

Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance

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Abstract Removing predatory fishes has effects that cascade through ecosystems via interactions between species and functional groups. In Kenyan reef lagoons, fishing-induced trophic cascades produce sea urchin-dominated grazing communities that greatly reduce the overall cover of crustose coralline algae (CCA). Certain species of CCA enhance coral recruitment by chemically inducing coral settlement. If sea urchin grazing reduces cover of settlement-inducing CCA, coral recruitment and hence juvenile coral abundance may also decline on fished reefs. To determine whether fishing-induced changes in CCA influence coral recruitment and abundance, we compared (1) CCA taxonomic compositions and (2) taxon-specific associations between CCA and juvenile corals under three fisheries management systems: closed, gear-restricted, and open-access. On fished reefs (gear-restricted and open-access), abundances of two species of settlement-inducing CCA, *Hydrolithon reinboldii* and *H. onkodes*, were half those on closed reefs. On both closed and fished reefs,

juveniles of four common coral families (Poritidae, Pocilloporidae, Agariciidae, and Faviidae) were more abundant on *Hydrolithon* than on any other settlement substrate. Coral densities were positively correlated with *Hydrolithon* spp. cover and were significantly lower on fished than on closed reefs, suggesting that fishing indirectly reduces coral recruitment or juvenile success over large spatial scales via reduction in settlement-inducing CCA. Therefore, managing reefs for higher cover of settlement-inducing CCA may enhance coral recruitment or juvenile survival and help to maintain the ecological and structural stability of reefs.

Keywords Trophic cascades · Crustose coralline algae · Coral settlement · Early life history · *Hydrolithon* · Sea urchins

Introduction

Factors and processes affecting recruitment have major consequences for the adult distributions and abundances of species whose life histories involve an early dispersal phase followed by a sessile or sedentary adult phase. Settlement is a critical part of the recruitment process, representing the culmination of pre-settlement reproductive and dispersal processes (Birrell et al. 2008). For benthic marine organisms, larval settlement onto substrata and their subsequent metamorphosis constitute one of the most vulnerable periods of the life cycle (Vermeij and Sandin 2008; Pineda et al. 2009); subsequent juvenile survival may also be perilous but is likely to improve with increasing age and size.

Settlement and metamorphosis of many marine larvae are induced by biological, chemical, or environmental stimuli (Morse et al. 1988). Many diverse taxa (including

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sea urchins, abalones, scleractinian corals, and octocorals) appear to have similar mechanisms for induction of larval settlement based on chemosensory recognition of particular chemical cues from crustose coralline algae (CCA) or their associated bacterial biofilms (Morse and Morse 1996). CCA form thin calcareous sheets on reef substrates and have been among the most abundant and widespread hard substrata in marine photic zones for many millions of years (Littler et al. 1995).

The distributions of scleractinian corals can be influenced by larval habitat selection (Raimondi and Morse 2000). For many corals, encountering an appropriate settlement-inducing CCA is the trigger that induces settlement (Morse et al. 1988; Heyward and Negri 1999). Some coral species will not settle in the absence of settlement-inducing CCA, and others can delay metamorphosis for up to 30 days in the absence of a chemical cue from either CCA or their bacterial biofilms (Morse and Morse 1991). Members of three diverse coral families (Acroporidae, Faviidae, and Agariciidae) have similar chemosensory signal recognition systems responding to similar CCA morphogens (Morse et al. 1996). CCA recognition is associated with both reproductive modes found in corals: brooding and broadcast spawning (Morse et al. 1994; Morse and Morse 1996; Raimondi and Morse 2000; Harrington et al. 2004). CCA abundance may also be correlated with post-settlement coral survival because CCA may be indicators of appropriate light, water motion, or water quality for corals (Fabricius and De'ath 2001), and because CCA can exclude other space competitors. However, McClanahan (2005) found that corals transplanted to CCA-dominated habitat suffered higher mortality through grazing than those transplanted to non-CCA habitats.

Not all CCA induce coral settlement, and some CCA species are inappropriate substrates because they can overgrow live corals or because epithallial sloughing can remove recruits (Harrington et al. 2004). Further, not all corals require CCA for induction of settlement and metamorphosis: bacterial biofilms alone can induce settlement for some corals, including the widespread and common *Pocillopora damicornis* (Negri et al. 2001; Webster et al. 2004). While the ability of some CCA to induce settlement and metamorphosis of individual scleractinian larvae is well documented (especially in laboratory settings), it remains largely unknown whether CCA facilitate coral recruitment over large spatial scales or whether CCA abundance and distribution patterns are useful predictors of successful coral recruitment.

If settlement-inducing CCA are an important determinant of coral recruitment, predicting successful recruitment requires knowledge of the factors affecting these CCA. On Kenyan reefs, fishing induces trophic cascades that change the dominant grazers from fishes to sea urchins

(McClanahan 1997; McClanahan et al. 2008) and, as a consequence of urchin grazing, the cover of CCA is very low on open-access (fished) reefs (<5% cover) compared to closed reefs (>20% cover; O'Leary and McClanahan 2010). In addition to altering CCA cover, the different effects of fish and sea urchin grazing may also affect CCA taxonomic composition. CCA taxa with thicker thalli (>200 μm) can withstand deep, infrequent bites of large herbivorous fish (e.g., parrotfish with an average bite depth of 290 μm ; Woelkerling et al. 1993), but not the frequent grazing of sea urchins (Steneck 1986). Conversely, thin CCA taxa (<200 μm) can better withstand frequent, shallow bites of sea urchins (average bite depth of 90 μm ; Steneck 1986), but not the deep bites of fishes. Hence, if settlement-inducing CCA also have thick thalli, they may be disproportionately harmed by sea urchin grazing on fished reefs.

Fisheries management traditionally considers only the species targeted by the fishery, but the consequences of fishing are often complex, indirect, likely to cascade through high-diversity ecosystems, and difficult to predict (Polis and Strong 1996). Knowing how trophic-level interactions affect the abundances and taxonomic composition of CCA, along with a more thorough understanding of coral-CCA relationships, should lead to better predictions of coral recruitment and juvenile success under different fisheries management systems. We build on previous experimental work that demonstrated that predation of sea urchins by fishes in areas closed to fishing results in greater CCA cover (O'Leary and McClanahan 2010). We hypothesize that coral recruitment will be higher on closed reefs due in part to the enhanced CCA cover, assuming that settlement-inducing CCA respond positively to closures and that corals respond strongly to settlement-inducing CCA. To explore this hypothesis, we quantified the abundances and taxonomic compositions of CCA and juvenile corals under three management systems in the back-reef lagoons of coastal Kenya. Our specific objectives were to determine whether (1) taxonomic composition of CCA is influenced by fisheries management practices, (2) the relative strengths of associations between corals and CCA differ among coral families and CCA taxa, and (3) large-scale patterns of juvenile coral abundance can be attributed (at least partially) to patterns of CCA distribution.

