

NOTE

# Contact with seaweed alters prey selectivity in a coral-feeding reef fish

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**ABSTRACT:** Human-driven disturbance is fundamentally altering the composition of benthic marine communities. For instance, many coral reefs are experiencing declining coral cover alongside increased macroalgae (seaweed) abundance. While the responses of herbivorous fishes to seaweeds are comparatively well understood, little is known regarding the responses of other important trophic guilds that interact with the benthic community, such as corallivores. To this end, we investigated how 2 species of seaweed (*Galaxaura filamentosa* and *Sargassum polycystum*) affected foraging in an obligate corallivorous fish, *Oxymonacanthus longirostris*. Corals with no seaweed contact were preferred over corals in contact with seaweed, regardless of the seaweed species. However, following seaweed removal, fish associated with, and fed on, all corals equally, suggesting that corals in contact with these seaweeds do not produce repellent chemical cues. This second finding contrasts with patterns seen in other corallivores, indicating that, while seaweeds may be generally repellent, sensory cues used to make foraging decisions may vary. Regardless, these findings provide further evidence that seaweeds negatively affect foraging in non-herbivorous fishes, which could have far-reaching impacts as habitat quality declines.

**KEY WORDS:** Macroalgae · Corallivory · Phase shifts · *Oxymonacanthus longirostris* · Disturbance

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## INTRODUCTION

Global changes in resource availability, brought on by human-driven disturbance and climate change (Clavel et al. 2011), may have unforeseen flow-on effects for associated species, community composition, and resilience. These changes are especially visible on coral reefs worldwide, where declining coral cover is often mirrored by increasing seaweed abundance (Hughes et al. 2007). Reef-building corals are an essential component of coral reefs, creating structure and promoting biodiversity. While seaweeds are also naturally occurring, their growth is generally suppressed by nutrient limitation (Lapointe

1997) and grazing (Hughes et al. 2007). However, coastal eutrophication (Lapointe 1997), declining herbivore abundance (Edwards et al. 2014), and the compounding effects of disturbances associated with climate change (Hughes et al. 2017) have created conditions unfavorable to corals but ideal for fast-growing seaweeds (Mumby et al. 2007). Increased seaweed abundance can limit settlement substrate availability (Birrell et al. 2008) and negatively affect established coral condition (McCook et al. 2001). While the positive and negative responses of coral reef-associated herbivores to increased seaweed has been the focus of substantial research (e.g. Hughes et al. 2007, Hoey & Bellwood 2011), identifying how

non-herbivores respond is also important. For instance, numerous reef-associated species depend on corals for food; thus, it is necessary to determine how seaweed-driven changes to coral abundance or condition will affect their trophic dynamics.

A taxonomically diverse range of fishes feed on corals (Cole et al. 2008), with species often displaying highly specialized trophic morphology and behavioral preferences for certain coral genera, species, or structures (Berumen et al. 2005, Pratchett 2007, Brooker et al. 2013a, Huertas & Bellwood 2017). Coral preferences appear to reflect nutritional value, with preferred corals positively correlated with corallivore growth, condition, and fitness (Berumen et al. 2005). Corallivory by fishes is ecologically important, influencing coral distribution, composition, and health (Cole et al. 2008). However, how corallivores respond to abundant seaweed remains unclear, although fitness and population resilience will likely decline as corals become scarce (Kokita & Nakazono 2001, Berumen et al. 2005). Corallivore communities can consume a large proportion of coral productivity (Cole et al. 2012). For this reason, how corallivorous fishes forage could have flow-on effects for coral resilience; if corals in contact with seaweed are targeted, energy reallocation towards repair may restrict recovery (Henry & Hart 2005). However, if corals in contact with seaweed are avoided, greater foraging on remaining corals could increase vulnerability to subsequent disturbance.

Recent evidence suggests many corallivorous species avoid corals in contact with seaweed due to both visual and chemical cues (Venera-Ponton et al. 2011, Clements & Hay 2015, Brooker et al. 2016), suggesting seaweed negatively affects prey quality or foraging efficiency. However, to determine whether seaweed avoidance is a generalized response in corallivores, and why, further studies examining whether taxonomically disparate species display similar behavioral aversions are needed. As many corallivores are highly habitat-associated, it is also important to determine if species distinguish between these corals as prey, as habitat, or both. One such species is the harlequin filefish *Oxymonacanthus longirostris*. Its highly specialized diet, largely composed of *Acropora* corals (Brooker et al. 2013a), makes it especially vulnerable to benthic community changes (Kokita & Nakazono 2001). Foraging behavior in *O. longirostris* is similar to many tissue-feeding corallivores (Pratchett 2007). This, along with its amenability to captivity, make it ideal for experimentally testing responses to seaweed. Our objectives were to determine (1) if the physical presence of seaweed affected coral selection

(both in terms of which corals fish associated with and which ones they foraged on), and if so, (2) if patterns of preference or avoidance continued following seaweed removal, thus indicating a chemical residue.

