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Supplementary Materials for

Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery

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Materials and Methods

Our investigations of both corals and fishes were conducted on reefs associated with the villages of Votua, Namada, and Vatu-o-lailai along the Coral Coast of Viti Levu, Fiji (Fig. S1). Each village has a no-take marine protected area (MPA) with high coral (38-56%) and low macrophyte (0.8-2.4%) cover on hard substrate immediately adjacent to non-protected, fished reefs (non-MPA) that have low coral (4-16%) and high macrophyte (49-91%) cover on hard substrate(*9*). In 2004, shortly after MPA establishment and a significant coral bleaching event, coral cover was low in all areas (6-7%), did not differ significantly between MPA and non-MPA areas, and macrophyte cover varied from ~35-45% across all areas. Currently, biomass of herbivorous fishes is 6.6-16.2 fold greater in MPAs than in adjacent fished areas and grazing rates are high on macroalgae moved from non-MPAs into MPA areas(*9*). The three villages are spread along an 11Km stretch of coast line, the paired MPA and non-MPA areas we sampled are separated by ~300-900m, and physical conditions (depth, wave exposure, etc.) appear similar between MPA and adjacent areas (Fig. S1). The three, spatially paired MPA and fished areas allow replicated contrasts of behavior in response to waters collected from healthy versus degraded reefs in close proximity and experiencing similar oceanographic conditions. Because these protected and fished areas differ more dramatically than many MPA versus non-MPA areas, these data may represent comparisons of healthy and degraded reefs rather than average MPA and non-MPA areas *per se*.

Assays with coral larvae:

To obtain coral planula, we used colonies of *Acropora millepora*, *A. nasuta*, and *A. tenuis*. These are broadcast-spawning, simultaneous hermaphrodites with one gametogenic cycle per year. Reproductive condition was assessed by breaking branches below the expectant sterile zones to expose the developing oocytes. Four individual colonies of each of species containing mature pigmented oocytes were carefully dislodged from the reef using a hammer and chisel four days following the October full moon of 2012. Colonies were transported from the reef to experimental holding pools each night for spawning and gamete collection. Different species were maintained in separate stagnate 1,000L pools. Each night before corals were brought into the laboratory, holding pools were filled with 5 μm filtered ocean water and complete water changes occurred each day to ensure highest water quality.

Using previously established spawning procedures*(37)* gametes were collected, held in still 10L aquaria and left to fertilize for 2 h. Once fertilization had been confirmed by examining a sample of embryos from each aquarium, the positively buoyant embryos were removed from the aquaria, taking as little water as possible. Embryos were transferred into new 10L still aquaria to "wash" the embryos of excess sperm. This was repeated twice before embryos were placed in their rearing aquaria.

Rearing aquaria had no flow for the first 24 h, a steady drip for the next 24 h, and aeration was added after that. The water surface was skimmed regularly to remove excess lipids and dead embryos. Larvae were competent to settle when they elongated and displayed swimming and settlement behavior; this occurred approximately 6-7 days post fertilization.

To assess the response of planula to waterborne chemical cues from different sources, individual planula were tested using an Atema choice flume (13cm x 4cm)*(24)*. Briefly, pair-wise choice experiments were conducted, with coral planula choosing between water of different treatments flowing at equivalent volumes (100ml min^{-1}) from two different sources. Water was gravity fed into the choice flume, a coral planula was pipetted into the center of the flume at the downstream end where it could move to either side or swim toward the preferred water source. A two-minute acclimation period was followed by a three-minute testing period where the position of the planula, on either the right or left side of the chamber, was recoded at five-second intervals. At the conclusion of this, the planula was removed from the flume via pipette for one minute, during this time the water in the flume was flushed and the water sources were exchanged from one side to the other. The test was then repeated, including the acclimation period, to ensure planula were displaying a preference for the chemical cues rather than one side of the chamber. Flow rates were measured using a flow meter, and dye tests were conducted at each water change to ensure that the two channels exhibited parallel water flow, with no turbulence or eddies. All planula were tested only once. Kolmogorov-Smirnov tests evaluated differences in chemical preferences, assessing the time spent in one side of the flume when chemical cues were present compared to the time spent on one side of the flume when untreated filtered seawater water was tested against itself. Although coral planula have limited swimming capabilities, they swam forward in the flume despite the 100 ml min^{-1} flow rate.

