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

Danielle L Dixson[1], **David Abrego**[2], and **Mark E Hay**[1,*]

[1]School of Biology, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA

[2]Department of Natural Sciences and Public Health, Zayed University, Abu Dhabi, United Arab Emirates

Abstract

Coral reefs are in global decline, converting from dominance by coral to dominance by seaweed. Once seaweeds become abundant, coral recovery is suppressed unless herbivores return to remove seaweeds, and corals then recruit. Variance in the recovery of fishes and corals is not well understood. We show that juveniles of both corals and fishes are repelled by chemical cues from fished, seaweed-dominated reefs but attracted to cues from coral-dominated areas where fishing is prohibited. Chemical cues of specific seaweeds from degraded reefs repulsed recruits, and cues from specific corals that are typical of healthy reefs attracted recruits. Juveniles were present at but behaviorally avoided recruiting to degraded reefs dominated by seaweeds. For recovery, degraded reefs may need to be managed to produce cues that attract, rather than repel, recruiting corals and fishes.

Corals are foundation species, creating the biogenic matrix on which reef structure, function, and biodiversity depend (1, 2). However, corals are in decline. Coral cover has declined by 80% in the Caribbean and 50% throughout the tropical Pacific (3, 4). As corals decline, species-rich and topographically complex reefs transition to flattened, species-poor beds of seaweeds and coral rubble with compromised ecosystem function (1, 5). Once degraded, reefs can recover if the right mix of herbivores recolonizes them to remove seaweeds and facilitate corals (5–9), but this process sometimes fails because of poorly understood feedback mechanisms that facilitate seaweeds and suppress corals (10–13).

Adequate coral cover is essential for producing the topographic complexity that supports reef fishes (2, 7, 11). Loss of corals leads to loss of reef fishes (2). Loss of reef fishes leads to coral decline, because intact fish communities aid coral recovery after coral loss to bleaching, predation, or other disturbances (5, 7, 8). Loss of both fishes and corals is catastrophic for coral reefs, which make up <0.1% of oceanic areas but support 32 of 34

*Corresponding author. mark.hay@biology.gatech.edu.

animal phyla (rainforests support 9); are valued at $29 billion/year for fisheries, tourism, and other uses; and provide critical protein to hundreds of millions of humans (14).

Reef decline is driven by many factors, including overfishing, climate change, disease, pollution, and predation (5, 7), but stresses affecting adult corals are better understood than are processes preventing juvenile recruitment (10–12). Some seaweeds chemically reduce the recruitment and survival of corals for centimeters around seaweed perimeters (15), possibly selecting for coral larvae that use chemical cues to reject seaweed-dominated reefs. If so, recovery could be suppressed by larval behavior, rather than just post-recruitment mortality. Understanding these chemical cues could be critical to developing effective conservation strategies (7, 11), such as protecting producers of positive cues or managing to remove producers of negative cues.

If coral larvae respond to chemical cues of reef quality, they might avoid degraded reefs, thus promoting the stability of seaweed-dominated reefs and preventing coral recovery. The nervous systems of planula larvae display a high level of histological, cytological, and biochemical complexity (16), suggesting that such responses are possible.

We tested the potential role of chemical cues from healthy versus degraded reefs in coral and fish recruitment, using pairs of no-take marine protected areas (MPAs) and adjacent non-MPAs associated with three villages along the coast of Viti Levu, Fiji (fig. S1). Coral cover on hard substrates in the MPAs was 38 to 56% (versus 4 to 16% in non-MPAs), seaweed cover on hard substrates was 1 to 2% (versus 49 to 91% in non-MPAs), and herbivorous fish biomass was 660 to 1615% greater in the MPAs than in fished areas (9). Although we used MPAs and non-MPAs, these reefs may represent functioning coral-dominated versus degraded seaweed-dominated reefs, regardless of the factors creating these divergent communities. Our paired MPAs and degraded reefs were adjacent, on the same continuous reef flat; were oriented similarly; and were exposed to the same oceanic waters, storm swell, and presumably other physical conditions (fig. S1). Our non-MPA reefs have higher seaweed and lower coral cover than many nonprotected reefs, but some unprotected reefs in the Carib-bean (5), Red Sea (17), and Indian Ocean (18) are similar in seaweed and coral cover, and numerous reefs are trending toward the conditions on our non-MPA reefs (3, 4). Thus, the contrasts of juvenile fish and coral behavior toward the divergent reef states we investigated may be informative about some present and numerous future reefs.

Responses of coral larvae

Coral larvae discriminate among environments, as shown by their behavior in response to different waters (19), substrates (20), settlement-inducing crustose coralline algae (21), or biofilms (22). Additionally, some seaweeds chemically suppress the settlement and survival of coral larvae within centimeters of their thalli (15). The low survival of coral recruits at sites occupied by certain competitors (23) suggests that the avoidance of specific competitors by settling larvae could be adaptive. If so, chemically mediated larval behavior could affect recruitment densities and reef resilience.

To test this possibility, we exposed larvae of corals within the genus *Acropora* to cues from divergent environments. Acroporid corals are major providers of topographic complexity,

which is negatively related to algal cover and positively related to fish density, biomass, diversity, and coral recovery after disturbances (2).