## MATERIALS AND METHODS

### Study species and location

Research was conducted during January 2014 at Lizard Island Research Station (LIRS), northern Great Barrier Reef, Australia (14° 40' S, 145° 27' E). Twenty-two *Oxymonacanthus longirostris* were collected on SCUBA using hand nets and clove oil and maintained in groups of either 5 or 6 individuals in four 500 l flow-through aquaria. As *O. longirostris* forages throughout the day, sufficient equal amounts of *Acropora spathulata* and *Pocillopora damicornis* corals were held in each aquaria to allow foraging to satiation.

### Effects of seaweed on prey selection and habitat use

A 2-part cafeteria-style experiment examined what effect coral–seaweed interactions had on habitat and feeding preferences. Trials were conducted in a 1.2 m diameter circular tank with 40 cm water depth. Each trial presented a fish with 3 *A. spathulata* colonies, each representing a different treatment. *A. spathulata* is a common prey of *O. longirostris*. Treatments in Part 1 were *A. spathulata* in contact with *Sargassum polycystum* seaweed, *A. spathulata* in contact with *Galaxaura filamentosa* seaweed, and a control treatment where *A. spathulata* was unassociated with seaweed. Treatments in Part 2 were *A. spathulata* post-contact with *S. polycystum*, *A. spathulata* post-contact with *G. filamentosa*, and the control.

Part 1 examined the effect that the physical presence of seaweed has on coral use. The 2 seaweeds used, *S. polycystum* and *G. filamentosa*, were selected as they naturally occur near LIRS and can rapidly increase in abundance following disturbance. However, as they are morphologically and chemically disparate, the way they interact with corals differs. Most notably, *G. filamentosa* can damage coral tissue via allelochemicals within the thallus not found in *S. polycystum* (Rasher et al. 2011). Seaweed was collected from LIRS reefs, with full plants used to ensure seaweed did not deteriorate over the trial period. For each treatment, 7 small discreet *A. spathulata* colonies (~15 cm diameter) were col-

lected. Corals were maintained in shaded 500 l aquaria supplied with oxygenated seawater. Prior to trials, coral–seaweed contact was initiated by securing a plant to the base of each coral using cable ties, ensuring that ties did not contact live tissue. Cable ties were also attached to control coral bases to account for any effects of the tie on preferences. In this fashion, coral–seaweed interactions were maintained without physical damage to seaweed or coral. Following attachment, corals were left for 12 h prior to trials. For each trial, 1 coral from each treatment and control were placed into the test tank, around the perimeter at randomly selected, equal distance, locations. A perforated section of PVC pipe (15 cm diameter  $\times$  45 cm height) was positioned at the tank center into which a fish was placed. Fish were left to habituate for 10 min, during which time they could receive coral visual and chemical cues but could not access them. Following this, the pipe was gently drawn upwards, releasing the fish and beginning the 15 min trial. The total number of bites on each coral was recorded with bites per coral standardized to the proportion of bites per coral per trial. The relative time spent next to each coral was determined as the proportion of total seconds (900) a fish spent within 15 cm of that coral. All time spent beyond 15 cm of any coral was recorded as ‘unassociated with coral’. Trials were simultaneously filmed using a HD camera (GoPro, Woodman Labs) to determine total time associated with each coral.

Part 2 examined whether chemical cues produced by coral–seaweed interactions affected foraging independent of visual cues. Following Part 1, corals were left for 1 wk with seaweed attached. Seaweed was then removed and trials repeated as for Part 1. To increase to number of coral replicates used, both parts of the study were completed twice using 7 coral sets. No physical signs of damage or tissue loss were visible on corals after the 1 wk of contact. Following experiments, healthy corals were secured back on their original reef using epoxy.