Materials and methods

Study sites

The Kenyan reef system consists of an extensive back-reef lagoon, protected by fringing reefs, along 250 km of coastline from Malindi in the north to the Tanzanian border

in the south (Fig. 1; McClanahan and Arthur 2001). In most areas, the back-reef lagoon is <2 m deep at low tide, with a 4-m tidal range during spring tides (Brakel 1982). Within the Kenyan reef system, there are four well-enforced fisheries closures (the Malindi, Watamu, Mombasa, and Kisite marine protected areas; Fig. 1) where all fishing had been successfully prohibited for more than 15 years prior to this study. Fish biomass in these closures is two orders of magnitude greater than on open-access, fished reefs (McClanahan et al. 2007). On closed reefs, surgeonfish (Acanthuridae) and parrotfish (Scaridae) account for most algal grazing, and a triggerfish, *Balistapus undulatus*, is the dominant predator of sea urchins (McClanahan 2000). On open-access reefs, nine sea urchin species are the main grazers, and their total biomass is two orders of magnitude higher than on closed reefs, due to the absence of predatory fishes (McClanahan 1997, 2008). Adjacent to each fisheries closure, there is a gear-restricted zone (or reserve) where certain types of fishing are excluded. Gear-restricted zones allow artisanal fishing using such traditional methods as hook and line, traps, and gill nets of <4 in (10.2 cm) mesh size while excluding spear guns and beach seines (Lambo and Ormond 2006), but these restrictions are not well enforced. CCA cover has not previously been evaluated on gear-restricted reefs.

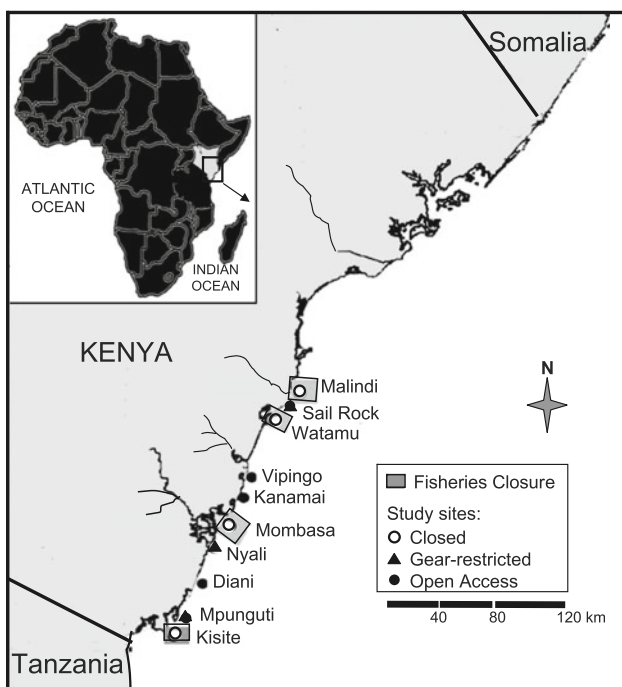


Fig. 1 Locations of study reefs along the Kenyan coastline. Gear-restricted zones are immediately adjacent to the closed reefs (marine protected areas)

CCA surveys

CCA cover and taxonomic composition were surveyed between November 2006 and April 2007 on 3–4 reefs within each of the three management systems: open-access (Vipingo, Kanamai, and Diani), gear-restricted (Sail Rock, Nyali, and Mpunguti), and fisheries closures (Malindi, Watamu, Mombasa, and Kisite; Fig. 1). On each reef, CCA cover (%) was quantified along three 10-m line-intercept transects, except for Watamu, a small closed reef where only one transect was completed. Transects were parallel to the coastline and at least 50 m apart. While the 10-m transect length was a straight line, CCA cover was measured following the surface rugosity beneath that line and included substratum below and on the underside of ledges. The length (in cm) of each CCA plant's intercept with the transect line was recorded, and its morphology was noted. The cover of CCA was calculated as a percentage of total hard substrate by dividing the total CCA length (per transect) by the contour transect length, including the vertical rugosity plus lengths of overhanging surfaces, but excluding any soft substrata such as sand or rubble. Transects were averaged to obtain a single percent cover value for CCA for each reef.

CCA percent cover data met assumptions of normality and homogeneity of variances and were analyzed in a two-way ANOVA comparing differences in percent cover of CCA among management systems, with CCA percent cover as the dependent variable, and management and site nested within management as independent variables. The ANOVA was followed by Tukey's honestly significant difference (HSD) tests to assess pair-wise comparisons among management systems (open-access, gear-restricted, or closed) with reefs ($n = 9$; three reefs in each management system) as replicates. We also compared the total available space for coral settlement across reefs by summing the percent cover of bare, turf-dominated, and CCA substrates for each reef. After checking for data normality, we analyzed differences in the total percent cover of these potential settlement substrates among management systems in a two-way ANOVA as above, with percent cover as the dependent variable and management and site nested within management as independent variables.

CCA identification

Because external morphology is rarely diagnostic, CCA are very difficult to identify in the field. Therefore, we used a sequence of field and laboratory observations to identify CCA. We began by collecting a small piece (using a hammer and chisel) from each visually distinguishable CCA plant encountered along the CCA abundance transects. Each CCA length was treated independently: even if

a section of CCA appeared to be the same morphotype as one previously sampled, we repeated the full procedure to avoid taxonomic mistakes. A total of 1,896 CCA specimens were collected and air-dried for subsequent laboratory examination.

We examined the external morphology of each sample under a 25× hand-held microscope. Based on color, texture, and conceptacle size, shape, and spacing (the only characters visible in hand specimens), we initially recognized 50 groups that appeared morphologically distinct. After assigning every specimen to a group, we calculated the cumulative length (summed along all transects) of CCA within each of the 50 morphological groups. We then selected the 20 commonest morphological groups, defined as those covering at least 1 m over all of the transects, and which collectively represented >85% of total CCA cover. From each of the 20 groups, we haphazardly selected 8 specimens for further microscopic study. Each of these specimens was identified to the lowest taxonomic level possible (usually species) by examining whole specimens and petrological thin sections first under a Leica MZ12 stereomicroscope and then with an Environmental Electron Scanning Microscope (FEI Quanta 400).

Eleven species were identified among the 160 specimens subjected to detailed microscopic analysis. Nine of the 20 morphological groups contained multiple CCA taxa and hence were taxonomically uninformative and were excluded from further analyses. The remaining 11 morphological groups examined were deemed internally consistent: 7 groups were taxonomically uniform (all 8 specimens were identical); and the other 4 had at least 6 (of 8) specimens

from the same taxon. We restricted subsequent analyses to these 11 morphological groups. Since some of these 11 groups were also taxonomically identical, they condensed into 5 consistently identifiable CCA taxa (Table 1) that accounted for 60% of all coralline algal cover and were found in all management regimes. Four of these consistently identifiable CCA contained a single species, while the fifth consisted of two species of *Hydrolithon*.

