

Alternate benthic assemblages on reef restoration structures and cascading effects on coral settlement

M. W. Miller^{1,*}, A. Valdivia², K. L. Kramer^{2,4}, B. Mason³, D. E. Williams², L. Johnston³

¹NOAA-Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida 33149, USA

²Cooperative Institute of Marine and Atmospheric Science, and ³Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, Florida 33149, USA

⁴Present address: National Park Service, Pacific Island Network Inventory and Monitoring (PACN I&M)
PO Box 52 Hawai'i National Park, Hawaii 96718, USA

ABSTRACT: In coral reefs, restoration actions often involve artificial construction since physical structure enhances physico-chemical conditions for benthic communities and provides habitat for reef-associated fauna. We evaluated the performance of 4 restoration structures (RS, aged 5 to 12 yr) by comparing convergence of their benthic assemblages to adjacent reference reefs (REF). Multivariate clustering indicated that benthic assemblages were significantly distinct between RS and REF, as well as among sites. Differences were primarily attributable to weedy macroalgal and cyanobacterial groups, not slow-growing corals and crustose coralline algae. RS had a higher abundance of cyanobacterial turfs that can negatively affect adult and larval corals. To elucidate potential cascading effects on reef development, we tested whether exudates of the distinct RS and REF assemblages inhibit settlement by planulae of 3 coral species in laboratory assays. Relative settlement deterrence (versus seawater controls) was variable both between sites and among coral species. For example, both RS and REF exudates from one site were deterrent to settlement for *Acropora palmata* and *Diploria strigosa*, but, for *Montastraea faveolata*, RS (but not REF) exudates from a second site were deterrent, while RS exudates from the first site were not. Overall, results indicate that divergence of benthic assemblages is not simply attributable to incomplete succession, but appears to be a persistent, possibly stable state and that benthic algal/cyanobacterial assemblages on both RS and REF in these locations impair 'recruitment potential' for framework-building corals to some degree.

KEY WORDS: Coral larvae · Cyanobacteria · *Acropora palmata* · *Montastraea faveolata* · *Diploria strigosa* · Succession · Florida Keys

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

A basic principle of restoration ecology is that primary successional processes can be accelerated by prudent interventions to physico-chemical and/or biotic attributes of a degraded ecosystem (Hobbs & Norton 1996, Dobson et al. 1997). Enhancement of physical habitat structure is a promising intervention in aquatic systems because of its importance in mediating ecological processes. For example, physical structure affects hydrodynamic conditions such as flow and boundary layer dynamics, as well as potential expo-

sure to anoxia, both of which can influence feeding, metabolism, and recruitment of benthic organisms (Genin et al. 1986, Lenihan 1999, Carbindale et al. 2002). Physical structure and heterogeneity are also important to ecosystem function in providing habitat for associated fauna, thereby controlling trophic interactions including crucial herbivory processes in coral reef systems (Gladfelter & Gladfelter 1978, Lindahl et al. 2001, Grabowski & Powers 2004, Lee 2006).

Indeed, because coral reef biodiversity (e.g. Jones et al. 2004), ecological services (Moberg & Folke 1999), and aesthetic values are largely owed to architectural

*Email: margaret.w.miller@noaa.gov

complexity created by reef-building corals, management often responds to acute physical injury by re-creating artificial physical structure. Under a legal mandate provided by the US National Marine Sanctuaries Act to restore areas affected by natural resource damage to pre-disturbance conditions, so-called 'structural restoration' is commonly undertaken within the Florida Keys National Marine Sanctuary (FKNMS) at reef sites affected by large ship groundings (Symons et al. 2006). At least 5 such projects have been constructed in the FKNMS at major ship grounding sites. These structural restoration projects are often performed in the absence of other ecological interventions, such as coral transplantation or proactive enhancement of grazing processes (e.g. Kaufman 2006), and at times in the absence of comprehensive monitoring or subsequent evaluation to confirm the presumed trajectory toward convergence with adjacent reference reefs.