### Statistical analysis

To compare the relative consumption of each treatment, the proportion of bites on each seaweed-contact coral was compared to the total bites on the control using a nested ANOVA, with the 3 treatments nested within each trial. The proportion of time associated with each coral per trial was analyzed using the same nested ANOVA design using a mixed ef-

fects model. Preliminary models using generalized least squared and other mixed-effects linear models compared the magnitude of the particular effect of each treatment and evaluated any correlation structures with other variables. This allowed us to investigate the variance correlation structures of multiple models to directly address possible additional complexity by comparing estimates due to the included fixed and random effects. For each aspect of the study design (i.e. comparing bites and comparing time associated with each coral, with or without seaweed), multiple models using fixed and random correlation structures (e.g. Bites  $\sim$  Treatment, random =  $\sim$ 1|Round) were compared using maximum likelihood estimation and Akaike information criteria (AICc package MuMIn; Barto 2015). These models investigated the possible effects of the different rounds and individual corals using random intercept and random intercept/random slope correlation structures. For every model comparison, the models with the lowest AICc values also compared log-likelihood ratios (function ANOVA), but the parsimonious model was always selected based on these criteria (e.g. Time  $\sim$  Treatment), and more complex models did not justify the additional degrees of freedom. Final models investigated the effect of Treatment on proportional Time/Bites with a random intercept model for Trial (i.e. each trial could have a slightly different intercept but the same slope). Data conformed to linear regression model assumptions. Tukey’s comparison of means was used for post hoc tests. Statistical analyses were conducted in R (R Core Team 2015) using the stats and nlme packages (Pinheiro et al. 2016).

## RESULTS

Fish took proportionally fewer bites on corals in contact with seaweed (Fig. 1). On average, 67% of the total bites taken were on the control (mean  $\pm$  SE:  $77.62 \pm 8.27$  bites), with 23% taken on the *Galaxaura filamentosa* treatment ( $4.71 \pm 2.19$  bites) and 8% taken on the *Sargassum polycystum* treatment ( $20.17 \pm 3.68$  bites) ( $F_{2,82} = 42.6$ ,  $p < 0.0001$ ). The average proportion of bites on the control was significantly greater than the proportion on either seaweed treatment ( $p < 0.01$ ). However, while close to significant, the proportion of bites did not differ between seaweed treatments ( $p = 0.06$ ). Following seaweed removal, there was no significant difference in the proportion of bites taken among corals (control:  $52.14 \pm 8.64$  bites; *G. filamentosa*:  $40.95 \pm 6.06$  bites; *S. polycystum*:  $40 \pm 6.92$  bites) ( $F_{2,82} = 0.51$ ,  $p = 0.598$ ) (Fig. 1).

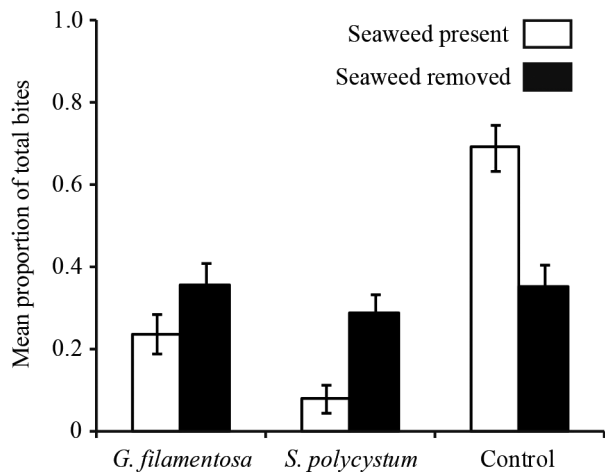


Fig. 1. Proportion of total bites (mean  $\pm$  SE) on each experimental coral when seaweeds were present or removed. Treatments: *Acropora spathulata* coral plus *Sargassum polycystum* seaweed, *A. spathulata* plus *Galaxaura filamentosa* seaweed, or seaweed-free *A. spathulata* control. Sample sizes: seaweed present  $n = 42$ , seaweed removed  $n = 42$

Fish avoided corals in contact with seaweed (Fig. 2). Fish spent on average  $50.7 \pm 5.4\%$  (mean  $\pm$  SE) of time near the control,  $21 \pm 4.3\%$  of time near the *G. filamentosa* treatment,  $13.6 \pm 3.4\%$  of time near the *S. polycystum* treatment, and  $14.6 \pm 3.1\%$  of time unassociated with coral ( $F_{2,123} = 17.34$ ,  $p < 0.0001$ ). Only time associated with control was significantly different to either treatments or unassociated time ( $p < 0.01$ ). Following seaweed removal, a significant difference in the time associated with each habitat category was observed ( $F_{2,123} = 7.377$ ,  $p < 0.0001$ ); however, Tukey's comparisons showed this was between unassociated time and all corals, with no difference seen between corals themselves (Fig. 2).

Model comparisons indicated that the main effects of seaweed presence during trials reduced both the proportion of bites taken and time associated with coral. Overall, variance due to random effects in all models was very low, indicated by the standard deviation of residuals and marginal and conditional  $R^2$  values.

