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Chemically cued suppression of coral reef resilience: Where is the tipping point?

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Abstract

Coral reefs worldwide are shifting from high-diversity, coral-dominated communities to low-diversity systems dominated by seaweeds. This shift can impact essential recovery processes such as larval recruitment and ecosystem resilience. Recent evidence suggests that chemical cues from certain corals attract, and from certain seaweeds suppress, recruitment of juvenile fishes, with loss of coral cover and increases in seaweed cover creating negative feedbacks that prevent reef recovery and sustain seaweed dominance. Unfortunately, the level of seaweed increase and coral decline that creates this chemically cued tipping point remains unknown, depriving managers of data-based targets to prevent damaging feedbacks. We conducted flume and field assays that suggest juvenile fishes sense and respond to cues produced by low levels of seaweed cover. However, the herbivore species we tested was more tolerant of degraded reef cues than non-herbivores, possibly providing some degree of resilience if these fishes recruit, consume macroalgae, and diminish negative cues.

Keywords

Macroalgae; Phase shifts; Recruitment; Fishes; Fiji

Introduction

The synergistic effects of climate change, overfishing, eutrophication, and other anthropogenic drivers are changing the composition and biodiversity of marine communities (Dulvy et al. 2003; Pauly et al. 2005; Worm et al. 2006; Doney et al. 2012). On tropical coral reefs, this can occur as a shift from species-rich, topographically complex systems dominated by corals to topographically flattened, low-diversity systems dominated by seaweeds (Gardner et al. 2003; Pandolfi et al. 2003; Hughes et al. 2007; Graham and Nash 2013). Once established, seaweeds can damage adult corals and suppress coral recruitment, causing further coral declines and reducing the ability of systems to recover (McCook et al. 2001; Rasher et al. 2011; Webster et al. 2015; van de Leemput et al. 2016). Reef degradation

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reduces ecosystem function, productivity, resilience (Hughes et al. 2003; Bellwood et al. 2004), and socioeconomic value (Micheli et al. 2014; Pratchett et al. 2014), making it critical to implement strategies that slow coral decline and preserve reef biodiversity (Kennedy et al. 2013). To ensure that reefs do not slip beyond thresholds where they cannot recover, we need a better understanding of the feedback mechanisms that either allow or prevent recovery and the levels of degradation beyond which recovery becomes unlikely. However, defining management targets is hindered by our incomplete understanding of how coral reef organisms react to degradation of reef quality and how this affects community resilience, especially via changes in critical processes such as recruitment by reef fishes (Wilson et al. 2010; Dixon et al. 2014; Adam et al. 2015).

Fishes play critical functional roles on coral reefs, with healthy fish communities being essential for reef function, resilience (Bellwood et al. 2012; MacNeil et al. 2015), and the maintenance of socioeconomic value (Bellwood et al. 2012; MacNeil et al. 2015). Though all species are threatened to some degree by anthropogenic disturbance, habitat and trophic requirements will affect relative risk following reef degradation (Munday et al. 2008; Holbrook et al. 2015). For instance, while many species are dependent on the presence of live coral (Cole et al. 2008; Bonin 2012; Coker et al. 2014), other reef-associated species appear resilient to coral declines (Jones et al. 2004; Graham et al. 2011). Likewise, while a greater abundance of seaweed will negatively affect many species (Dixon et al. 2014; Brooker et al. 2016), some fishes, such as rubble dwellers and small herbivores, may benefit from a greater abundance of seaweeds and rubble on degraded reefs (Munday et al. 2008).

Shifts from coral to seaweed dominance may suppress reef resilience and lock areas into degraded states by preventing fish and coral recruitment via an absence of key settlement habitats (Bonin 2012), increased post-settlement mortality (Coker et al. 2009), or by producing cues that juveniles use to identify unsuitable reefs and thus suppressing recruitment (Dixon et al. 2014; Lönnstedt et al. 2014). Critically, recent evidence shows that the larvae of reef fishes, as well as several corals, are repelled by the odor of highly degraded habitats and by those of common seaweeds that bloom as reefs decline; in contrast, they are attracted to odors of certain corals (Dixon et al. 2014). Thus, as corals decline and seaweeds increase, stimulatory cues are lost, suppressive cues accumulate, and this sensory landscape may suppress the recruitment of juveniles that is critical for reef recovery.