CCA community composition

The program PRIMER 6 was used for a multivariate analysis to evaluate differences in CCA abundance among management systems and to determine which CCA taxa were driving any differences. After calculating a Bray–Curtis similarity matrix, we determined whether CCA taxa differed among the management systems using a nested analysis of similarities (ANOSIM) with two factors: management system and site (nested within management). If management was significant in the nested ANOSIM, we used a similarity of percentages (SIMPER) analysis to determine the contribution of each CCA taxon to the differences among management systems.

Coral recruitment

Because it is very difficult to detect newly settled coral recruits (≤ 1 mm) in the field, we treated juvenile corals as proxies for recruits. We defined proxy recruits as juvenile corals ≤ 30 mm diameter. In Kenya, corals (Poritidae and Pocilloporidae) settled and grew to 30+ mm on artificial substrata immersed for 6–9 months (J.O. pers. obs.), so we assumed that juveniles <30 mm are probably recruits less than 1 year old. We searched for juveniles using 30-min searches of exposed and cryptic habitats in six 5 × 5 m areas on each of nine reefs (excluding Watamu, the small, closed reef) between November 2008 and December 2008. Searched areas were in the center of coral-dominated habitat, were ~100 m apart, and were arrayed parallel to the reef crest. Because juvenile corals often lack morphological features associated with adult colonies, digital images were taken in the field for subsequent identification, which was based primarily on corallite structure. Each juvenile was measured and identified to genus.

Coral–substrate associations

To determine the probable substrate on which each juvenile coral had settled, we recorded substrates surrounding and touching the edges of each coral. Although many sessile organisms (e.g., sponges, anemones, soft corals, fleshy

Table 1 The eleven CCA taxa among the 168 specimens identified to species

<i>Hydrolithon</i> spp. (<i>H. reinboldii</i> and <i>H. onkodes</i> ⁺)*
<i>Neogoniolithon fosliei</i> *
<i>Pneophyllum conicum</i> *
<i>Spongites yendoii</i> *
<i>Mastophoroid</i> sp.
<i>Lithophyllum insipidum</i>
<i>Lithophyllum kotschyianum</i> *
<i>Lithophyllum pustulatum</i>
<i>Leptophytum ferox</i>
<i>Mesophyllum funafutiense</i>

* Indicates the 5 CCA taxa identified consistently in field surveys and used in analyses

⁺ The species *onkodes* was transferred to *Hydrolithon* by Penrose and Woelkerling (1992). Most publications treat the species as *H. onkodes*. However, this year, based on molecular phylogenetics, Kato et al. (2011) have suggested that the species might be within the genus *Porolithon*. This change has not yet been made, so we have used the Penrose and Woelkerling (1992) taxonomy

algae) surrounded the corals, we only recorded substrates suitable for coral settlement, that is, CCA, bare carbonate rock, and carbonate rock with algal turf. Because more than one potential settlement substrate often touched a coral, suitable substrate types were weighted as follows: if only one suitable substrate touched the coral (regardless of any non-suitable substrates present), it received a weighting of 1; if two suitable substrates touched the coral, each substrate received a weighting of 0.5; if all three suitable substrates touched the coral, each received a weighting of 0.333. In every case where a CCA touched a juvenile coral, a small CCA sample ($\sim 1 \text{ cm}^2$ in size) was collected for laboratory identification of species via the thin section protocol described above.

The availability of substrates suitable for coral settlement (CCA, bare, and turf) on each reef was assessed using three 10-m line-intercept transects in the center of coral-dominated habitat and spaced 50 m apart. The relative abundance of each suitable substrate was calculated by dividing the percent cover of each substrate by the sum of the cover of all suitable substrates.

To determine whether juvenile corals were associated with CCA substrate in general, or with specific CCA taxa, we used a series of χ^2 analyses to compare the observed numbers of juveniles associated with each substrate to the numbers that would be expected on that substrate if settlement were random. The expected numbers for each substrate were calculated by multiplying the total number of observed juvenile corals (across all substrates) by the proportional abundance of that substrate. If the χ^2 test was significant, 95% confidence intervals were calculated to determine which categories were different, using Systat 12 and methods described by Bailey (1980). When data were compared by coral family and among the five CCA taxa, there were cases in which the expected number of juveniles on some substrates was <5 , so χ^2 tests were inappropriate. In these cases, data were graphed to show patterns, but no statistical analyses were done.

We grouped juvenile coral abundances in three ways for separate χ^2 analyses. First, to determine whether associations of juveniles with substrates were non-random, we compared the observed with the expected numbers of juveniles on each suitable substrate (bare, CCA, turf-dominated) for (a) all corals combined and (b) separately for each of the four most abundant coral families (Poritidae, Pocilloporidae, Agariciidae, and Faviidae). Second, to assess whether observed associations with substrate reflected larval preferences for pre-existing substrates at settlement or reflected later (post-settlement) establishment of those substrates, juvenile corals were assigned to four size classes (indicative of increasing age): 1–5, 6–10, 11–20, and 21–30 mm. If substrates surrounding juveniles did not change as the corals aged, patterns of coral–

substrate association should remain similar from the smallest to the largest size class. Third, we compared the observed with the expected numbers of recruits associated with the five consistently identifiable CCA taxa for (a) all juvenile corals and (b) separately for each of the four most abundant coral families.

Corals may not recruit to different reef sites from a well-homogenized larval pool and may not suffer identical post-recruitment survival across sites. Therefore, we also analyzed the observed and expected distributions of juvenile corals at each of nine sites (three from each management regime), first with each suitable settlement substrate (bare, CCA, and turf; Electronic Supplemental Material, ESM Appendix Fig. 1) and then with the five consistently identifiable CCA taxa (ESM Appendix Fig. 2). If results are similar across sites, it indicates that, regardless of environmental or other potential ecological differences between sites, juvenile corals responded consistently to substrate availability.

Juvenile coral density

We quantified densities of juvenile corals (≤ 30 mm) in 48–60 quadrats (each 0.33 m^2) on each of nine reefs (all except Watamu) between December 2009 and March 2010. The number of quadrats was proportional to the extent of hard substrate on the reef. Quadrats were placed haphazardly by throwing the quadrat along the reef, parallel to the shore, with 5–10 m between quadrats. To minimize possible bias, the observer (J.O.) throwing the quadrats stood in waist-deep water, was unable to see the bottom and had no visual references for where the quadrat landed. Quadrats with more than 1/3 of the area on non-hard substrata were re-thrown. Each juvenile coral found was identified to genus using the method described above.