## DISCUSSION

Contact with seaweeds altered coral selectivity, with fishes associating with, and feeding on, seaweed-free corals more than those in contact with either *Sargassum polycystum* or *Galaxaura filamentosa*. This suggests seaweeds are a powerful foraging deterrent,

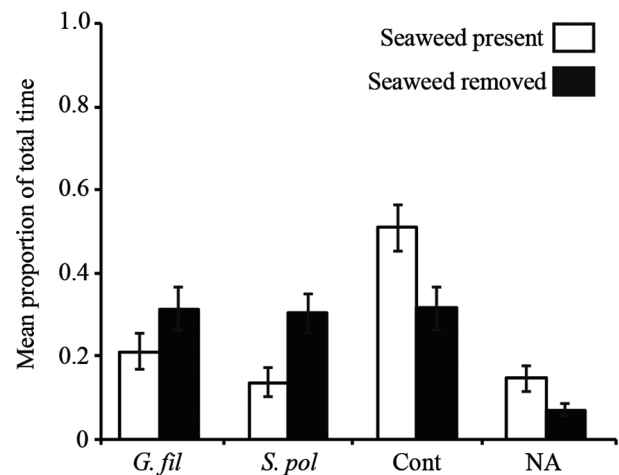


Fig. 2. Proportion of total time associated (mean  $\pm$  SE) with each experimental coral when seaweeds were present or removed. Treatments: *Acropora spathulata* coral plus *Sargassum polycystum* seaweed (*S. pol*), *A. spathulata* plus *Galaxaura filamentosa* seaweed (*G. fil*), or seaweed-free *A. spathulata* control (Cont). NA: proportion of time unassociated with coral. Sample sizes: seaweed present  $n = 42$ , seaweed removed  $n = 42$

possibly indicating reduced nutritional quality or foraging efficiency. Many other corallivorous species display similar behavioral patterns, e.g. an aversion to seaweed is also seen in butterflyfishes (Brooker et al. 2016), parrotfishes (Venera-Ponton et al. 2011), and crown-of-thorns sea stars (Clements & Hay 2015). However, while seaweed negatively affected coral selection, this did not continue following seaweed removal. This contrasts with evidence from butterflyfishes, which continued to avoid corals that had been in contact with alleopathic seaweed, suggesting a lasting repellent cue is produced by the interaction (Brooker et al. 2016). That *Oxymonacanthus longirostris* was not repelled suggests that either the interactions here did not produce residual chemical cues, or these are not universally repellent. Given recent evidence, it appears likely that seaweed would have affected coral tissue biochemistry and odor to some degree (Rasher et al. 2011). This is especially the case for the *G. filamentosa* treatment, as coral contact increases concentrations of alleopathic compound within the thallus, damaging coral tissue (Rasher & Hay 2014). Such negative chemical cues may not repel species if they rely on visual cues during foraging. Nonetheless, the physical removal of seaweeds will likely be limited on degrading reefs where herbivores are scarce. Therefore, avoidance of corals in contact with seaweed will likely be the dominant behavioral pattern seen in obligate corallivores on seaweed-rich reefs.

While this avoidance could temper some negative impacts of seaweed contact, a predation shift onto remaining seaweed-free corals could also have implications for the broader reef community. As reefs degrade, the persistence of remaining corals becomes increasingly critical, forming a vital source of larvae that can support resilience (Doropoulos et al. 2017). Foraging by corallivores that do not damage the skeleton, such as butterflyfishes and *O. longirostris*, is often thought to minimally affect coral health (Harmelin-Vivien & Bouchon-Navaro 1983). However, these fishes can remove up to 3 g of coral tissue per day (Cole et al. 2011), with corallivore communities consuming up to 13.5% of total available coral biomass and 79% of targeted coral productivity annually (Cole et al. 2012). Chronic predation on a restricted number of corals could increase their energetic expenditure in repair, reducing growth and fitness. In addition, sub-lethal effects could decrease coral resilience to subsequent disturbance.

However, corallivore avoidance of corals in contact with seaweed will likely have the greatest impact on corallivores themselves if it limits access to preferred prey. For instance, *O. longirostris* pairs often maintain a territory in areas of highly preferred coral abundance (Brooker et al. 2013b). If these become overgrown, fishes may expend energy locating seaweed-free colonies and defending larger territories, or forage on less nutritious coral, negatively affecting condition and fitness over time. Regardless, this study provides further evidence that greater seaweed abundance will negatively affect the behavior of non-seaweed associated species.

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