There are recent demonstrations that odors of highly degraded habitats are strongly avoided by juvenile fishes (Dixon et al. 2014), but the minimal level of seaweed increase or coral decline that produces negative cues is not known. It is also unknown whether the response to lesser levels of degradation is consistent among species. With this in mind, the aims of this study were to determine whether juvenile fishes avoid the odor of less severely degraded habitats and at what ratios of healthy reef to degraded reef cues this behavioral aversion occurs. In addition, we investigated whether interspecific differences in habitat or trophic requirements impact the level at which degradation cues affect behavior. Finally, we examined whether variable responses to degraded reef cues are driven by seaweed abundance and whether this is reflected in patterns of habitat selection.

Materials and methods

Study site and species

This study was conducted at Votua Reef, Viti Levu, Fiji (18°13.049'S, 177°42.968'E), during the larval recruitment period of January 2015. This section of fringing reef is split into a locally managed no-take marine protected area (MPA), defined by approximately 56% coral cover, 2.4% seaweed cover, and associated high biodiversity, and a directly adjacent non-protected, fished area with only ~4% coral cover and 91% seaweed cover on hard substrates (Rasher et al. 2013). Juveniles of four common fish species were selected for this study due to the differential trophic and habitat usages they represent: the blue-green damsel, *Chromis viridis*, the humbug damsel, *Dascyllus aruanus*, the twin spot wrasse, *Halichoeres trimaculatus*, and the bullethead parrotfish, *Chlorurus sordidus*. Both *Chr. viridis* and *D. aruanus* are planktivorous species that recruit in high numbers to branching scleractinian corals, remaining closely associated with live coral throughout their lives. *Halichoeres trimaculatus* occurs mainly in areas of sand and rubble where it feeds on small benthic invertebrates. Finally, recruits of herbivorous *Chl. sordidus* are generally found foraging as small roving assemblages closely associated with macroalgae. This species is known to feed on *Sargassum* seaweed (Chong-Seng et al. 2014). All experimental protocols were approved by Georgia Institute of Technology. Methods were carried out in accordance with the approved guidelines.

Effects of chemical cue concentration on juvenile fish behavior

Newly settled recruits (1.5–2 cm total length) of all four species were collected from Votua Reef using hand nets and clove oil. Clove oil has only short-term effects on the behavior and olfactory responses of fishes (Yamamoto et al. 2008). Newly settled juveniles were used instead of pre-settlement larvae because larval collection methods such as light traps often fail to collect significant numbers of non-pomacentrids while other methods, such as crest nets, could not be used due to wave action at this site. However, naïve larvae and post-settlement recruits display similar behavioral responses to environmental chemical cues (Dixson et al. 2008, 2011). While recruits were collected from within and outside the MPA and tested in equal numbers, previous work has shown that recruits from MPA and non-MPA locations exhibit identical olfactory preferences in assays like the ones conducted here (Dixson et al. 2014). Following collection, fishes were maintained overnight in fresh aerated MPA water prior to testing.

Choice tests were conducted using an Atema choice flume (13 cm × 4 cm) where individual fish were presented with a choice between two separate flows of water: water from the MPA versus water from the degraded non-MPA; or water from the MPA versus various ratios of MPA/non-MPA waters. Previous work on these Fijian reefs demonstrated that juvenile fishes from three separate pairs of reefs all acted equivalently in terms of behavior toward chemical cues from MPA versus non-MPA reefs regardless of collection site (Dixson et al. 2014). This suggests that tests of fishes from this one MPA/non-MPA pairing will be generally predictive.

To achieve a spectrum of chemical signatures found under degraded conditions, while also controlling for chemical variability due to site or other factors, MPA water was diluted with non-MPA water at specific ratios dependent on treatment. Thus, as the proportion of water from the MPA decreased the proportion of water from the non-MPA increased, hopefully mimicking chemical cues from reefs differing in the relative ratios of cues from coral-dominated versus seaweed-dominated reefs. Four different assays were run comparing 100% MPA water to: a) 100% non-MPA water; b) a 50% MPA/50% non-MPA water mix; c) a 75% MPA/25% non-MPA water mix; or d) a 90% MPA/10% non-MPA water mix. The ratio at which fishes stop distinguishing between water sources was taken to indicate the degree of degradation below which juvenile fishes will not detect and begin avoiding degrading reefs. Each assay consisted of 20 replicate trials. Each trial used a single untested individual with all recruits only used once. Water was gravity fed into the flume at equivalent volumes (100 mL min^{-1}) from each of the two sources, with dye tests confirming that each water source remained separate on each side of the flume. A fish was then placed into the center of the flume at the downstream end. Following a 2-min habituation period, the position of the fish (left or right side of chamber) was recorded at 5-s intervals for a period of 2 min. The source of water to each side of the chamber was then reversed and a second, 2-min habituation period allowed. The initial test was then repeated for an additional 2-min period to control for any side preference.