Juvenile densities were averaged for each reef. After square-root transformation to meet assumptions of normality and homogeneity of variances, densities under each management system were compared in a one-way ANOVA, using reefs as replicates. The ANOVA was followed with pair-wise comparisons of management systems (open-access, gear-restricted, and closed) using Tukey's honestly significant difference (HSD) tests. Because there were no differences in densities between open-access and gear-restricted reefs, these management systems were grouped as "fished." We then asked whether the density of each coral family responded in similar or different directions in the management systems. We did this in a two-way ANOVA with log-transformed densities as the dependent variable and with management (closed/fished) and family as the independent variables. A significant interaction term would indicate that the densities of coral families changed in different directions.

Factors affecting juvenile coral densities

Where densities differed among management systems, we evaluated two factors that might contribute to these differences: the abundance of the settlement-inducing CCA, *Hydrolithon*, and grazing by sea urchins. Sea urchin grazing may influence coral recruitment by altering post-settlement survival, either negatively (via feeding or bioerosion) or positively (via removal of competing fleshy algae).

We used data on sea urchin density and biomass from 2007 to 2009 obtained during an independent annual monitoring program, using methods described in McClanahan and Shafir (1990), and based on 9 to 18 non-overlapping, 10 m radius, circular areas per reef. The center of each area was determined haphazardly by tossing a weight. Biomass (kg/m^2) of each of 9 urchin species was estimated by multiplying the average density by the average wet weight of 20–200 haphazardly selected individuals per species (depending on abundance). Biomass samples were collected only on open-access reefs because urchin sizes did not differ greatly among reefs (T.M. pers obs). The biomass of all urchin species was summed and average sea urchin biomass per reef calculated.

We used urchin biomass rather than counts because urchin size is important in determining bioerosion rates (O’Leary and McClanahan 2010). Urchin data were available for three closed reefs (Malindi, Mombasa, and Kisite) and five fished reefs (Vipingo, Kanamai, Diani, Nyali, and Mpunguti). Since juvenile coral densities were surveyed between December 2009 and March 2010, and because they had likely settled within the last year (based on size ≤ 30 mm, and observed growth nearby), we used the average sea urchin biomass from 2008 to 2009 in most analyses, except for Mpunguti (fished), which had sea urchin data only for 2007. Data on cover of *Hydrolithon* spp. were collected between November 2006 and April 2007 during the CCA abundance surveys (above), and a year before the likely settlement of most coral recruits. However, these data should be reliable since we previously demonstrated that year to year fluctuations in CCA cover are small in the absence of strong El Niño Southern Oscillation warming (O’Leary and McClanahan 2010). There were no strong ENSO effects or distinct changes in CCA cover over the course of this study (T.M. pers obs).

To determine whether *Hydrolithon* cover was correlated with juvenile coral densities, after accounting for effects of sea urchin grazing, we used a multiple linear, non-sequential regression model with juvenile coral density as the dependent variable, *Hydrolithon* cover and sea urchin biomass as independent variables, and reefs as replicates (for the eight reefs listed above with sea urchin data available). All data were square-root transformed to meet assumptions of normality. We also did a second linear

regression to test for correlations between juvenile density (dependent variable) and *Hydrolithon* (independent variable) on the three closed reefs where *Hydrolithon* is relatively abundant. While a sample size of three gives very low power, a strongly significant effect is interpretable despite the low power (Quinn and Keough 2002). We did not include sea urchin biomass in this second analysis because the number of reefs (the replicates) was too low to allow enough degrees of freedom, and because sea urchin abundances are uniformly low on closed reefs in Kenya.

Results

CCA surveys

The overall percent cover of CCA was significantly different among management systems (Fig. 2; ANOVA $df = 2,16$, $F = 10.10$, $P = 0.001$) and by site within management system (ANOVA $df = 6,16$, $F = 2.90$, $P = 0.04$). In pairwise comparisons, CCA cover on open-access and gear-restricted reefs did not differ significantly from each other (Tukey’s HSD $P = 0.26$), but closed reefs had significantly higher CCA cover than both open-access and gear-restricted reefs (Tukey’s HSD $P = 0.002$ and 0.02 , respectively). CCA cover in fisheries closures was 2.7 times that of the fished (open-access and gear-restricted) reefs.

In contrast to the results for CCA cover, we did not find significant differences among management systems in overall available settlement substrate (bare, turf-dominated, and CCA cover combined; ANOVA, $df = 2,16$, $F = 1.15$, $P = 0.89$) or by site within management system (ANOVA $df = 6,16$; $F = 0.69$, $P = 0.66$).

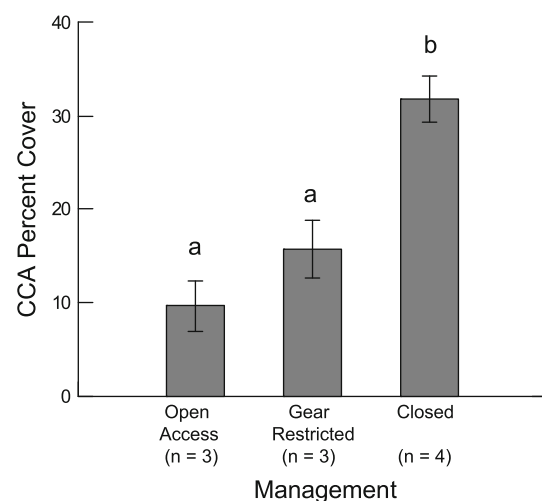


Fig. 2 Percent cover of CCA substrate (\pm SD) on reefs under three management systems. n = number of reefs surveyed. Letters above bars indicate significant differences

Table 2 SIMPER analyses (following nested ANOSIMs) comparing CCA abundances between closed and fished management systems

Taxa	CCA (%)		Contribution to differences (%)	Dissimilarity/SD
	Fished	Closed		
<i>Hydrolithon</i> spp.	2.9	7.3	36.5	1.2
<i>N. fosliei</i>	0.6	5.2	30.9	1.3

Only those taxa that contributed more than the expected amount to differences are shown

CCA identification

There were eleven taxa identified among the 160 CCA specimens subjected to laboratory analysis, and five of these were consistently identifiable in the field: four to species and to one genus, *Hydrolithon*, with two species (Table 1). Four of the taxa were identified with 100% accuracy and *Hydrolithon*, the one taxon identified to genus, was identified with 85% accuracy. These five taxa accounted for 60% of the total CCA cover across the three management systems. Among these five taxa, the two *Hydrolithon* species and *Neogoniolithon fosliei* have relatively thick thalli (>200 μm), while *Pneophyllum conicum* and *Spongites yendoi* have thin thalli (<200 μm). *Lithophyllum kotschyianum* typically branches, but it occurred only as thin crusts with small protuberances in our surveys.