To evaluate potential side preferences in the flume and for statistical purposes, larvae of all coral species were tested in blank trials, where filtered seawater was tested against itself. All species spent equal time in either side of the flume indicating that this was an appropriate apparatus for testing chemical preferences ($p= 0.12$), and that the planula exhibited no detectable side preference in the flume unrelated to the treatments.

To determine if coral larvae could use chemical cues for reef assessment, planula were offered a choice between water collected from the marine protected area (MPA) compared to the non-protected area (non-MPA) from each village. Because all three species we assessed showed indistinguishable levels of attraction to MPA vs non-MPA water and because planula of some species were limited, we used planula of *A. tenuis* alone to evaluate the effects of common benthic species in producing chemical cues that attracted or repelled planula. Trials conducted included: 1) MPA water versus MPA water treated (to add chemical cues) with the non-allelopathic brown alga *Padina gymnospora(25)*; 2) MPA water versus MPA water treated with the non-allelopathic, but abundant, brown alga *Sargassum polycystum(25)*; 3) MPA water compared to MPA water treated with the allelopathic red alga *Galaxaura filamentosa(25),* 4) water from the MPA versus water from the fished area treated with the settlement-inducing crustose coralline alga (CCA), *Hydrolithon reinboldii(21)*, 5) MPA water versus MPA water treated with conspecific *A. tenuis* , 6) MPA water versus MPA water treated with a mix of five corals (*Porites cylindrica*, *Pocillopora damicornis*, *Montipora digitata, Merulina*

scabricula, *Acropora formosa)*, and 7) non-MPA water treated with CCA versus MPA water. Chemical cues were created by soaking 20 g of each upright seaweed, 50g of CCA chips, or 100g of coral (different masses used to counter balance the differences in density) in 10L of the water source indicated above for 60 min. The mixed coral cue was created by soaking 20g of each coral species (i.e., 100g total, so that it was equal to the total cue concentration from the conspecific assay). To ensure settlement competency of assay larvae, each day prior to chemical trials, 10 planula were placed in a 2 L aquarium for one hour with *H. reinboldii* chips, a minimum of 7 planula needed to settle for larvae to be deemed settlement competent. Complete settlement (flattening along oral-aboral axis with clear radial messenterial subdivisions) was not observed during this short period but substantial modifications to larval behavior (larvae stopped swimming and remained in one spot on or near the CCA and began flattening along oral-aboral axis) occurred, and we deemed these larvae to be competent. All chemical preference trials were conducted on days 7-8 post-fertilization. Analysis of each assay was by the Kolmogorov-Smirnov test.

To test for the possibility that lipophilic molecules from macroalgal surfaces*(25, 26)* were being transferred to surrounding substrata and that these could deter settlement of coral larvae upon contact, we conducted choice settlement assays using *A. tenuis* planula in 10L glass aquaria. Each aquarium held a pair of 2cm x 2cm ceramic tiles placed 5 cm apart. Using underwater paper a grid was made on the bottom of each aquaria displaying a 20mm boundary around each tile. Planulae were counted as settling on the tile if they were on it or within this 20 mm boundary near it. Tiles were soaked over night in either control water (offshore water) or treatment water (water containing the chemical cues of each algal species made as described above). Additionally, immediately prior to trails, treated tiles were brushed 5 times with the corresponding alga species, to mimic substrate in brushing contact with each seaweed species. Control tiles were brushed with a plastic algal mimic. Six replicate aquaria were set up for each algal species with an additional two aquaria testing the settlement competency of the planula using a control tile and a tile rubbed with CCA. At the beginning of the trial, 10 coral planula were pipetted into each aquaria. Each planula's position was recorded at 2h, 6h, 12h and 24h post-injection. Corals were also recorded as either crawling or settled once they settled or metamorphosed. Analysis was by multi-factorial repeated measures ANOVA.