Water from both MPA and non-MPA areas was collected at low tide and stored in chemically inert containers until trials were conducted within several hours. Prior to trials, containers were held in a large water bath until temperatures were equivalent; this prevented temperature from confounding preferences or flow lamination. Significant differences in the proportion of time spent in each water source at each dilution were determined using separate paired-sample *t* tests.

Effect of seaweed abundance on microhabitat preferences

As coral cover declines in non-protected areas, it is often replaced by seaweeds. On Votua Reef, the non-MPA benthic community is dominated by *Sargassum polycystum*, which covers >50% of hard substrates (Rasher et al. 2013). Thus, chemical and visual cues given off by *S. polycystum* probably contribute substantially to the sensory landscape of the degraded area and may drive patterns of avoidance (Dixon et al. 2014). With this in mind, a 'cafeteria'-style choice experiment was conducted to examine the effects of increasing *S. polycystum* on microhabitat preference. In the field, juvenile fishes were presented with a choice of four patch reefs, each constructed from equal parts coral rubble and live coral (*Pocillopora damicornis*). As *P. damicornis* commonly occurs as unattached colonies among rubble, patch reefs could be constructed without causing damage to corals. Once constructed, each patch reef had a diameter of 40 cm. Each reef was encircled by a weighted rope containing *S. polycystum* that obscured the patch reef by 100, 50, 25, or 0% (did not contain any seaweed). These percentages were achieved by attaching 8, 4, 2, or 0 *S. polycystum* plants of approximately 30 cm in length to the respective ropes. The same species of fish used in dilution assays were used for this experiment. They were collected using hand nets and clove oil and held in situ in a mesh basket prior to use.

For each trial, the four patch reefs were arranged in a circle at equal distance (1.5 m) from each other, with seaweed treatment applied in a random order. Patch reefs were set up in an area of hard substratum within Votua's MPA, 10 m from any other reef structure to ensure fish selected from among the experimental patch reefs. A mesh cylinder enclosing the single test fish in each assay was placed in the middle of the circle, allowing the fish to receive visual and chemical cues from each of the four patches. After a 10-min habituation period, the mesh cylinder was gently lifted upward releasing the fish. The patch reef that the fish swam to was recorded, as was its location after 5 min; all fishes remained on the initial patch reef selected. Observations were conducted on snorkel from a distance of 3 m with the observer's location around the patch reefs randomized for each trial. Fish did not appear affected by the observer's presence, with patch reef selection not reflecting the location of the observer. Data were analyzed using a Chi-squared goodness-of-fit test (χ^2), with the null hypothesis (H_0) that fishes would settle next to each patch reef in equal frequency, suggesting no preference. Where a significant χ^2 was found, standardized residuals (sr) determined what choices were driving the deviation from H_0 . An $sr > 2.00$ meant a choice was selected significantly more than expected, whereas an $sr < 2.00$ meant a choice was selected less.

Results

Effects of chemical cues from degraded versus MPA habitats on fish behavior

All four species preferred 100% MPA over 100% non-MPA water, spending significantly more time in the MPA water (between 31 and 45.2%) (Table 1; Fig. 1). Diluting the non-MPA water with 50% MPA water did not increase the attractiveness of the non-MPA mixture for the two damselfishes or the wrasse (all still spent 20.6–43.2% more time in the MPA water), but it did become more attractive to the parrotfish (its time spent in 100% MPA water dropped from 45.2% more than the alternative to only 18.1%). In general, when MPA and degraded reef waters were mixed, the strength of preference for 100% MPA water declined as the percent of MPA water in the alternative mixture increased and water sources became more chemically similar (Table 1; Fig. 1). However, the rate of decline and point where this preference ceased entirely varied among species. *Chr. viridis*, *D. aruanus*, and *H. trimaculatus* showed a significant preference for 100% MPA water against degraded reef water mixes of 100% non-MPA, 50% non-MPA, and 25% non-MPA water, but this preference was lost when water from degraded reefs constituted only 10% of the mixture. The tolerance of the parrotfish, *Chl. sordidus*, for degraded reef cues was higher; it differed from the other fishes in ceasing to prefer the 100% MPA water when water from degraded reefs constituted 25% of the mixture.