We obtained larvae from *Acropora millepora, A. nasuta*, and *A. tenuis* by holding four fertile colonies of each species in separate pools, collecting gametes, facilitating fertilization, collecting embryos, and raising these to competent planula after 6 to 7 days. We evaluated planula preferences for water collected from the centers of MPA versus non-MPA sites using two-channel Atema flumes (24), offering organisms a pairwise choice of each water source flowing at 4.2 mm s^{-1}. A planula was pipetted into the downstream center of the flume, where it swam toward its preferred water source. A 2-min acclimation period was followed by a 3-min testing period in which the planula's position was recorded at 5-s intervals. After 3 min, the planula was removed for 1 min, the water was flushed, the water sources were exchanged from one side to the other, and the test was repeated to ensure that preferences were not biased for one side of the chamber.

All *Acropora* larvae expressed a 558 to 561% preference for MPA over non-MPA water ($P < 0.001$, Fig. 1A); this was consistent across all pairs of MPA versus non-MPA reefs [$P > 0.9$ for among-site contrasts, factorial analysis of variance (ANOVA); table S1]. Thus, their preference was for healthy reefs within MPA sites and was not a location effect. We therefore pooled data for all MPAs versus non-MPAs for subsequent comparisons ($n = 60$ per species, Fig. 1).

To identify the sources of water-borne cues, we hypothesized that larvae might cue to corals and crustose coralline algae (CCA) from healthy reefs or be repelled by seaweeds from degraded reefs. We tested these hypotheses by holding upright seaweeds (20 g), CCA (50 g), or corals (100 g) in 10 liters of MPA- or non-MPA–sourced water for 1 hour (the variable masses were due to density differences among species) and testing the effects of leached cues on the preferences of *A. tenuis* larvae in flumes. Cues from conspecifics were 389% more attractive than cues from a congeneric (*A. millepora*), but cues from a mix of five corals (*Porites cylindrica, Pocillipora damicornis, Montipora digitata, Merulina scabricula, and A. formosa*) were 570% more attractive than an equal mass of the conspecific alone (Fig. 1A). Adding cues from the CCA *Hydrolithon reinboldii* to MPA water increased larval attraction by 800%; the same magnitude of CCA cue added to non-MPA water increased preference by only 184% and did not fully counter larval avoidance of non-MPA water (Fig. 1A). Chemical cues from the common seaweeds *Padina gymnospora, Sargassum polycystum*, and *Galaxaura filamentosa* decreased larval attraction by 28, 81, and 86%, respectively ($P < 0.001$ for all contrasts, Fig. 1A).

In the above assays, larvae responded to cues dissolved in the water. However, known seaweed allelochemicals are lipophilic molecules on algal surfaces that damage corals after contact (25, 26). Using larvae of *A. tenuis*, we evaluated the possibility that such lipids could deter coral settlement if transferred to benthic surfaces. We brushed settlement tiles with five strokes of either CCA, *Padina, Galaxaura*, or *Sargassum* (mimicking contact via wave motion) and compared settlement on these tiles to settlement on control tiles brushed with inert, plastic seaweeds. Paired treatment and control tiles were placed into aquaria ($n = 6$),

10 competent larvae were added to each, and larval settlement was monitored at 2, 6, 12, and 24 hours.

Rubbing tiles with CCA increased settlement by 1600% as compared to control tiles (Fig. 1B), with 70% of all larvae settling within 2 hours and 90% within 24 hours. In contrast, rubbing tiles with *Galaxaura*, which produces allelopathic loliolide derivatives (25), resulted in 0% settlement. Rubbing tiles with *Sargassum* produced no differential effect between treatment and control tiles, but at 12 and 24 hours, 62% [±4.0 SE] and 48% [±3.1] of larvae were still swimming and had delayed settling. Rubbing tiles with *Padina* slightly increased settlement on treatment versus control tiles, but at 12 hours, 47% (±3.3) of larvae were still swimming. The presence of cues from *Sargassum*, *Padina*, or *Galaxaura* suppressed settlement in general ($F_{(3, 16)} = 7.58$, $P = 0.002$, repeated measures ANOVA); after 24 hours in aquaria, only 10% (±0.0) of larvae in CCA treatments had not settled, compared to 33% (±4.2) for treatment with *Padina*, 31% (±6.5) for *Galaxaura*, and 48% (±3.1) for *Sargassum* (Fig. 1B and table S2).

To see whether attraction to cues from MPAs, corals, and CCA, and repulsion by cues from non-MPAs and upright seaweeds, occurred in the field, we established 18 2 × 2 m benthic plots in MPA and non-MPA areas at two villages. From 9 of the 18 quadrats at each site, we removed all upright seaweeds at 2- to 4-week intervals and monitored coral recruits to the natural substrate monthly during the week of the new moon through the November–February recruitment pulse. Juvenile corals fluoresce under black light, so surveys were conducted nocturnally using an ultraviolet filter and black light.

We also erected four T-shaped poles holding eight 15 × 15 cm settling tiles 50 cm above the benthos. Two poles adjoined seaweed removal plots and two adjoined control plots at each location. These tiles evaluated settlement above the benthic boundary layer, where chemical cues from benthic organisms might be reduced. After 6 months, tiles were collected and examined for recruits.