Succession on reef restoration structures is taking place upon a shifting baseline of declining ecological condition of reference reef communities in the Florida Keys (Pandolfi et al. 2005, Callahan et al. 2007), the Caribbean (Gardner et al. 2003, Wilkinson & Souter 2008), and worldwide (Pandolfi et al. 2003, Bruno & Selig 2007). Benthic assemblages have become increasingly dominated by macroalgae and cyanobacteria under conditions of high adult coral mortality, declines in herbivory pressure, and/or anthropogenic nutrient enrichment (e.g. Hughes 1994, Thacker & Paul 2001, Paul et al. 2005). Experimental studies have shown that the presence of macroalgae may allelopathically inhibit larval settlement of marine invertebrates, including corals, over and above the simple pre-emption of space (Walters et al. 1996, Kuffner & Paul 2004, Kuffner et al. 2006), such that increased abundance of macroalgae may create feedbacks further inhibiting coral recruitment. Indeed, recruitment failure by framework-building coral species on Caribbean reefs, at least relative to high observed rates of adult mortality, has been documented (Hughes & Tanner 2000, Edmunds & Elahi 2007).

In the current study, we sought to evaluate the presumption that replacing physical reef structure would result in the reassembly of the reference reef benthic community. We did this by testing the convergence of benthic assemblages on reef restoration structures (RS) of varying age with those on adjacent reference reef substrates (REF; biogenic carbonate reef substrates adjacent to the RS). In addition, we investigated one potential cascading impact such differences in benthic assemblages might propagate: namely, the allelopathic deterrence of settlement by reef-building coral larvae. Specifically, we tested the hypotheses that: (1) benthic assemblages on 4 RS in the Florida Keys did not differ from REF assemblages and (2) exudates from

macroalgal assemblages on RS versus REF substrates did not affect settlement success (relative to seawater controls) of framework-building coral larvae.

MATERIALS AND METHODS

Assemblage surveys. Four RS of varying ages within the FKNMS were surveyed in 2007 (Fig. 1; characteristics given in Table 1). All RS had a similar composition of locally quarried limestone surfaces secured in a varying amount of concrete. All RS provided ~1 m of structural relief above the surrounding reef surface, though the architectural structure of the reference reefs differed between sites (Table 1), ranging from high-relief, spur-and-groove (Iselin and Wellwood) to low-relief, hard-bottom habitats dominated by gorgonians (Maitland). Ten meter long, haphazardly placed line-intercept transects were used ($n = 4$ to 7, according to the size and layout of the structure), scoring the taxa underlying 1 point every 10 cm, yielding 100 points transect⁻¹. Points were scored as occupied by organisms or substrates at varying levels of resolution. Upright macroalgae were recorded by genus (most commonly, *Dictyota*, *Halimeda*, *Lobophora*); other algae, by morphological group (crustose corallines, turf >2 mm, turf <2 mm, and turfs dominated by cyanobacteria which were scored separately); hard corals, by species; other cnidarians, by genus (most commonly, *Pseudopterogorgia*, *Gorgonia*, *Palythoa*); and sponges, as a single group. The relatively short transect length was employed to fit multiple replicates within the RS, which were of limited size. Adjacent reference areas (natural reef substrate, REF) were sampled similarly at each site within 100 m of the RS boundary. There is no way to determine the degree of disturbance experienced in these adjacent REF areas, either from the original grounding or the subsequent RS construction activities. However, there was no visually obvious difference in the community between the REF areas we sampled and the reef as a whole.

Data were analyzed via multivariate clustering of samples (i.e. individual transects, with full taxonomic resolution of the collected data) as well as via multi-dimensional scaling ordination, based on Bray-Curtis similarity coefficients and group average linkage (PRIMER-E, V.6). A 2-way crossed layout utilizing the factors substrate (RS vs. REF) and site was used for analysis of similarity (ANOSIM) to test for significant influence of these factors on determining similarity of assemblages and for SIMPER analysis of species contribution to group dissimilarity (Clarke & Warwick 2001). Community data was pooled for major taxa (comprising more than 10 % cover overall plus hard corals) for illustration and to examine abundance patterns.