To determine if our laboratory behavioral assays predicted recruitment patterns in the field, 18 2x2m plots were constructed in adjacent MPA and non-MPA locations at two villages (Votua and Namada) along Fiji's coral coast. The first plot was randomly selected, and subsequent plots were added based on the initial plot location (6 rows of 3 plots running parallel to shore, separated by 5m). Using randomized selection half of the plots were cleared of macroalgae by hand and half were left in the natural state (each row contained at least one cleared and one natural plot). Macroalgal removal plots were maintained bi-weekly initially; this was reduced to monthly once algal re-growth was determined to be slow. Directly adjacent to 2 sets of cleared and natural plots in each MPA and non-MPA per village tile arrays mounted on PVC poles were cemented into the benthos. Each tile array stood 50 cm off of the seafloor and contained 8-15x15 cm unglazed tiles (=16 unglazed surfaces) as potential coral settlement sites. Tiles were arranged in pairs, with two pairs horizontal and two pairs parallel to the benthos, in an

effort to maximize recruitment onto arrays. Plots were initiated in March 2012 and maintained through the coral recruitment season, ending on April 2013. Tile arrays were deployed in September and 2012 and deconstructed in March 2013 (after 6 months in the field) to look for coral recruitment on each tile. To determine recruitment to the natural benthos, each month during the week of the new moon we conducted nocturnal surveys to count coral recruitment in the plots using a UV filter and black light – juvenile corals fluoresce under black light and are easier to see reliably using this method(*38)*. Each individual plot was surveyed for 10 minutes, and a map was constructed of recruit locations in each plot to ensure that new recruits were differentiated from those mapped previously so we could accumulate an accurate cumulative total. Newly recruited corals were simply counted and not identified to species because we were not confident of our ability to visually identify larvae at this small size in the field. Analyses of total settlement densities were by multi-factor ANOVA. Because we experienced considerable settlement in some treatments and none in others, data distributions violate some assumptions of ANOVA. However, this test accounts for the hierarchical approach of the design and for potential interaction between factors such as village (Votua or Namada), protection status (MPA or Non-MPA), and treatment (cleared or uncleared). Using this test potentially biases for detection of significant differences. However, as no significant effect of clearing seaweeds or village location was detected, (village [$F_{(1,72)}$=0.04; p=0.84]; clearing status [$F_{(1,72)}$= 1.64 p=0.21]), but effects of protection status (MPA vs non-MPA) were highly significant ($p<0.0001$; Table 1), we felt justified in using this approach. Additionally, ANOVA is robust to heteroscedasticity if the design is balanced*(39)*. Additionally, if we ran the non-parametric Mann-Whitney on density of settlers in MPA vs non-MPA, we also found protection status to be significant at $p<0.0001$.

Assays with juvenile fishes:

Newly settled recruits of coral reef fishes were collected from each of the three MPAs and non-MPAs using hand nets and clove oil, which does not affect the olfactory responses of juvenile fishes, when necessary. We focused on new recruits (identified as new by both size and coloration) rather than larvae because we could collect a broader range of species for testing. Light traps attracted primarily damselfishes and crest nets could not be used at these sites due to wave force. Following collection, all fishes were held overnight in aerated aquariums filled with water from the collection location and tested the following day for preferences for chemical cues contained in water from MPAs versus non-MPAs or for waters treated with different reef organisms. As chemical stimuli can be important settlement cues for a variety of species, we collected recruits from a wide range of taxonomic and functional groups – including: 6 pomacentrids (*Chromis viridis* [mean $\pm$ SE = 8.6 $\pm$0.34 mm]*, Chrysiptera biocellata* [11.5 $\pm$ 0.24mm]*, C. cyanea* [11.5 $\pm$ 0.23 mm], *Dascyllus aruanus* [10.1 $\pm$ 0.23 mm]*, D. trimaculatus* [11.7 $\pm$ 0.15 mm]*, and Pomacentrus spilotoceps* [13.0 $\pm$ 0.16 mm]), 2 cheatodontids (*Chaetodon raffelsi* [15.1 $\pm$ 0.16 mm] and *C. vagabundus* [15.5 $\pm$ 0.22 mm]), 2 acanthurids (*Acanthurus triostegus* [18.5 $\pm$ 0.31 mm] and *Ctenochaetus striatus* [19.6 $\pm$ 0.35 mm]), 1 siganid (*Siganus spinus* [20.1 $\pm$ 0.26 mm]), 3 labrids (*Chlorurus sordidus* [15.8 $\pm$ 0.27 mm]*, Halichoeres trimaculatus* [15.9 $\pm$ 0.19 mm], *Scarus sp.* [15.8 $\pm$ 0.22 mm]), and 1 apogonid (*Apogon angustatus* [15.5 + 0.91 mm]).