For both the natural benthos and the elevated tiles, there were no effects of village or seaweed removal (table S3). Thus the same patterns occurred in both locations, and larvae were reacting to chemical cues from areas larger than our 4-m^2 removal areas; we therefore pooled results by MPA and non-MPA and ignored location and removal treatment.

Protection status (MPA or non-MPA) had a significant, but opposite, effect on settlement in the field ($P < 0.001$). Corals settled onto the benthos in the MPAs (1.0 ± 0.1/m^2; mean ± 1 SE) but not in the non-MPAs (0 ± 0/m^2; $P < 0.0001$; factorial ANOVA). Settlement onto tiles deployed above the benthos was 4.75 ± 0.4 recruits per tile array (~13/m^2) in the non-MPAs but 0 ± 0 per array in the MPAs ($P < 0.0001$, factorial ANOVA). Thus, larvae occurred in both areas, but in the MPAs they recruited exclusively to the benthos, whereas in the non-MPAs they recruited exclusively to the elevated tiles.

Field recruitment of coral larvae was consistent with laboratory assays. In the non-MPAs where chemical cues from seaweeds would be strong, larvae never settled on the benthos despite occurring there and being competent—as evidenced by their settlement on elevated tiles. In contrast, within the MPA where positive cues from corals and CCA would be

abundant, settlement to the benthos was common, and larvae completely avoided the raised tiles. These opposing patterns indicate that larvae make nuanced decisions regarding the relative attractiveness of substrata in differing environmental contexts and act on these complex decisions despite flow and turbulence in the field. These divergent patterns of settlement could be generated by positive cues in MPAs causing larvae to swim down to explore the bottom in search of additional contact cues (such as CCA) and negative cues in non-MPAs causing larvae to avoid swimming down (thus avoiding the benthos in the non-MPAs), but possibly contacting CCA or stimulatory biofilms on the raised tiles and these being sufficient to induce settlement in this otherwise unappealing environment.

Responses of juvenile reef fishes

Given that juvenile fishes respond to chemical cues from predators, conspecifics, their home reef, and reefs differing in community composition or proximity to terrestrial vegetation (27–30), juveniles might also respond to chemical cues from coral- versus seaweed-dominated reefs. If so, this could compromise healthy reefs as sources for larval export and help explain why seaweed-dominated reefs may fail to recover (5, 7, 10, 11).

Using the paired MPAs and non-MPAs described above, we asked (i) whether juvenile fishes were differentially attracted to chemical cues from coral-dominated MPAs versus seaweed-dominated non-MPAs, (ii) whether attraction varied among fish trophic groups, (iii) whether fishes used chemical cues from sessile species to assess habitat desirability, and (iv) whether densities of new recruits in the field were consistent with predictions from juvenile behavior in flumes.

To test juvenile attraction to MPAs versus non-MPAs, we used 20 recently settled juveniles of each of 15 reef fish species (see Fig. 2 for species) from each MPA and adjacent non-MPA at the three villages. We tested recently settled juveniles instead of larvae because we could acquire more species (yields from light traps were taxonomically limited). Attraction to waters from MPAs versus paired non-MPAs was assessed using flumes as described for corals, except that fish observations were for 2 rather than 3 min because their greater mobility produced faster reactions. Assay species represented six families, including six planktivores (Pomacentrids), two coralivore/invertivores (Chaetodonts), five herbivores (Acanthurids, Siganids, and Labrids), and two predators (a Labrid and an Apogonid; see Fig. 2).

Regardless of species, family, or trophic group, each of the 15 species showed a 432 to 844% preference for water from MPAs versus non-MPAs ($P < 0.001$ for all species; Fig. 2). Juveniles collected from MPAs and non-MPAs exhibited equivalent preferences ($P > 0.10$ for all species), indicating no effect of postsettlement experience and suggesting that these preferences are innate. Additionally, responses to MPA versus non-MPA waters from the "home" MPA did not differ from responses when offered this choice of waters from other MPAs ($P > 0.10$ for all species; table S4).

To evaluate habitat cues, common seaweeds or corals were added to 10 liters of water (50 g of coral or 10 g of seaweed) for 1 hour, the organisms were then removed, and flume assays were run using this water versus equivalent water without the cues (as in the coral assays).

Cues from the common seaweed *S. polycystum* suppressed attraction to MPA water by 65 to 86% (Fig. 3A, *P* < 0.001 for all species). In contrast, cues of the common coral *Acropora nasuta* enhanced attraction to non-MPA water by 107 to 343% for all 15 fishes (Fig. 3B, *P* < 0.001).

We then assessed variance in response to cues from different corals and seaweeds. We hypothesized that the corals most susceptible to stresses would be reliable indicators of healthy reefs, because they would be among the first lost from stressed reefs, and that seaweeds abundant on stressed reefs would be reliable indicators of reef degradation. We selected *Acropora* corals as appropriate sentinels, because they commonly bleach, are favored by coral predators, and are strongly affected by algal competition (25, 31, 32). In contrast, *Porites* corals are more resistant to disturbances (25, 32), and *Pocillopora* corals are susceptible to stresses but often recolonize rapidly after disturbances. These latter genera are found on both healthy and degraded reefs, making them poor predictors of reef quality. Consistent with these hypotheses, chemical cues from *A. millepora* or *A. formosa* were preferred by 313 to 1036% over those from *Porites cylindrica* or *Pocillipora damicornis* (Fig. 4, *P* < 0.001 for all species).