Effect of seaweed abundance on microhabitat preferences

All four fish species strongly preferred some patch reefs over others based on algal abundance, but preferences varied among species (Table 2; Fig. 2). *Chr. viridis*, *D. aruanus*, and *H. trimaculatus* all exhibited a strong preference for the seaweed-free patch reef with between 51 and 55% of individuals selecting it over the other three choices. However, *Chl. sordidus* exhibited a significant preference for the patch reef with 50% seaweed coverage; 51% of individuals selected this treatment. An additional 43% of individuals selected the

patch reef with 25% seaweed coverage. Unlike the other species, *Chl. sordidus* avoided the patch reef with no seaweed—only 3% of individuals selected it (Fig. 2).

Discussion

While juveniles of both damselfishes and of the wrasse began significantly avoiding chemical cues from the degraded reef when these were mixed in with MPA water at only 25% of the water volume, the parrotfish did not show a significant avoidance of the non-MPA cues until they constituted 50% of the water volume. Algal cover is high on hard substrates in the non-MPA (~90%), but hard substrates (i.e., not sand or rubble) only constitute around 30% of the non-MPA area (Bonaldo and Hay 2014; Rasher et al. 2013). Thus, a 50% MPA/50% non-MPA water mix could hold macroalgal cues representative of a continuous reef with seaweed coverage of only 13–14%. Many reefs support such macroalgal coverage and may therefore already be producing sufficient negative feedback cues to discourage fish recruitment. If the mix of signals here mirrors natural mixes of seaweed and coral cues, our results suggest that even modest losses of corals and increases in macroalgae may alter the sensory landscape so as to cue fishes to avoid habitats in the early stages of decline, potentially reinforcing that decline.

The protected and non-protected areas of Votua Reef present a stark contrast in benthic community structure, with the abundance of biodiversity-promoting organisms such as hard corals, soft corals, and turf algae greater within the MPA, while fleshy macroalgae are more abundant in the non-MPA. For instance, corals cover approximately 56% of hard substrates within the MPA but only ~4% in the adjacent non-MPA, while seaweeds cover only 2.4% of hard substrates within the MPA but 91% in the non-MPA (Rasher et al. 2013). Dramatic differences in benthic composition within this localized area appear primarily due to direct and indirect effects of fishing activities that remove herbivores and damage benthic structure (Burkepile and Hay 2008; Rasher et al. 2013). Although both corals and seaweeds occur throughout the reef, their species composition varies between the protected and non-protected areas, with the sparse coral community in the non-MPA dominated by relatively hardy *Porites* and relatively weedy *Pocillopora* colonies, whereas the species-rich coral community in the MPA includes numerous *Acropora* species that are particularly susceptible to anthropogenic and natural stresses (Marshall and Baird 2000; Bonaldo and Hay 2014) and produce cues that attract juvenile fishes (Dixon et al. 2014). Similarly, the seaweeds dominating the non-MPA are large brown macroalgae such as *S. polycystum* and *Turbinaria conoides* that bloom on reefs when herbivores are removed (Lewis 1986; Hughes et al. 2007; Burkepile and Hay 2008) and that produce cues avoided by settling fishes and corals (Dixon et al. 2014). These species are rare within the MPA where the macroalgae community is composed of species such as *Chlorodesmis fastigiata* or *Galaxaura filamentosa* that are less palatable to herbivores, occur on both fished and unfished reefs, and are minimally suppressive of settling fishes (Dixon et al. 2014). Thus, chemical cues from healthy and degraded reefs may be produced primarily by specific seaweeds and corals rather than by any seaweeds or corals. This is consistent with the results from our patch reef experiment which suggest that *S. polycystum* alone can affect fish attraction; both damselfishes and the wrasse selected the *S. polycystum*-free patch reefs despite the similarity in concentration of live coral and rubble cues among them. In contrast, the

parrotfish preferentially recruited to the patch reef with 50% cover of *S. polycystum* and significantly avoided the reef with no macroalgal cover (Fig. 2).