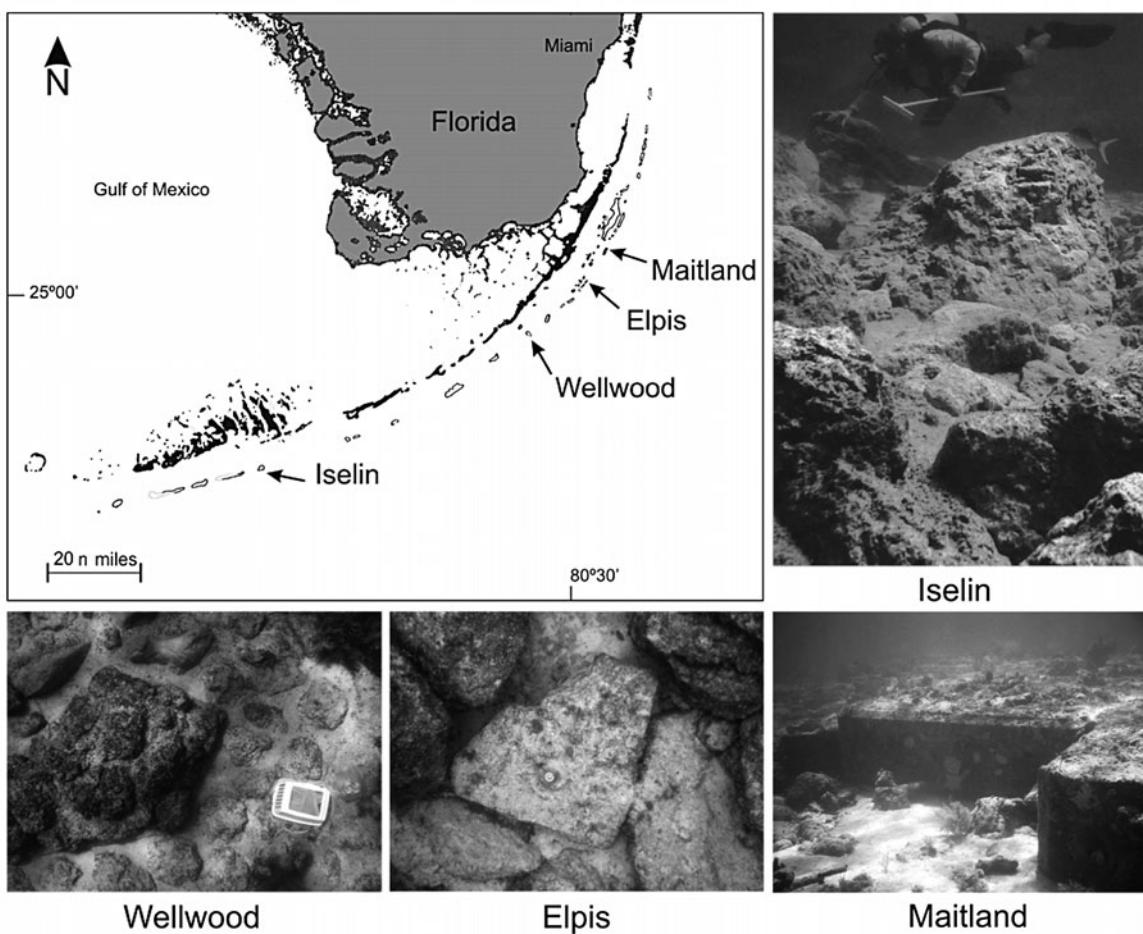


Fig. 1. Florida Keys National Marine Sanctuary showing approximate location and representative view of the 4 restoration structures sampled in the current study. Scale varies in the photographs. See Table 1 for further characteristics of each structure

Larval settlement assays. To test one possible mechanism of influence of distinct macroalgal assemblages on potential coral recruitment to each substrate type, we conducted larval settlement assays using seawater

exudates of the macroalgal community from 2 RS/REF site pairs (Maitland and Wellwood). Larvae of 3 dominant reef-building coral species were cultured from gametes collected during an annual spawning event

Table 1. Characteristics of reef restoration structures (RS) surveyed in the present study. All sites are within the Florida Keys National Marine Sanctuary and are named for the ship that grounded there. Age of structure is at time of sampling. Adjacent natural reef substrates were sampled similarly at each site. n: number of 10 m long point-intercept transects sampled at each site.