Fishes' responses to different seaweeds also varied. Fishes avoided water containing cues from the seaweeds *S. polycystum* or *Turbinaria conoides*, which are abundant on degraded reefs (6, 12, 33), as compared to water containing cues from *Chlorodesmis fastigiata* or *Hypnea pannosa*, which occur at low abundance on both healthy and degraded reefs (Fig. 4, *P* < 0.001 for all species).

Fishes use visual, auditory, and olfactory cues when selecting settlement sites, but chemical cues should be important because they can extend over long distances, provide directional information, and provide a recent history of the site (24, 28). All 15 fishes distinguished between healthy versus degraded habitats by swimming toward coral and away from seaweed chemical cues (Fig. 3), but this behavior was nuanced (Fig. 4). The stress-sensitive acroporid corals were more attractive than the stress-tolerant *Porites* or the weedy *Pocillopora*, and common seaweeds that dominate herbivore-impoverished reefs (*Sargassum* and *Turbinaria*) were more deterrent than uncommon seaweeds such as *Chlorodesmis* and *Hypnea* that occupy both healthy and degraded reefs (Fig. 4, *P* < 0.001 for all contrasts). The behavior was not biased by postsettlement experiences. Recently settled juveniles from both MPAs and non-MPAs exhibited an equally strong preference for water from coral-dominated as opposed to seaweed-dominated reefs and for specific corals and seaweeds. These preferences appear innate, could strongly affect settlement choice, and should be included in models of dispersal and connectivity (34).

Surveys of recent recruits in each village's MPA and non-MPA during recruitment season documented a 537 to 794% higher density and 80 to 344% greater diversity of recruits on the MPAs versus adjacent fished reefs (Fig. 5). These density differences parallel the degree of preference we found for chemical cues from MPAs in laboratory assays. Additionally, because predators of recruits were 186 to 228% more dense in the MPAs (Fig. 5C), enhanced recruitment in MPAs was not associated with having fewer predators there. However, if predators in non-MPAs were more effective, then postsettlement predation

could confound patterns generated by habitat choice. We tested this possibility by building 30 rubble habitats ~30 cm tall by 30 cm in diameter in each of two villages' MPAs and non-MPAs, stocking each with five marked juveniles of the abundant damselfishes *Chromis viridis* and *Dascyllus aruanus* and monitoring survival each morning, noon, and evening for 3 days. Fifteen equivalent structures were stocked and individually enclosed in 1-cm wire mesh in each location to exclude predators, controlling for migration or other losses unrelated to predation. Survival and retention in cage controls was 100% across all sites. Mortality on uncaged structures was ~20% over 3 days in all sites and did not differ between MPAs and non-MPAs (*P* = 0.67 and 0.77 for *C. viridis* and *D. aruanus*, respectively). Thus, if predation on small juveniles is similar to predation on new recruits, then based on our results, postrecruitment predation appears similar between MPAs and non-MPAs, suggesting that differential recruitment may explain the much greater density of juveniles in the MPAs.

Conclusion

MPAs are established to protect contained communities and to provide larvae for export to aid the recovery of more-degraded habitats (34). However, export to degraded reefs will be constrained if recruits avoid chemical cues from degraded reefs. In some locations, export occurs (35), but in other areas, there is minimal connectivity, even between protected and exploited populations separated by small distances (36). These divergent outcomes could occur if intact reefs export larvae to similar communities but not to degraded, seaweed-dominated communities. The protected and fished areas we studied differ in coral cover, seaweed cover, herbivory rates, and biomass of herbivorous fishes (9). Thus, organisms settling only 100 m apart experience dramatically different environments. Our findings suggest that once degradation passes some critical but as yet undetermined threshold, recruit behavior may constrain the value of healthy reefs as larval sources for populations in degraded habitats.

To produce the desired connections between healthy reefs as a source of larvae and degraded reefs as targeted settlement sites where recruitment can promote reef resilience, managers will have to suppress the chemical barrier produced by seaweeds and enhance the chemical "call" of corals and CCA. A promising strategy could be to reduce the harvest of critical species of herbivorous fishes beyond MPA borders. Feeding by specific mixes of these fishes can remove seaweeds, enhance CCA, enhance corals (6, 9, 12, 33), and replace chemical cues of degradation with chemical stimulants for recruitment.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

REFERENCES AND NOTES

1. Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. Proc Biol Sci. 2009; 276:3019–3025. [PubMed: 19515663]

2. Graham NAJ, Nash KL. Coral Reefs. 2013; 32:315–326.

3. Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. Science. 2003; 301:958–960. [PubMed: 12869698]

4. Bruno JF, Selig ER. PLOS ONE. 2007; 2:e711. [PubMed: 17684557]

5. Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. Trends Ecol Evol. 2010; 25:633–642. [PubMed: 20800316]