A two-channel Atema choice flume (13cm x 4cm) was used to assess preference of recent recruits for chemical cues in water from different locations, or water containing chemical cues from different benthic organisms*(24)*. Methods were as described above for coral larvae. Flow rates were set equal using a flow meter, and dye tests were conducted at each water change to ensure that the two channels exhibited parallel water flow, with no turbulence or eddies. Twenty recruits per species were used for each trial from each of the six collection sites; individual recruits were never reused (i.e., all replicates were independent).

Reef fishes rarely move more than a few meters to a few 100 meters from their initial settlement site(*40*), nearly 60% of recruits are consumed within 1-2 days of settlement(*41*), and post-settlement survival can be enhanced by high coral cover*(42)*. These conditions should create strong selection for settlement in response to reliable cues of reef habitat quality. We hypothesized coral reef fishes would favor areas with high coral cover and low seaweed cover (i.e., healthy versus degraded reefs), and coral species that were critical for producing topographic complexity and that are most at risk of being damaged when reefs degrade would produce the most reliable cues for a healthy reef, while seaweeds that commonly bloom as reefs degrade would be reliable cues of reefs to avoid.

MPA and non-MPA water for our flume assays was collected during low tide from mid way through the water column at a depth greater than 1 meter at the degraded or healthy reef sections of each village. Waters were used in flume assays within 12h of collection. Offshore seawater was collected from 2 km offshore and used as a control to test for side bias when tested against itself (blank trial; n=20 individual fish per species per location; n=1800 when pooled). Cues created to contain the chemical cues of specific corals or seaweeds were made by soaking 50g of coral or 10g of algae in 10L of seawater for 1h. The organism was removed before olfactory preferences were tested.

Because there were no significant differences in preference patterns of fishes collected from the multiple MPAs compared against each other, or of the non-MPAs compared against each other (Kolmogorov Smirnov test, $p>0.10$, see Table S4), recruits from within each habitat type were pooled by species. Separate Kolmogorov-Smirnov tests were used to compare the proportion of time that individuals of a species spent in the water containing the focal chemical cue compared to the proportion of time spent on one side of the chamber when no cue was present (i.e. the blank trial).

To assess patterns of natural recruitment at each of the 3 paired fished and MPA sites, we evaluated density of newly settled juveniles, species richness of newly settled juveniles, and density of predators that prey on recruits in 30 non-overlapping transects of 30x2m located randomly at each site. Transects were conducted during the annual recruitment pulse (December-January 2012-2013) with densities assessed by slowly swimming a 30 m line and carefully searching 1 m on each side of the line. New recruits were identified by their immature color pattern and predators were counted based on known predators of recruits on Pacific reefs. Each day of the observation period, 5 transects were run in the MPA and adjacent non-MPA of one village during high tide. The next day, a similar evaluation was run at the next village. This continued each day until a total of 30 transects were completed for each site in each village.

Supplemental Figure:

Fig S1

Map of field site locations indicating the village locations (black circles), water collection points for choice comparisons (red circles) and PMA (white) and non-MPA (yellow, dashed) areas used in the study.

Supplementary Tables

Table S1: Mean percent time (SE) coral planula (n=20) spent in MPA water when compared to non-MPA water of three replicate paired MPA/fished locations ($p>0.9$ Factorial ANOVA).