CCA composition

In the nested ANOSIM analysis, percent cover of the five consistently identifiable CCA taxa differed significantly between sites within management systems ($P = 0.002$) and between management systems ($P = 0.028$). Closed reefs differed from both open-access and gear-restricted reefs (ANOSIM pair-wise tests, $P = 0.001$ and 0.005 , respectively), but open-access and gear-restricted reefs did not differ ($P = 0.2$). Therefore, the two fished management types (open-access and gear-restricted) were pooled for the subsequent SIMPER analysis. Differences between the closed and fished reefs were due mainly to differences in cover of the two thicker taxa (Table 2), *Hydrolithon* spp. and *Neogoniolithon fosliei*, which were 2.3 \times and 8 \times more abundant, respectively, on closed than on fished reefs (Fig. 3).

Coral recruitment

Coral–substrate associations

A total of 427 juveniles, from 9 scleractinian families and 1 hydrozoan coral family, were recorded in surveys of

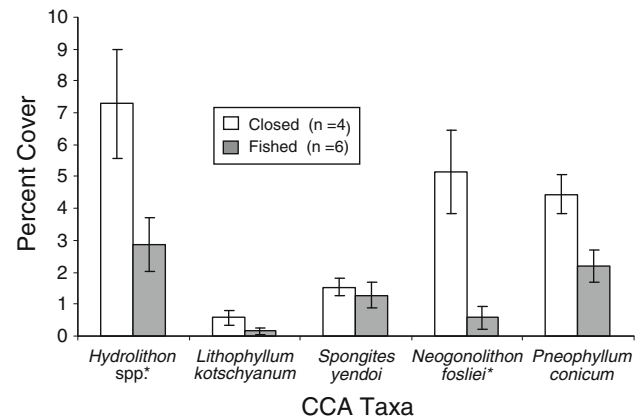


Fig. 3 Percent cover (\pm SD) of identifiable CCA taxa on fished and closed reefs. *Taxa that contributed most to driving differences in CCA cover between management systems (see Table 2)

coral–substrate associations (Table 3). All but two of the poritids were *Porites*, and all agaricids were *Pavona*. Most pocilloporid juveniles were *Pocillopora* (70%), with some *Stylophora* (21%) and *Seriatopora* (7%). Juvenile faviids included seven identifiable genera (*Cyphastrea*, *Echinopora*, *Favia*, *Favites*, *Goniastrea*, *Platygyra*, and *Plesiastrea*).

Percent covers of the three substrates suitable for settlement, averaged across all reefs, were turf ($28.3 \pm 2.3\%$ SD), bare ($11.4 \pm 1.7\%$), and CCA ($10.7 \pm 1.9\%$). Based on these values, we calculated the relative availability of suitable substrates as turf (0.561), bare (0.226), and CCA (0.213), and we used these values to determine the expected (random) distribution of juvenile corals. There were significant differences between the observed and expected distributions of juveniles (Fig. 4a1) with more than twice the expected numbers associated with CCA substrate, only half the expected numbers associated with bare substrate, and about three-quarters the expected numbers associated with algal turf (Fig. 4a1; 95% confidence intervals). All four common coral families had similar patterns, with significantly more juveniles associated with CCA than expected in every family (Fig. 4a2–5).

Approximately half of the juvenile corals were associated with CCA substrate (Fig. 4a1), and of these, 84% were associated with the five consistently identifiable CCA taxa. Among the CCA taxa, more juvenile corals than expected were found associated with *Hydrolithon* spp. and *Spongites yendoi*, and fewer than expected were associated with *Neogoniolithon fosliei* and *Pneophyllum conicum* (Fig. 4b1; 95% confidence intervals). *Lithophyllum kotschyianum* was the only CCA for which the observed number of juveniles was not significantly different from expected (Fig. 4b1). When each coral family was analyzed separately (Fig. 4b2–5), the patterns of coral association with CCA were similar to that for all coral families combined.

Table 3 Taxonomic distribution of coral recruits assessed for CCA association (total = 427) with previously published reports of settlement preferences of coral larvae for CCA. *n* refers to the number of corals found in our surveys

Family	<i>n</i>	Genus	<i>n</i>	Previously reported settlement preferences for CCA
Acroporidae	17	<i>Acropora</i>	15	Strongly preferred (Morse et al. 1996; Negri et al. 2001; Price 2010)
		<i>Montipora</i>	2	
Agariciidae	49	<i>Pavona</i>	49	Astroceoniidae
		<i>Stylocoeniella</i>	4	
Faviidae	31	<i>Cyphastrea</i>	4	Required (Morse and Morse 1996)
		<i>Echinopora</i>	8	Required (Morse and Morse 1996)
		<i>Favia</i>	2	
		<i>Favites</i>	1	Required (Morse and Morse 1996; Golbuu and Richmond 2007)
		<i>Goniastrea</i>	2	
		<i>Leptoria</i>	1	
Fungidae	1	<i>Fungia</i>	1	No preference (Harrison and Wallace 1990; Baird and Hughes 2000; Baird and Morse 2004); Preference for CCA (Price 2010)
		<i>Plesiastrea</i>	1	
		Unknown	12	
Milleporidae	7	<i>Millepora</i>	7	No preference (Harrison and Wallace 1990)
Mussidae	4	<i>Acanthastrea</i>	3	
Oculinidae	1	<i>Lobophyllia</i>	1	No preference (Harrison and Wallace 1990)
		<i>Galaxia</i>	1	
Pocilloporidae	101	<i>Pocillopora</i>	71	No preference (Goreau et al. 1981)
		<i>Seriotopora</i>	7	
		<i>Stylophora</i>	21	
		Unknown	2	
Poritidae	166	<i>Goniopora</i>	1	No preference (Goreau et al. 1981)
		<i>Porites</i>	164	
		Unknown	1	
Unknown	46	N/A	N/A	

When juveniles were grouped into four size classes, the same general pattern was found in each size class: twice as many corals as expected were associated with CCA and fewer than expected were associated with bare and turf substrates (Fig. 5a–d). Two exceptions were that the

observed and expected numbers of corals were similar on turf-dominated substrate for the largest size class (Fig. 5a) and on bare substrate for the 6- to 10-mm size class (Fig. 5c). However, in every case, more than the expected numbers of juvenile corals were on CCA. Because there was no consistent change in coral distributions with increasing size, it is likely that the substrates observed touching juvenile corals were the same ones present at the time of settlement.