The choice of initial settlement habitat can have dramatic consequences for survival and fitness of larvae (Munday 2001). If certain seaweeds are strong indicators of declining habitat quality (Lapointe 1997), or deleterious coral–seaweed interactions (Bonaldo and Hay 2014; Brooker et al. 2016), even limited odor or visual cues from these species may repel juveniles when a better alternative is available. If seaweed cue concentration influences whether a habitat will attract or repel juveniles, annual fluctuations in seaweed growth have the potential to deter larvae from settling into otherwise acceptable habitats if blooms overlap with periods of peak larval recruitment. For instance, in the tropical Indo-Pacific, fish recruitment and abundance of brown macroalgae such as *Sargassum*, *Turbinaria*, and *Dictyota* both peak during the warm summer months (Ferrari et al. 2012; Fulton et al. 2014). When such overlaps occur, ecologically critical fishes could fail to recruit and help restore reef resilience even if habitat quality is high during portions of the year when macroalgae senesce and reach seasonal lows.

While seaweed odors may act as repellants to juvenile fishes, it seems likely that fishes may also respond positively to odors of the corals with which they associate (Dixson et al. 2014). The strongest preference for MPA water was seen in the two coral-associated damselfishes. For such coral specialists, coral odor may act as a powerful attractant. Many coral-associated species exhibit strong preferences for certain coral species or genera, so it is possible that they distinguish between concentration of cues originating from these specific corals instead of, or as well as, the odor of degraded and non-degraded coral habitats. The concentration of *Acropora* coral odor, for instance, is likely to be a good indicator of habitat health (Dixson et al. 2014). There is also evidence that larvae use the odor of conspecifics to identify and orientate toward settlement habitat (Lecchini et al. 2005). As both *Chr. viridis* and *D. aruanus* preferentially settle on corals that contain conspecifics (Lecchini et al. 2005; Sweatman 1988) and the abundance of each species is much higher within coral-rich habitats, it is possible that the concentration of conspecific cues could assist larvae to differentiate between habitats via a positive feedback mechanism of successful prior settlement. While it generally does not associate with coral microhabitats, the rubble-dwelling *H. trimaculatus* also exhibited a significant preference for the MPA water, suggesting that unless there is a direct benefit to associating near algae (i.e., for herbivorous species) species will select coral- over algal-dominated habitats. For non-coral-associated species, recruiting to structurally complex, coral-rich reefs is likely beneficial because these habitats provide refuge from predators (Almany 2004).

A diverse fish community bolsters the function and resilience of coral reefs, but certain species, or mixes of species, are critical for preserving critical function on reefs (Bellwood et al. 2004; Burkepile and Hay 2008; Rasher et al. 2013). For instance, herbivorous fishes are often highlighted as essential for coral reef resilience. Because seaweeds employ a diverse range of differing anti-herbivore defenses, specific mixes of herbivorous species are often needed to effectively control seaweeds and prevent their suppression of corals (Burkepile and Hay 2008; Rasher et al. 2013). As fishing commonly removes key herbivores, their recovery may depend on larval replenishment from adjacent protected reefs (Harrison et al.

2012). In this study, the herbivorous parrotfish *Chl. sordidus* exhibited a greater tolerance for cues from degraded reefs and also preferentially selected patch reefs with 50% *S. polycystum* cover as opposed to no macroalgae. Thus, larvae of herbivorous species (or at least this herbivorous species) may be less repelled by degraded reefs and may continue to settle onto habitats in the early stages of algal overgrowth, potentially promoting resilience if these settlers grow and consume macroalgae. However, even *Chl. sordidus* was repelled by the 50%/50% healthy/degraded mix, suggesting that even the greater tolerance of this species is exceeded once macroalgae become too common. This result is in line with recent findings from Moorea (Adam et al. 2011) where total abundance of *Chl. sordidus* in degraded areas increased with seaweed abundance. However, this was driven by migrations of small adults; juveniles were virtually absent. Juveniles recruited to coral-rich habitats before moving into the seaweed-rich areas once they reached a certain size. This suggests that, while continued recruitment of herbivorous fishes could help to reduce seaweed growth on mildly degraded reefs, if reefs degrade too far then seaweed removal will depend on movement of adult fishes. However, migration of small adults is likely limited to modest spatial scales. If spatially isolated reefs degrade, or more integrated reefs degrade over large areas, resilience may be lost due to the absence or suppression of juvenile recruits which can disperse over greater distances.