	Namada	**Vatu-o-lailai**	**Votua**
A. tenuis	87.9% (±1.8)	86.8% (±1.3)	85.8% (±2.2)
A. nasuta	87.8% (±1.8)	86.8% (±1.3)	85.8% (±2.1)
A. millepora	88.3% (±1.3)	90.8% (±2.5)	87.2% (±1.7)

Table S2: Summary of repeated measures ANOVA comparing behavioral recruitment choice for *Acropora tenuis* larvae over 24hrs

Algae	Factor	df	F	p-value
CCA	Choice	3	35.77	**0.002**
	Time	3	0.00	1
	Choice *Time	9	2.41	0.079
Post-hoc Tukey HSD Test (24hrs)				
	CCA tile vs Water Column			**0.049032**
	CCA tile vs No choice			**0.031677**
	CCA tile vs Untreated			**0.039209**
	Untreated tile vs. No Choice			1
	Untreated tile vs. Water Column			1
	No choice vs. Water Column			0.999
Padina	Choice	3	16.28	**<0.0001**
	Time	3	0.03	0.995
	Choice *Time	9	1.03	0.428
Post-hoc Tukey HSD Test (24hrs)				
	Padina tile vs. Water Column			1
	Padina tile vs. No choice			0.899004
	Padina tile vs. Untreated tile			0.99657
	Untreated tiles vs. no choice			1
	Untreated tile vs. water column			0.979590
	No Choice vs. water column			0.826536
Sargassum	Choice	3	342.73	**<0.0001**
	Time	3	0.087	0.967
	Choice *Time	9	3.349	**0.0022**
Post-hoc Tukey HSD Test (24hrs)				
	Sargassum tile vs. Water Column			**0.000179**
	Sargassum tile vs. No choice			**0.019289**
	Sargassum tile vs. Untreated tile			0.919972
	Untreated tiles vs. no choice			**0.000970**
	Untreated tile vs. water column			**0.000187**
	No Choice vs. water column			**0.000146**
Galaxura	Choice	3	40.30	**<0.001**
	Time	3	0.0185	0.9965
	Choice *Time	9	2.8028	**0.008**
Post-hoc Tukey HSD Test (24hrs)				
	Galaxura tile vs. Water Column			**0.001821**
	Galaxura tile vs. No choice			0.072940
	Galaxura tile vs. Untreated tile			**0.000277**
	Untreated tiles vs. no choice			0.120650
	Untreated tile vs. water column			0.973006

No Choice vs. water column	0.774382

Table S3: In situ mean (±SE) cumulative settlement of coral larvae/m^2 on natural benthos plots that had been either cleared or not cleared of upright seaweeds or on adjacent tile arrays throughout the experiment. * = a significant difference between MPA and non-MPA at $p<0.001$.

Substrate	Village	Treatment	MPA	Non-MPA
Natural Benthos	Namada	Cleared (n=9)*	1.2 (±0.2)	0.0 (±0)
		Algae (n=9)*	0.83 (±0.2)	0.0 (±0)
	Votua	Cleared (n=9)*	1.1 (±0.1)	0.0 (±0)
		Algae (n=9)*	0.86 (±0.2)	0.0 (±0)
Tile Array	Namada	Cleared (n=2)*	0.0 (±0)	13.9 (±0)
		Algae (n=2)*	0.0 (±0)	13.9 (±2.7)
	Votua	Cleared (n=2)*	0.0 (±0)	12.5 (±4.2)
		Algae (n=2)*	0.0 (±0)	12.5 (±1.4)