The graphical and χ^2 analyses of patterns of juvenile coral distribution by site closely paralleled those for all sites combined. On all nine reefs, regardless of location or management status, juvenile corals were associated with CCA substrate more than expected by random chance (ESM Appendix Fig. 1). Similarly, juvenile corals appeared to be associated with turf-covered substrate less than expected by chance on all nine reefs (ESM Appendix Fig. 1). On six reefs, juvenile corals also appeared to be associated less than expected with bare substrate (ESM Appendix Fig. 1). In terms of juvenile coral association among the five consistently identified CCA taxa, on seven out of nine reefs, juvenile corals appear to be associated more than expected by chance with inductive *Hydrolithon* spp. substrate and with *Spongites yendoi* (ESM Appendix Fig. 2). In all eight reefs where *Neogoniolithon fosliei* was present, juvenile corals appeared to be associated less than expected with this species (ESM Appendix Fig. 2). Juvenile corals also appeared to be associated less than expected with *Pneophyllum conicum* (on six out of nine reef sites; ESM Appendix Fig. 2). Associations with *Lithophyllum kotschyannum* are difficult to evaluate as this species was only present on 4 out of 9 reefs and was never very abundant.

Juvenile coral density

In the density surveys, we counted a total of 547 juvenile corals on hard substrates on 9 reefs. Juvenile densities differed significantly among the management systems with the highest densities in fisheries closures (Fig. 6; ANOVA $df = 2,6$; $F = 9.0$; $P = 0.02$). In pair-wise comparisons, juvenile densities on open-access and gear-restricted reefs did not differ significantly (Tukey's HSD $P = 0.90$, Fig. 6), so they were pooled into a single fished category for subsequent analyses.

As found in the surveys of juvenile-substrate association, most juveniles in the density surveys were from four families: Poritidae (55%), Pocilloporidae (17%), Agariciidae (8%), and Faviidae (6%). The remaining 14% either belonged to six other families or could not be identified. In a two-way ANOVA (four families, two management systems; Table 4a), the effects of management and family were both significant, but there was no interaction between

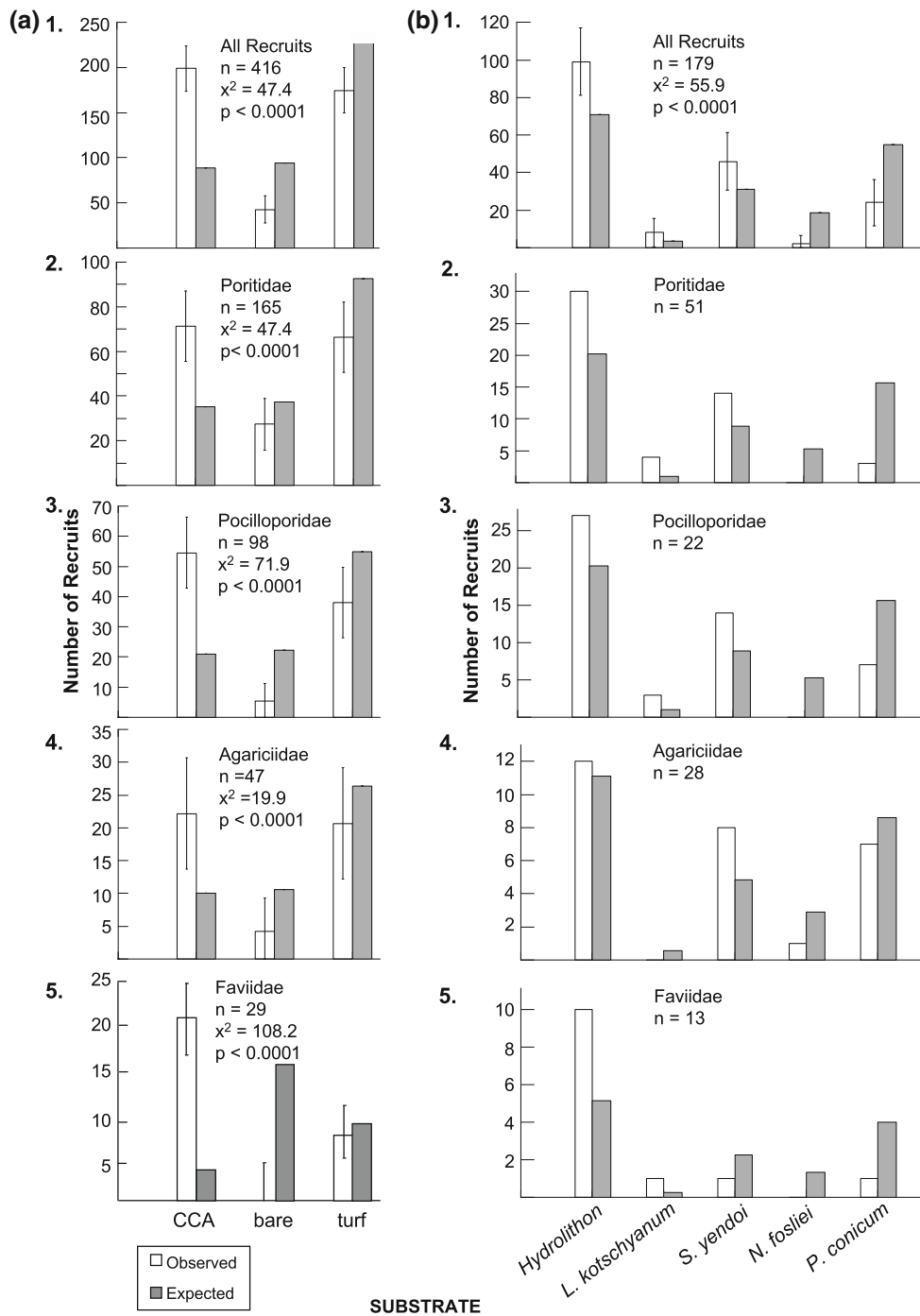


Fig. 4 Observed (*open bars*, with 95% confidence intervals) versus expected (*solid bars*) numbers of juvenile corals associated with **a** suitable substrate and **b** the five identifiable CCA taxa. χ^2 results are shown where expected sample sizes were >5

management and family (Table 4b), indicating that all families tended to be more abundant on closed than on fished reefs.

Factors affecting juvenile coral densities

Mean sea urchin biomass was 7.7 times greater on fished reefs ($5,376 \pm 3,572$ kg/ha) than on closed reefs

(695 ± 671 kg/ha). Total juvenile coral densities (all families pooled) across eight reefs (three closed, five fished) were positively correlated with *Hydrolithon* cover (Table 5a; $P = 0.04$) but were not significantly correlated with sea urchin biomass ($P = 0.07$). Total juvenile densities on three closed reefs were also significantly correlated with *Hydrolithon* cover (Table 5b; $P = 0.01$).