6. Burkepile DE, Hay ME. Proc Natl Acad Sci USA. 2008; 105:16201–16206. [PubMed: 18845686]

7. Mumby PJ, Steneck RS. Trends Ecol Evol. 2008; 23:555–563. [PubMed: 18722687]

8. Cheal AJ, et al. Coral Reefs. 2010; 29:1005–1015.

9. Rasher DB, Hoey AS, Hay ME. Ecology. 2013; 94:1347–1358. [PubMed: 23923498]

10. Wilson SK, et al. Conserv Biol. 2012; 26:995–1004. [PubMed: 22971046]

11. Nyström M, et al. Ecosyst. 2012; 15:695–710.

12. Hughes TP, et al. Curr Biol. 2007; 17:360–365. [PubMed: 17291763]

13. Cheal AJ, Emslie M, MacNeil MA, Miller I, Sweatman H. Ecol Appl. 2013; 23:174–188. [PubMed: 23495645]

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

15. Kuffner IB, Paul VJ. Coral Reefs. 2004; 23:455–458.

16. Watanabe H, Fujisawa T, Holstein TW. Dev Growth Differ. 2009; 51:167–183. [PubMed: 19379274]

17. Benayahu Y, Loya Y. Bull Mar Sci. 1981; 31:514–522.

18. McClanahan TR, Arthur R. Ecol Appl. 2001; 11:559–569.

19. Gleason DF, Danilowicz BS, Nolan CJ. Coral Reefs. 2009; 28:549–554.

20. Golbuu Y, Richmond RH. Mar Biol. 2007; 152:639–644.

21. Harrington L, Fabricius K, De'ath G, Negri A. Ecology. 2004; 85:3428–3437.

22. Tebben J, et al. PLOS ONE. 2011; 6:e19082. [PubMed: 21559509]

23. Arnold SN, Steneck RS. PLOS ONE. 2011; 6:e28681. [PubMed: 22194883]

24. Atema J, Kingsford MJ, Gerlach G. Mar Ecol Prog Ser. 2002; 241:151–160.

25. Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. Proc Natl Acad Sci USA. 2011; 108:17726–17731. [PubMed: 22006333]

26. Andras TD, et al. J Chem Ecol. 2012; 38:1203–1214. [PubMed: 23108534]

27. Dixson DL, Pratchett MS, Munday PL. Anim Behav. 2012; 84:45–51.

28. Leis JM, Siebeck U, Dixson DL. Integr Comp Biol. 2011; 51:826–843. [PubMed: 21562025]

29. Lecchini D, Waqalevu VP, Parmentier E, Radford CA, Banaigs B. Mar Ecol Prog Ser. 2013; 475:303–307.

30. Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V. Proc Natl Acad Sci USA. 2007; 104:858–863. [PubMed: 17213323]