Fish Collection Site	Votua			Namada			Vatu-o-lailai		
MPA Water	Votua	Namada	Vatu-o-lailai	Votua	Namada	Vatu-o-lailai	Votua	Namada	Vatu-o-lailai
Chromis viridis	88% (±0.9)	92% (±0.8)	92% (±0.8)	92% (±0.8)	86% (±0.9)	88% (±0.7)	92% (±0.7)	89% (±0.7)	88% (±0.6)
Chrysiptera biocellata	88% (±0.8)	84% (±0.9)	82% (±0.7)	85% (±0.6)	86% (±0.8)	88% (±0.7)	83% (±0.8)	86% (±0.7)	86% (±0.7)
C. cyanea	89% (±0.7)	90% (±1.0)	89% (±0.8)	88% (±0.9)	85% (±1.0)	90% (±0.7)	89% (±0.8)	88% (±0.8)	88% (±0.9)
Dascyllus aruanus	90% (±0.6)	90% (±0.7)	89% (±0.7)	90% (±0.6)	89% (±0.7)	88% (±0.7)	90% (±0.4)	90% (±0.9)	90% (±0.6)
D. trimaculatus	90% (±0.8)	87% (±0.9)	89% (±0.8)	87% (±0.9)	83% (±1.2)	86% (±1.0)	88% (±1.0)	84% (±1.0)	86% (±1.0)
Pomacentrus spilotoceps	90% (±0.8)	90% (±0.7)	90% (±0.7)	88% (±0.9)	88% (±1.0)	88% (±1.0)	88% (±0.8)	90% (±1.0)	90% (±1.0)
Chaetodon raffelsi	88% (±0.7)	88% (±0.6)	83% (±0.6)	86% (±0.7)	87% (±0.6)	86% (±0.6)	89% (±0.7)	88% (±0.6)	89% (±0.6)
C. vagabundus	89% (±1.0)	87% (±0.8)	89% (±0.7)	87% (±1.0)	87% (±1.0)	87% (±1.0)	87% (±1.1)	87% (±0.9)	88% (±1.0)
Acanthurus triostegus	87% (±0.9)	87% (±1.3)	89% (±0.8)	86% (±1.0)	87% (±0.7)	86% (±1.1)	87% (±0.9)	86% (±0.9)	87% (±0.9)
Ctenochaetus striatus	90% (±0.9)	87% (±1.0)	89% (±0.9)	90% (±0.8)	85% (±0.8)	87% (±1.2)	88% (±0.9)	89% (±1.0)	86% (±0.8)
Siganus spinus	89% (±1.0)	86% (±1.1)	83% (±0.8)	88% (±0.8)	83% (±0.9)	87% (±0.9)	89% (±0.8)	84% (±0.9)	84% (±1.2)
Scarus forsteni	89% (±0.9)	87% (±1.0)	89% (±0.9)	87% (±0.7)	86% (±0.8)	87% (±1.2)	87% (±0.8)	85% (±0.8)	89% (±1.0)
Chlorurs	90%	85%	87%	88%	84%	85%	90%	83%	85%

sordidus	(±0.9)	(±0.8)	(±0.9)	(±0.7)	(±0.7)	(±1.0)	(±0.7)	(±0.7)	(±0.9)
Apogon	89%	88%	90%	90%	90%	91%	89%	90%	90%
angustatus	(±0.8)	(±0.7)	(±0.7)	(±0.7)	(±0.8)	(±0.7)	(±0.7)	(±0.9)	(±1.0)
Halichoeres	90%	88%	90%	88%	88%	88%	87%	89%	88%
trimaculatus	(±0.9)	(±0.7)	(±0.7)	(±0.6)	(±0.8)	(±0.8)	(±0.7)	(±0.8)	(±0.7)

Table S4: Behavioral response of each species, towards MPA water (mean % time spent in MPA water ±SE) grouped by "home" collection village, compared against adjacent non-MPA reefs, (n=40 per species [20 from each MPA and 20 from each non-MPA]; $p>0.10$ for all trials; Kolmogrov-Smirnov Tests). Values for response to non-MPAs would be these values subtracted from 100%.

References

1. L. Alvarez-Filip, N. K. Dulvy, J. A. Gill, I. M. Côté, A. R. Watkinson, Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proc. Biol. Sci.* **276**, 3019–3025 (2009). Medline doi:10.1098/rspb.2009.0339

2. N. A. J. Graham, K. L. Nash, The importance of structural complexity in coral reef ecosystems. *Coral Reefs* **32**, 315–326 (2013). doi:10.1007/s00338-012-0984-y

3. T. A. Gardner, I. M. Côté, J. A. Gill, A. Grant, A. R. Watkinson, Long-term region-wide declines in Caribbean corals. *Science* **301**, 958–960 (2003). Medline doi:10.1126/science.1086050

4. J. F. Bruno, E. R. Selig, Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLOS ONE* **2**, e711 (2007). Medline doi:10.1371/journal.pone.0000711

5. T. P. Hughes, N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, R. S. Steneck, Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* **25**, 633–642 (2010). Medline doi:10.1016/j.tree.2010.07.011

6. D. E. Burkepile, M. E. Hay, Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 16201–16206 (2008). Medline doi:10.1073/pnas.0801946105

7. P. J. Mumby, R. S. Steneck, Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.* **23**, 555–563 (2008). Medline doi:10.1016/j.tree.2008.06.011