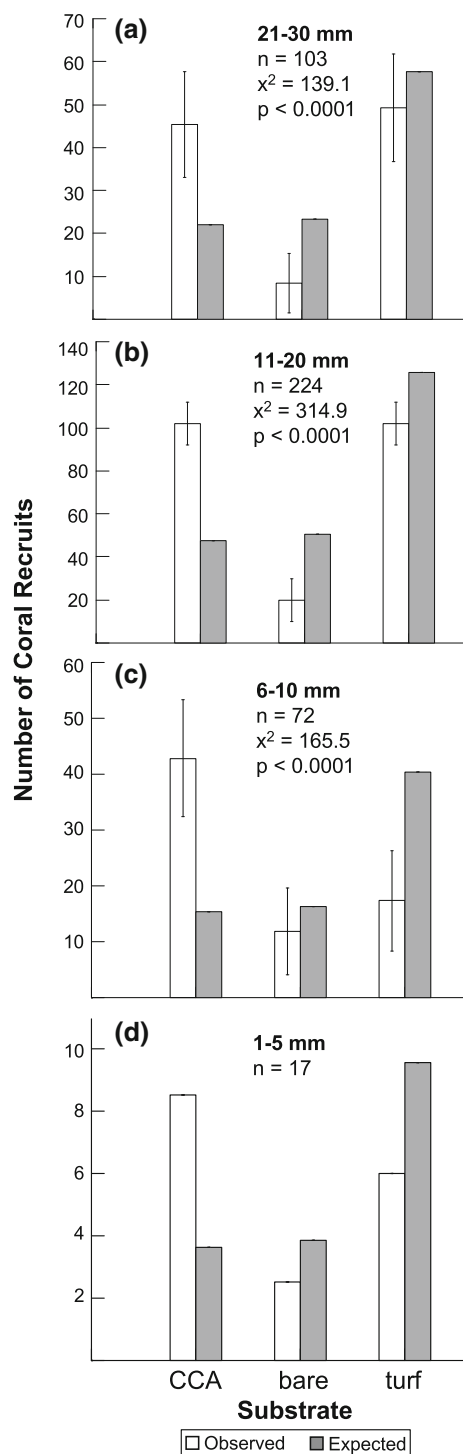


Fig. 5 Observed (*open bars*, with 95% confidence interval) versus expected (*solid bars*) numbers of juvenile corals associated with three suitable settlement substrates, within four coral size classes. χ^2 results are shown where expected sample sizes were >5

Discussion

O’Leary and McClanahan (2010) demonstrated that the high numbers of sea urchins on open-access reefs in Kenya

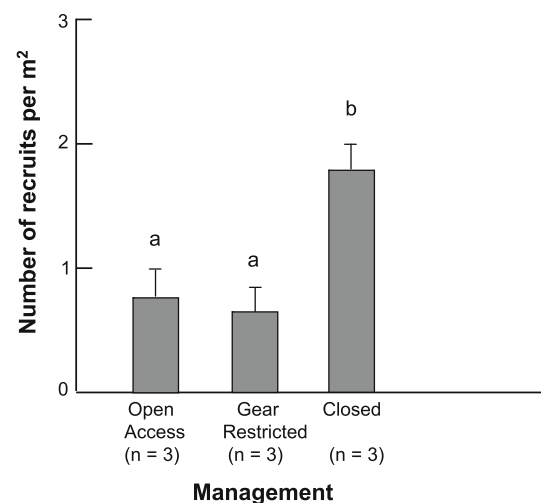


Fig. 6 Numbers of juvenile corals (per m² \pm SD) under three management systems. *n* = number of reefs surveyed. Letters above bars indicate significant differences

result in large reductions in CCA abundance. Here, we extend that work by showing that (1) the abundance of settlement-inducing CCA is lower on fished (open-access and gear-restricted) reefs than on reefs within fisheries closures; (2) juvenile corals are more abundant than expected on CCA in general, and on two settlement-inducing *Hydrolithon* species in particular; (3) juvenile coral density is higher on closed than on fished (open-access and gear-restricted) reefs; and (4) juvenile coral densities are positively correlated with the cover of *Hydrolithon* spp. These findings suggest that effects of fishing may cascade through the ecosystem, first by increasing urchin biomass by nearly an order of magnitude, then by reducing inductive CCA cover, and finally by reducing coral recruitment and/or juvenile survival.

Among the five CCA taxa that were consistently identifiable in the field, *Hydrolithon* spp., *Neogoniolithon fosliei*, and *Pneophyllum conicum* were more abundant on closed than on fished reefs. The first two taxa were the main driver of the differences in total CCA cover between the management systems, and we previously demonstrated experimentally that sea urchin grazing directly reduces the growth rate of *N. fosliei* (O’Leary and McClanahan 2010). Other work indicates that differential effects of grazers on CCA can be based on CCA thickness (Adey and Vassar 1975; Steneck 1983, 1986). Our results are consistent with the premise that sea urchin grazing (on fished reefs) is especially harmful to thick CCA taxa such as *Hydrolithon* spp. and *N. fosliei*, but that these species are better able to tolerate fish grazing (on closed reefs). The greater cover of both *N. fosliei* and *Hydrolithon* spp. on closed reefs is likely to reduce bioerosion and enhance reef stability since thick-crust CCA taxa are major binders of reefs and help

Table 4 (a) Recruit numbers per m² ± SD in fished and closed reefs; (b) two-way ANOVA testing whether the densities of recruits in the four most abundant families responded in the same direction (greater in closed reefs) to management (closed vs. fished)

Family	Fished	Closed	
<i>(a)</i>			
Poritidae	0.43 ± 1.02	0.91 ± 1.56	
Pocilloporidae	0.12 ± 0.41	0.32 ± 0.75	
Agariciidae	0.07 ± 0.28	0.14 ± 0.66	
Faviidae	0.02 ± 0.15	0.14 ± 0.41	
Treatment	<i>df</i>	<i>F</i> -Ratio	<i>P</i>
<i>(b)</i>			
Family	3,27	8.67	<0.0001
Management	1,27	11.54	0.002
Management*Family	3,27	0.54	0.66

Table 5 Regression testing correlations between coral recruit density (all recruits) and (a) sea urchin biomass and *Hydrolithon* cover across eight reefs (closed: Malindi, Mombasa, Kisite; fished: Vipingo, Kanamai, Diani, Nyali, Mpunguti), (b) *Hydrolithon* cover across three closed reefs (Malindi, Mombasa, Kisite)

Effect	Coefficient	Tolerance	<i>t</i>	<i>P</i>
<i>(a) Model F(2,5) = 6.5, P = 0.04</i>				
Constant	1.071		4.771	0.005
<i>Hydrolithon</i> % cover	0.080	0.998	2.863	0.035
Sea Urchin biomass (kg/ha)	-0.000085	0.998	-2.321	0.067
Effect	Coefficient		<i>t</i>	<i>P</i>
<i>(b) Model F(1,1) = 353.5, P = 0.034</i>				
Constant	1.37		55.5	0.01
<i>Hydrolithon</i> % cover	0.05		18.8	0.03

to build reef structure (Adey and Vassar 1975). However, for coral recruitment, the cover of inductive CCA species is likely to be more important than overall CCA cover.