31. Baird AH, Pratchett MS, Hoey AS, Herdiana Y, Campbell SJ. Coral Reefs. 2013; 32:803–812.

32. Pratchett MS, McCowan D, Maynard JA, Heron SF. PLOS ONE. 2013; 8:e70443. [PubMed: 23922992]

33. Lewis SM. Ecol Monogr. 1986; 56:183–200.

34. Sale PF, et al. Trends Ecol Evol. 2005; 20:74–80. [PubMed: 16701346]

35. Harrison HB, et al. Curr Biol. 2012; 22:1023–1028. [PubMed: 22633811]

36. Palumbi SR. Annu Rev Environ Resour. 2004; 29:31–68.
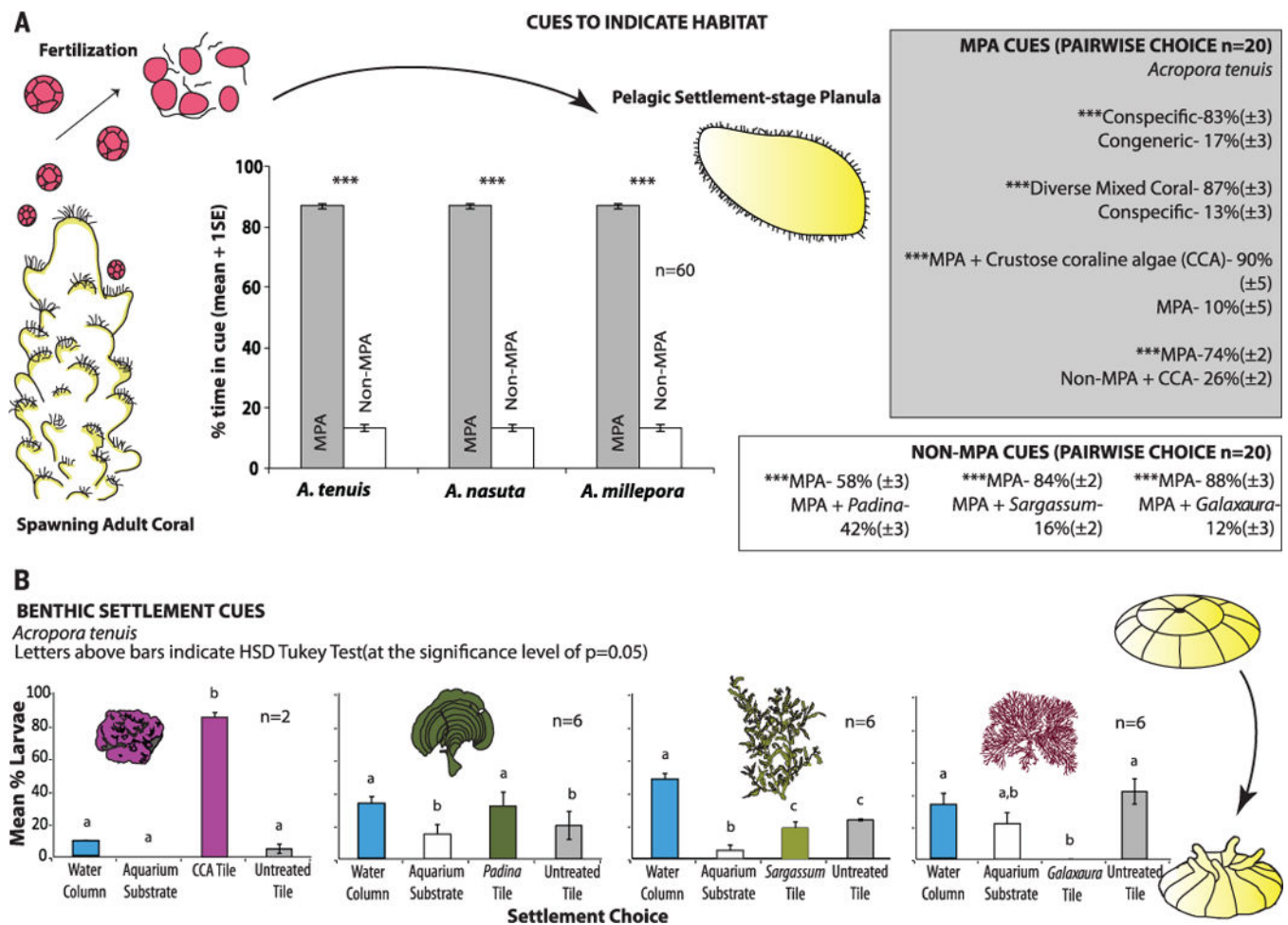
Fig. 1. Influence of chemical cues on coral larvae
(**A**) Larval tracking in a flume and (**B**) larval behavior when offered differently treated substrates. *** indicates $P < 0.001$ via the Kolmogorov-Smirnov test. Letters above bars indicate significant groupings by ANOVA and post-hocTukey test at 24 hours.
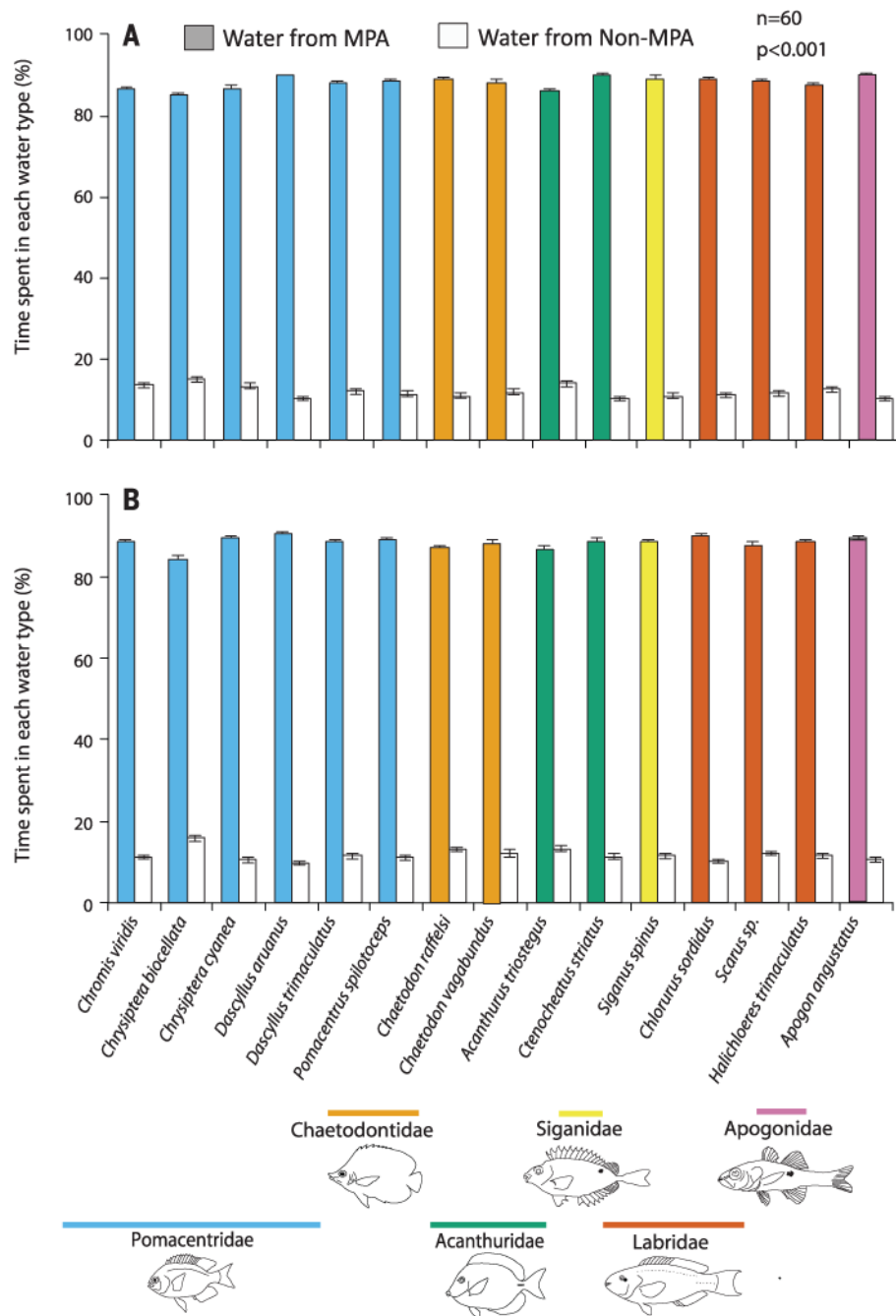
Fig. 2. Attraction of fishes to waters from MPA versus non-MPA areas as a function of fish collection site