Our findings suggest that as seaweeds reach ~15% cover on reefs, they may produce olfactory cues that generate negative feedbacks and begin suppressing recruitment of reef fishes. If our assays using recently settled juveniles are predictive for pre-settlement larvae, this could lead to reduced settlement into degraded habitats further exacerbating biodiversity losses. We tested only one herbivorous species, but if it is typical of other herbivores then increased tolerance for seaweed odors could allow for resilience of reefs in the initial stages of degradation. However, if degradation goes too far even these species may be repelled by seaweed cues. Overall, these findings suggest that the mass avoidance of degraded habitats predicted by Dixon et al. (2014) may be relevant to both highly degraded and less degraded coral reef systems worldwide, with subtle intraspecific differences in tolerance also altering the composition of reef fish communities.

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Fig. 1.

Results of dilution assays comparing attraction of fishes to water taken from an MPA versus a mix of water from MPA diluted with water taken from an adjacent non-MPA. Four species were tested: **a** *Chr. viridis*; **b** *Dascyllus aruanus*; **c** *Halichoeres trimaculatus*; and **d** *Chl. sordidus*. Assays are: 0/100 = 0% MPA/100% non-MPA mix; 50/50 = 50% MPA/50% non-MPA mix; 75/25 = 75% MPA/25% non-MPA mix; 90/10 = 90% MPA/10% non-MPA mix. Dotted line indicates the point between trials where fishes did (left of line) and did not (right of line) display a significant preference for MPA water, suggesting the theoretical threshold beyond which degradation will not negatively affect odor-driven larval recruitment behavior. Error bars are standard errors. Number of individual fish per assay, $n = 20$

Fig. 2.

Percentage of fishes that selected patch reefs depending on the proportion of associated *Sargassum polycystum* seaweed. Four species were tested: **a** *Chr. viridis*; **b** *Dascyllus aruanus*; **c** *Halichoeres trimaculatus*; and **d** *Chl. sordidus*. Gray bars indicate where a positive standardized residual was identified indicating selection for that reef type, while black bars indicate where a negative standardized residual was identified indicating avoidance of that reef type. $n = 28$ individual fish per species

Table 1

Summarized paired-sample *t* test results for two-channel flume-based assays using four species of juvenile coral reef fishes: *Chromis viridis*, *Dascyllus aruanus*, *Halichoeres trimaculatus*, and *Chlorurus sordidus*

Species	MPA/non-MPA mix (%)	<i>t</i> (19)	<i>p</i>
<i>Chromis viridis</i>	0/100	9.582	0.000 [*]
	50/50	7.503	0.000 [*]
	75/25	2.634	0.016 [*]
	90/10	−0.067	0.948
<i>Dascyllus aruanus</i>	0/100	9.877	0.000 [*]
	50/50	6.676	0.000 [*]
	75/25	2.316	0.032 [*]
	90/10	0.279	0.783
<i>Halichoeres trimaculatus</i>	0/100	6.400	0.000 [*]
	50/50	3.002	0.007 [*]
	75/25	2.425	0.025 [*]
	90/10	−0.636	0.532
<i>Chlorurus sordidus</i>	0/100	8.546	0.000 [*]
	50/50	4.216	0.000 [*]
	75/25	−0.184	0.856
	90/10	0.085	0.933

Assays compared the proportion of time spent in 100% MPA water versus a mix of MPA and non-MPA water (MPA/non-MPA mix) at four different ratios. Number of trials per assay *n* = 20

^{*} Assays where a significant difference in time was identified

Table 2

Summarized χ^2 goodness-of-fit test results for patch reef preference trials using four species of juvenile coral reef fishes: *Chromis viridis*, *Dascyllus aruanus*, *Halichoeres trimaculatus*, and *Chlorurus sordidus*

Species	χ^2 (3 df)	<i>p</i>	Sig. driven by	<i>sr</i>
<i>Chromis viridis</i>	8.00	0.04 *	0% <i>S. polycystum</i>	2.65
<i>Dascyllus aruanus</i>	10.29	0.01 *	0% <i>S. polycystum</i>	2.27
<i>Halichoeres trimaculatus</i>	12.00	<0.01 *	0% <i>S. polycystum</i>	2.27
<i>Chlorurus sordidus</i>	14.86	<0.01 *	0% <i>S. polycystum</i>	-2.27
			50% <i>S. polycystum</i>	2.27

Each individual fish was presented with a choice of four patch reef treatments, each with 0, 25, 50, or 100% *Sargassum polycystum* coverage

* Significant χ^2 test, indicating a preference. Standardized residuals (*sr*) were calculated to identify which patch reef treatments were driving this significance ('Sig. driven by'), being selected more (positive *sr*), or less (negative *sr*) than expected under a null hypothesis of no preference