8. A. J. Cheal, M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, H. Sweatman, Coral-macroalgal phase shifts or reef resilence: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* **29**, 1005–1015 (2010). doi:10.1007/s00338-010-0661-y

9. D. B. Rasher, A. S. Hoey, M. E. Hay, Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**, 1347–1358 (2013). Medline doi:10.1890/12-0389.1

10. S. K. Wilson, N. A. Graham, R. Fisher, J. Robinson, K. Nash, K. Chong-Seng, N. V. Polunin, R. Aumeeruddy, R. Quatre, Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. *Conserv. Biol.* **26**, 995–1004 (2012). Medline doi:10.1111/j.1523-1739.2012.01926.x

11. M. Nyström, A. V. Norström, T. Blenckner, M. la Torre-Castro, J. S. Eklöf, C. Folke, H. Österblom, R. S. Steneck, M. Thyresson, M. Troell, Confronting feedbacks of degraded marine ecosystems. *Ecosyst.* **15**, 695–710 (2012). doi:10.1007/s10021-012-9530-6

12. T. P. Hughes, M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, B. Willis, Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* **17**, 360–365 (2007). Medline doi:10.1016/j.cub.2006.12.049

13. A. J. Cheal, M. Emslie, M. A. MacNeil, I. Miller, H. Sweatman, Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecol. Appl.* **23**, 174–188 (2013). Medline doi:10.1890/11-2253.1

14. H. Cesar, L. Burke, L. Pet-Soede, *The Economics of World Wide Coral Reef Degradation* (Cesar Environmental Economics Consulting, Netherlands, 2003).

15. I. B. Kuffner, V. J. Paul, Effects of the benthic cyanobacterium *Lyngbya majuscule* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs* **23**, 455–458 (2004). doi:10.1007/s00338-004-0416-8

16. H. Watanabe, T. Fujisawa, T. W. Holstein, Cnidarians and the evolutionary origin of the nervous system. *Dev. Growth Differ.* **51**, 167–183 (2009). Medline doi:10.1111/j.1440-169X.2009.01103.x

17. Y. Benayahu, Y. Loya, Competition for space among coral reef sessile organisms at Eilat, Red Sea. *Bull. Mar. Sci.* **31**, 514–522 (1981).

18. T. R. McClanahan, R. Arthur, The effects of marine reserves and habitat on populations of east African coral reef fishes. *Ecol. Appl.* **11**, 559–569 (2001). doi:10.1890/1051-0761(2001)011[0559:TEOMRA]2.0.CO;2

19. D. F. Gleason, B. S. Danilowicz, C. J. Nolan, Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. *Coral Reefs* **28**, 549–554 (2009). doi:10.1007/s00338-009-0480-1

20. Y. Golbuu, R. H. Richmond, Substratum preferences in planula larvae of two species of scleractinian corals, *Goniastrea retiformis* and *Stylaraea punctate*. *Mar. Biol.* **152**, 639–644 (2007). doi:10.1007/s00227-007-0717-x

21. L. Harrington, K. Fabricius, G. De'ath, A. Negri, Recognition and selection of settlement substrata determines post-settlement survival in corals. *Ecology* **85**, 3428–3437 (2004). doi:10.1890/04-0298

22. J. Tebben, D. M. Tapiolas, C. A. Motti, D. Abrego, A. P. Negri, L. L. Blackall, P. D. Steinberg, T. Harder, Induction of larval metamorphosis of the coral *Acropora millepora* by tetrabromopyrrole isolated from a *Pseudoalteromonas* bacterium. *PLOS ONE* **6**, e19082 (2011). Medline doi:10.1371/journal.pone.0019082

23. S. N. Arnold, R. S. Steneck, Settling into an increasingly hostile world: The rapidly closing "recruitment window" for corals. *PLOS ONE* **6**, e28681 (2011). Medline doi:10.1371/journal.pone.0028681

24. J. Atema, M. J. Kingsford, G. Gerlach, Larval reef fish could use odour for detection, retention and orientation to reefs. *Mar. Ecol. Prog. Ser.* **241**, 151–160 (2002). doi:10.3354/meps241151