Because of the difficulty of identifying CCA in the field, previous CCA surveys are rarely taxon specific and the ability of CCA to induce coral settlement has been tested mainly in laboratory settings. The strong associations of juvenile corals with CCA in general and certain CCA taxa both across all reefs and within single reefs indicate consistency of our results over relatively large spatial scales (spanning the coral coast of Kenya) and across three management systems. Laboratory studies have demonstrated differences in inductive ability and suitability for coral settlement for three of the five CCA taxa we consistently identified (Table 3). Both *Hydrolithon* species (*H. onkodes* and *H. reinboldii*) are highly inductive (Morse

and Morse 1996; Negri et al. 2001; Harrington et al. 2004; Golbuu and Richmond 2007), and these species are common throughout the tropical Indo-Pacific (Adey and Vassar 1975). Conversely, *Neogoniolithon fosliei* is a poor inducer of coral recruitment and unsuitable for coral settlement. In a laboratory experiment using acroporid larvae, *N. fosliei* was the weakest inducer of settlement among five CCA, and the larvae that settled on it had 100% mortality due to epithelial shedding (Harrington et al. 2004). The inductiveness of *P. conicum* is unknown, but since this species can overgrow live adult corals (Antonius 2001), it should be adaptive for coral larvae to avoid settling on it.

No previous studies have assessed either inductive ability or suitability for coral settlement of the two other CCA taxa that we identified consistently. *Lithophyllum kotschyianum* occurred at low percent cover, did not have higher than expected numbers of corals associated with it, and is not likely to be inductive, since it has a branching morphology. While *Spongites yendoii* had more corals associated with it than expected, it is also unlikely to be a suitable settlement habitat as it has the most extreme form of cell shedding described for CCA species—twice annual deep-layer sloughing of material from well below the layer of meristematic cells (Keats et al. 1994). Deep-layer shedding minimizes colonization by burrowing invertebrates and helps maintain the thallus as a thin sheet, which enhances surface attachment. The relative contributions of grazing versus shedding to maintenance of thallus thickness are unknown (Keats et al. 1994). In Kenya, cover of *S. yendoii* was low (<2%) on both fished and closed reefs, and it is possible that grazing by urchins and fishes (respectively) keeps it in a thin state so that deep-layer shedding rarely occurs. Further testing of the suitability of *S. yendoii* as a settlement substrate for corals under different grazing conditions may be warranted.

The strong associations of juvenile corals from four families with CCA substrates in general, and with two inductive species of *Hydrolithon* in particular, suggest that many corals are likely to have affinities for CCA substrates under natural field conditions. Because the recruits we surveyed were up to 30 mm in diameter (and perhaps up to a year old), the substrates surrounding them could have developed after settlement, rather than before. However, two lines of evidence suggest this was not the case: the consistent coral–substrate associations across all juvenile size classes and the strong associations of corals with inductive CCA and their apparent avoidance of non-inductive CCA taxa.

The affinity of coral recruits in Kenya for inductive CCA substrates indicated by our data is consistent with published literature for some, but not all, coral families. Previous studies on the responses of coral larvae to CCA are limited to few taxa (Table 3). The association between CCA and the agaricid genus *Pavona* in Kenya is consistent

with that of another agaricid, *Agaricia humilis*, in the Caribbean, which also responds very strongly to species of *Hydrolithon* and other inductive CCA (Morse et al. 1994). By contrast, the associations of Kenyan Poritidae (*Porites*) and Pocilloporidae (mainly *Pocillopora*) with CCA were unexpected. In most previous studies, *Pocillopora* and *Porites* species did not require CCA for settlement (Goreau et al. 1981; Harrison and Wallace 1990; Baird and Hughes 2000; Baird and Morse 2004), though one study found that *Pocillopora* strongly preferred CCA substrate (Price 2010). Some CCA may play roles in post-settlement survival as well as pre-settlement substrate selection. However, the unchanging patterns of CCA association among size classes suggest that any differential post-settlement mortality on different substrate types (bare, turf, CCA) should have occurred prior to our surveys in very small size classes. In the only other relevant example, on Palmyra Atoll, there was no difference in the microhabitats of <1-mm and 4- to 5-mm corals (Roth and Knowlton 2009). Therefore, pocilloporids and perhaps poritids may either have a facultative response to CCA (i.e., they do not require it but prefer it when available), or settlement responses vary between species in these coral families.

The associations between juveniles from several large and abundant coral families and inductive CCA suggest that the reduced cover of CCA on fished reefs may be responsible for lower coral recruitment. Other possible explanations seem less likely. For example, differences in environmental conditions could have affected CCA cover and coral recruitment between reefs in similar ways. However, this seems unlikely because, while the gear-restricted reefs are directly adjacent to and almost identical physically to the closed reefs (e.g., depth, flow, and geomorphology), gear-restricted reefs had CCA cover and coral recruitment levels most similar to the more distant and shallow open-access reefs. Gear-restrictions are not well enforced, so these reefs effectively are fished, and we included them primarily as a control for differences in physical condition between open-access and closed reefs. Similarly, the proximity of gear-restricted and closed reefs makes it improbable that differences in larval delivery explain our results. If circulation was responsible for differential larval delivery, reefs in close proximity should have similar recruitment patterns, but the gear-restricted and closed reefs had very different juvenile densities. Another possible explanation of our results could be that fished and open-access reefs differed in available settlement space (e.g., through differences in the cover of fleshy algae). However, severe competition for space with fleshy algae is not likely a factor in Kenya as both sea urchins (in fished reefs) and herbivorous fishes (in closed reefs) are equally effective at removing fleshy algae (O'Leary and McClanahan 2010).

Crustose coralline algae have received little attention in scientific, management, or lay literature compared to corals (Miller et al. 2003), due in part to difficulties with field identification (Braga et al. 1993). However, the success of reef restoration and coral recovery may depend greatly on CCA abundance and taxonomic composition. Where coral populations are at low densities, settlement in response to a specific inducer (such as CCA) may enhance reproductive success by leading to aggregation of adults on a common substrate (Raimondi and Morse 2000). Management that increases the cover of inductive CCA might be used as a restoration measure for corals (Vermeij 2005) and recognized as one of the key benefits of effective fisheries management. Our results suggest that total CCA cover may be a good proxy for the abundance of inductive CCA, and that it might be used to indicate reef health and management effectiveness where time-consuming CCA identification is prohibitive.

As far as we know, this is the first field study to examine how fishing-induced differences in grazing pressures affect taxonomic composition of CCA and is one of a few studies documenting associations of coral recruits with different CCA taxa in the field. These findings provide evidence of pathways by which heavy fishing may fundamentally alter ecological processes and structures via sequences of species interactions. Any factor, abiotic or biotic, that reduces CCA abundance or shifts CCA species composition toward non-inductive taxa may reduce reef resilience by diminishing the likelihood of successful coral recruitment and thereby changing the dynamics of the many species depending on coral habitat.

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