	Depth (m)	Location	Age of structure (yr)	RS materials	Surrounding reef habitat	Date of survey	n
Iiselin	2.5–5	24° 32.67' N, 81° 24.51' W	8	Quarried limestone boulders with concrete	High-relief spur and groove	May 2007	7
Wellwood	4–5	25° 00.63' N, 80° 22.24' W	5	Quarried limestone boulders with concrete	High-relief spur and groove	Aug 2007	4
Elpis	9–11	25° 08.92' N, 80° 15.15' W	12	Quarried limestone boulders Low-relief hard bottom	Low-relief hard bottom	Aug 2007	4
Maitland	2.5	25° 11.98' N, 80° 13.57' W	12	Concrete with embedded quarried limestones	Low-relief hard bottom	Aug 2007	4

(*Acropora palmata* spawned 1 to 2 September 2007 at Elbow Reef; *Montastraea faveolata* and *Diploria strigosa* spawned 3 September 2007 at Grecian Rocks Reef) according to previously described methods (Miller & Szmant 2006).

Four algal exudates were prepared from 4 algal assemblages: Wellwood RS (WRS), Wellwood Reference (WREF), Maitland RS (MRS), and Maitland Reference (MREF). At each site, four 0.25 m² quadrats were haphazardly placed and all macroalgal biomass (including turf) that could be plucked by 2 divers in 5 min was harvested. This biomass was pooled for each site (i.e. 1 m² algae from each site) and soaked in ~5 l of seawater in a stainless steel bucket. After 24 h, the exudate was filtered (Whatman GF/A) and bubbled with an airstone for at least 2 h prior to use in the assays. Approximate wet mass of algae utilized in each exudate was recorded and varied by a factor of 5 (WRS ~ 94 g; WREF ~ 140 g; MRS ~218 g; MREF ~ 499 g), but represented the actual relative abundance of macroalgae among the different sites (i.e. the biomass that was present on 1 m² of reef substrate). Positive seawater controls (SWC) were performed using (5 µm) filtered reef water. While there is no way to determine the actual levels of such exuded substances in the field, this assay approach provided a standard means to compare potential settlement inhibition among the algal community types present at/in the different reef sites and substrates.

Assays were performed in polystyrene Petri dishes (100 mm diameter) to which small chips of natural reef rubble containing crustose coralline algae were added to provide natural settlement cues. Ten replicate dishes with 10 larvae each were used for each treatment of *Diploria strigosa* and *Montastraea faveolata*, while only 8 replicates with 8 larvae each were used for *Acropora palmata* due to limited larval availability. All 5 treatments were run with *M. faveolata* (WRS, WREF, MRS, MREF, SWC) during the period from 8 to 11 September 2007, whereas only 3 treatments were conducted with *D. strigosa* and *A. palmata* (WRS, WREF, SWC) from 7 to 10 September 2007. Larvae were left undisturbed in the assay for 3 d and were then scored under a

fluorescent dissecting microscope. The percent of larvae settled (attached and flattened with beginning differentiation of mouth and mesenteries) was the primary parameter of interest. The vast majority of the settlers were on chips, but a few settled on the dish and were included in the counts. The total number of larvae sighted (including settled plus live unattached) was also noted; not all larvae were re-sighted at the end of the assay due to mortality and/or settlement in cryptic crevices (bottom surfaces of the chips were observed), which could not be adequately observed under the microscope.