(**A**) MPAs, (**B**) Non-MPAs. $n = 60$ independent juvenile fish for each bar. Families are grouped by color below species names. $P < 0.001$ for all contrasts.
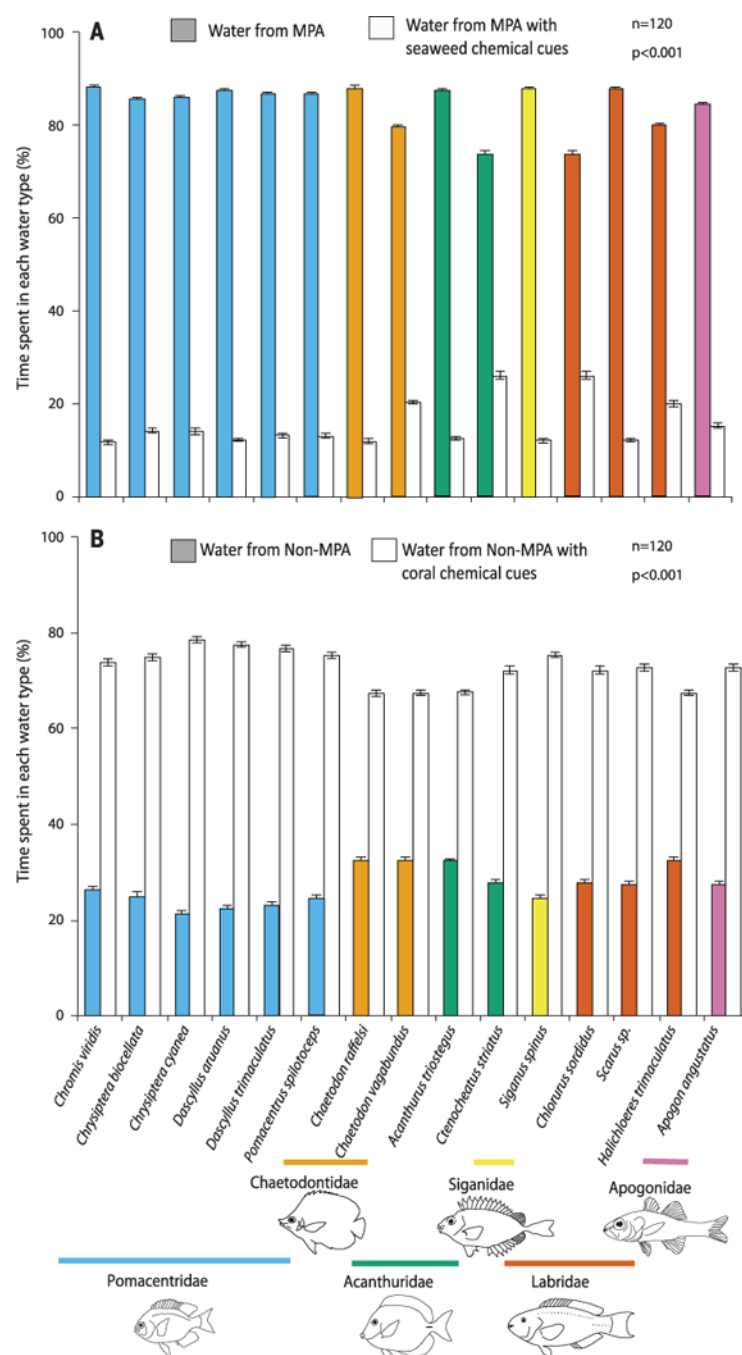
Fig. 3. Effects of seaweed or coral chemical cues on the behavior of recently settled fishes
(**A**) Effects of the seaweed *S. polycystum* and (**B**) the coral *A. nasuta*. $n = 120$ independent juvenile fish for each bar; $P < 0.001$ for all contrasts.
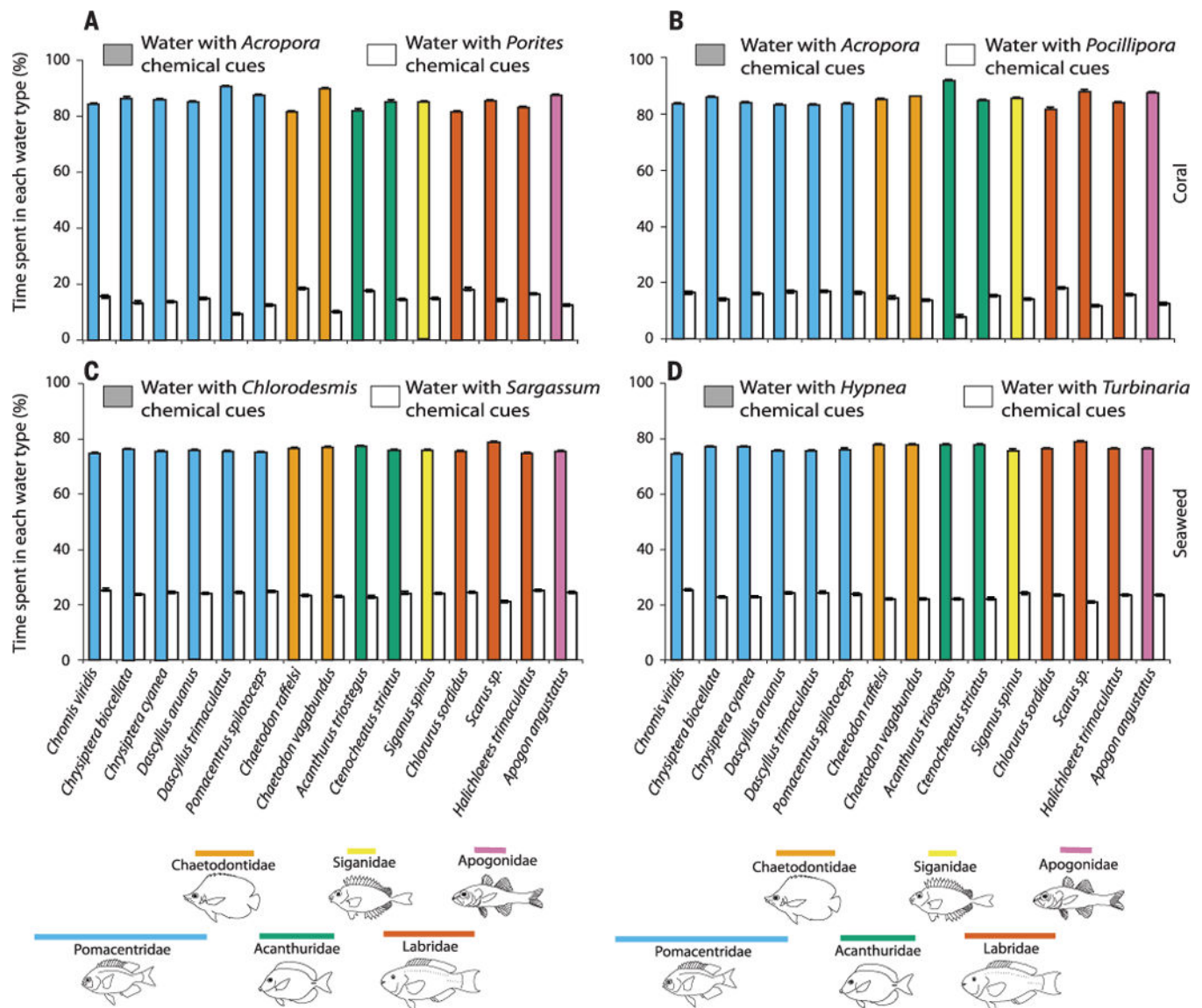
Fig. 4. Effects of chemical cues from different corals or seaweeds on fish behavior