25. D. B. Rasher, E. P. Stout, S. Engel, J. Kubanek, M. E. Hay, Macroalgal terpenes function as allelopathic agents against reef corals. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17726–17731 (2011). Medline doi:10.1073/pnas.1108628108

26. T. D. Andras, T. S. Alexander, A. Gahlena, R. M. Parry, F. M. Fernandez, J. Kubanek, M. D. Wang, M. E. Hay, Seaweed allelopathy against coral: Surface

distribution of a seaweed secondary metabolite by imaging mass spectrometry. *J. Chem. Ecol.* **38**, 1203–1214 (2012). Medline doi:10.1007/s10886-012-0204-9

27. D. L. Dixson, M. S. Pratchett, P. L. Munday, Reef fish innately distinguish predators based on olfactory cues associated with recent prey items rather than individual species. *Anim. Behav.* **84**, 45–51 (2012). doi:10.1016/j.anbehav.2012.04.001

28. J. M. Leis, U. Siebeck, D. L. Dixson, How Nemo finds home: The neuroecology of dispersal and of population connectivity in larvae of marine fishes. *Integr. Comp. Biol.* **51**, 826–843 (2011). Medline doi:10.1093/icb/icr004

29. D. Lecchini, V. P. Waqalevu, E. Parmentier, C. A. Radford, B. Banaigs, Fish larvae prefer coral over algal water cues: Implications of coral reef degradation. *Mar. Ecol. Prog. Ser.* **475**, 303–307 (2013). doi:10.3354/meps10094

30. G. Gerlach, J. Atema, M. J. Kingsford, K. P. Black, V. Miller-Sims, Smelling home can prevent dispersal of reef fish larvae. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 858–863 (2007). Medline doi:10.1073/pnas.0606777104

31. A. H. Baird, M. S. Pratchett, A. S. Hoey, Y. Herdiana, S. J. Campbell, *Acanthaster planci* is a major cause of coral mortality in Indonesia. *Coral Reefs* **32**, 803–812 (2013). doi:10.1007/s00338-013-1025-1

32. M. S. Pratchett, D. McCowan, J. A. Maynard, S. F. Heron, Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLOS ONE* **8**, e70443 (2013). Medline doi:10.1371/journal.pone.0070443

33. S. M. Lewis, The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* **56**, 183–200 (1986). doi:10.2307/2937073

34. P. F. Sale, R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. Polunin, G. R. Russ, Y. J. Sadovy, R. S. Steneck, Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* **20**, 74–80 (2005). Medline doi:10.1016/j.tree.2004.11.007

35. H. B. Harrison, D. H. Williamson, R. D. Evans, G. R. Almany, S. R. Thorrold, G. R. Russ, K. A. Feldheim, L. van Herwerden, S. Planes, M. Srinivasan, M. L. Berumen, G. P. Jones, Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* **22**, 1023–1028 (2012). Medline doi:10.1016/j.cub.2012.04.008

36. S. R. Palumbi, Marine reserves and ocean neighbourhoods: The spatial scale of marine populations and their management. *Annu. Rev. Environ. Resour.* **29**, 31–68 (2004). doi:10.1146/annurev.energy.29.062403.102254

37. R. C. Babcock, A. H. Baird, S. Piromvaragorn, D. P. Thomson, B. L. Willis, Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zool. Stud.* **42**, 211–226 (2003).

38. A. H. Baird, A. Salih, A. Trevor-Jones, Fluorescence census techniques for early detection of coral recruits. *Coral Reefs* **25**, 73–76 (2006). doi:10.1007/s00338-005-0072-7

39. B. J. Winer, D. R. Brown, K. M. Michels, *Statistical Principles in Experimental Design* (McGraw-Hill, New York. ed. 3, 1991).

40. K. M. M. Jones, Home range areas and activity centres in six species of Caribbean wrasses (Labridae). *J. Fish Biol.* **66**, 150–166 (2005). doi:10.1111/j.0022-1112.2005.00589.x

41. G. R. Almany, M. S. Webster, The predation gauntlet: Early post-settlement mortality in reef fishes. *Coral Reefs* **25**, 19–22 (2006). doi:10.1007/s00338-005-0044-y

42. M. C. Bonin, G. R. Almany, G. P. Jones, Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* **92**, 1503–1512 (2011). Medline doi:10.1890/10-0627.1