroalgal cover in French Polynesia, higher food availability increased herbivorous fish abundance via population processes (Adam et al., 2011), reinforcing the link between landscape and fishes.

A benthic community dominated by turf algae may be an alternative stable state on coral reefs (e.g. Goatley et al., 2016), and theory predicts positive feedbacks stabilizing one state simultaneously destabilize the alternate state, producing and stabilizing a bifurcation fold (Scheffer et al., 2001; Beisner et al., 2003; Schröder et al., 2005; Dudgeon et al., 2010). Alterations in top-down control by herbivores have been implicated in shifts to alternative stable states in kelp-forests (Estes et al., 1998), lakes (Carpenter et al., 1987), grasslands (Prins and van der Jeugd, 1993), and coral reefs (Lewis, 1986; Hughes et al., 2007; Muthukrishnan and Fong, 2014), though the latter is contentious (Dudgeon et al., 2010). Because healthy reefs have high herbivory rates, and herbivore exclusion results in shifts, strong herbivory may stabilize coral while simultaneously destabilizing algal states. Thus, alternative stable state theory predicts decreased herbivory in algal states, stabilizing this alternative state (for review of positive feedbacks see Cinquin and Demongeot, 2002; Schröder et al., 2005). In contrast, if herbivorous fishes track resource availability (e.g. Charnov 1976, Adam et al., 2011) and algal-dominated states experience increased herbivory, herbivorous fishes may destabilize these states, making them transient.

Our objective was to determine if herbivorous fish distribution and behavior differed in coral-versus turf algal-dominated states on a reef recently shifted from coral to algal turf and macroalgal dominance after an outbreak of the predacious crown-of-thorns sea star and a cyclone in 2010 (Adam et al., 2011). These disturbances resulted in a mosaic landscape with patches of coral- and algal-dominated states on fringing reefs of Moorea, French Polynesia. Moorean reefs have undergone multiple state shifts yet have consistently recovered (Adjeroud et al., 2009). This resilience may have been facilitated by a numeric response of herbivorous fishes to increased resources (Adam et al., 2011). We hypothesized resilience was also enhanced by fish behavior, with more intense foraging concentrated in turf algal-dominated states. We used an observational approach to assess differences in distribution and behavior of herbivorous fishes between states to explore if these differences may facilitate recovery.

#### 2. Methods

Our study was conducted in April of 2012 along a fringing reef on the north shore of Moorea in French Polynesia. This fringing reef was a mosaic of patches dominated by turf or coral alternatively (Fig. 1).

To understand the relationship between benthic state and fish abundance and behavior, we established three  $3 \times 3$  meter paired plots of high coral and high turf cover (n = 6). These plots were small and close enough that we observed herbivorous fish moving between plots. To characterize plots, we measured benthic community composition (% cover coral, turf algae (< 1 cm), crustose coralline algae, and macroalgae (> 1 cm)) using the point intercept technique within randomly placed 0.25 m<sup>2</sup> quadrats with 36 points (n = 4 per plot). We measured rugosity using the chain method, where a flexible chain was fitted over the benthos for a planar meter. Rugosity is calculated by dividing the fitted chain length by the planar length (n = 10 per plot). Plots were classified as turf-dominated (turf > 60%) or coral-dominated (coral > 60%). Data met assumptions of parametric statistics and we used a nested ANOVA to compare coral cover and rugosity with plot as a

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Fig. 1. Map of Moorea; the star indicates our field site (17° 28.944 S 149° 48.827 W).

random effect nested in benthic state.

To quantify the relationship between fish abundance and benthic state, we recorded the number of fish visiting each plot in 5-min periods (n = 9 per plot). We counted fish in the dominant grazing families on coral reefs: Acanthuridae, Labridae (tribe Scarinae), Kyphosidae, and Siganidae. Kyphosidae and Siganidae were rare (< 0.017%) and thus excluded from analysis. Abundances of Acanthuridae and Labridae (tribe Scarinae) met assumptions and were compared with a nested ANOVA with plot as a random effect nested in benthic state.

To characterize the species composition of the fish families at this site, we relied on annual survey data from the Moorea Coral Reef Long Term Ecological Research program (MCR LTER). Four surveys quantifying density of fish populations were conducted in August 2012 at the same site as our study. Fish were identified to species and counted along a 50 m transect 5 m wide for a surveyed area of 250 m<sup>2</sup>. We calculated average abundance  $\pm$  SE per 100 m<sup>2</sup> for each species. Low sample size limited our ability to approximate average size of each fish species so we calculated average fish length  $\pm$  SE for each fish family.

To quantify behavior in each state, we conducted focal observations on individuals and constructed time budgets. Between 1000 h and 1400 h, we haphazardly selected individuals as they entered plots and recorded their activity for 1 min. Focals were only conducted on Acanthuridae (n = 370) and Labridae (tribe Scarinae) (n = 173) because Kyphosidae and Siganidae were rare. Fish occupying the plot < 1 min were excluded from analysis. Fish behavior was categorized as feeding, swimming, hiding, chasing, or other. Feeding behavior was broken into 2 components-fish were scored as taking individual bites when singular bites were taken while swimming near the benthos and scored as foraying when bites were rapid and sequential while swimming near the benthos. Swimming fish actively moved through the water column without stopping to feed. Hiding fish took cover in structure. Chasing fish were pursuing another fish or being pursued. Fish behavior was classified as other if the individual was still in the water column and not close to structure. For each individual, the amount of time engaged in each behavior was recorded and then calculated as a proportion.

Because we were interested in foraging and anti-predator behaviors, we did not include the behavior categories of other or chasing in this analysis. We used a permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the R package vegan (R Core Team, 2015) to compare the four behaviors (Foray, individual bites, hiding, and swimming) by habitat type with site as a random effect. Our data had a Poisson distribution, and this technique has been found to be robust against violations of normality and heterogeneity of Download English Version:

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