(**A**) *A. millepora* versus *Porites cylindrica*, (**B**) *A. formosa* versus *Pocillipora damicornis*,
(**C**) *Chlorodesmis fastigiata* versus *S. polycystum*, or (**D**) *Hypnea pannosa* versus *Turbinaria conoides*. $n = 120$ independent juvenile fish for each bar; $P < 0.001$ for all contrasts.
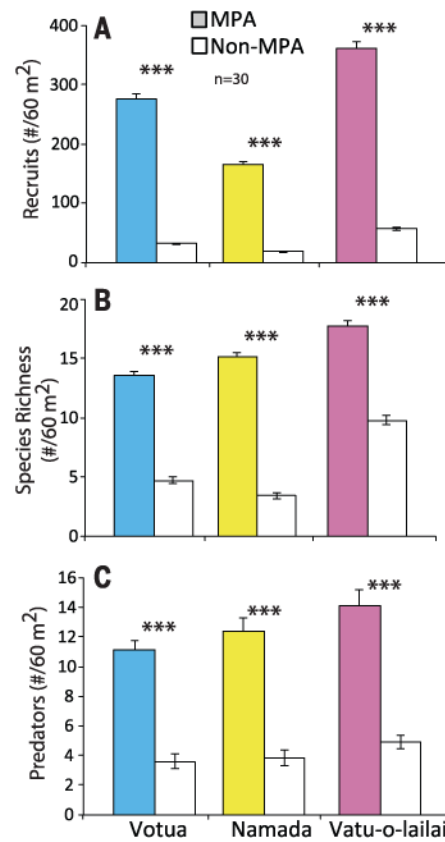
Fig. 5. Density and species richness of fish recruits, and density of predators, in MPAs and non-MPAs

(**A**) Density (±SE) and (**B**) species richness of recruits. (**C**) Density of predators. $n = 30$ transect per site. $P < 0.001$ for all contrasts