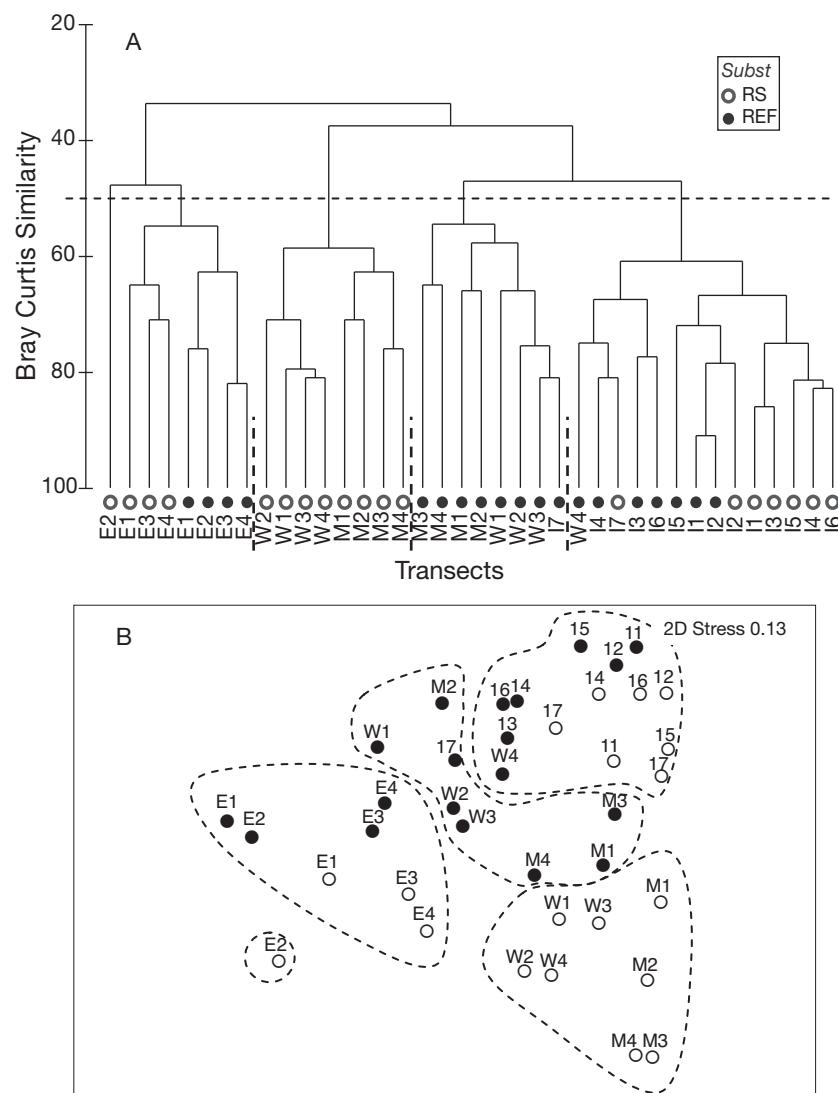


Fig. 2. (A) Dendrogram showing multivariate clustering of individual transect samples on restoration structures (RS) and reference (REF) substrates at 4 sites (W: Wellwood; M: Maitland; E: Elpis; I: Iselin). Clustering is based on Bray-Curtis similarity and group-average linkage of percent cover of benthic assemblages (PRIMERe, V. 6). (B) Multidimensional scaling ordination plot for the same data set with clusters of 50% similarity enclosed for illustration

For each species, 1-way ANOVA (*Montastraea faveolata* and *Diploria strigosa*) or ANOVA on ranks (for *Acropora palmata*, since assumptions were not fulfilled) was used to test for significant differences in percent of larvae settled among the different exudate treatments. Post hoc tests (Holm-Sidak or Dunn's test, respectively) were used to compare the effect of each exudate against the seawater control.

RESULTS

Assemblage surveys

Benthic assemblages differed significantly between RS and REF substrates (ANOSIM, Global R = 0.677, significance level of 0.1%) as well as among sites (ANOSIM Global R = 0.855, significance level of 0.1%). Cluster analysis (Fig. 2A) shows the Elpis site assemblage to be the most distinct from other sites (only ~30% similar), with REF transects clustering together at ~65% similarity, while 1 RS transect appears segregated from the other 3. The next cluster includes all the samples from the WRS and MRS, which are ~40% similar to the remaining samples. These last 2 clusters include one with all but 1 of the REF samples from the Maitland and Wellwood sites and a second containing, primarily, the Iselin samples, with a reasonable degree of separation by substrate. The multidimensional scaling ordination plot (Fig. 2B), despite moderately high stress of 0.13, shows a consistent pattern with the cluster diagram.

The contribution of the most distinguishing benthic taxa to the overall dissimilarity between RS and REF assemblages is given in Table 2. The top contributor to

dissimilarity between substrate types, turf <2 mm, had a similar mean abundance overall, but the 2-way crossed SIMPER analysis only compares dissimilarities within sites. The top 4 contributors are fast-growing algae, turfs, and a weedy encrusting cnidarian (*Palythoa caribaeorum*), which together account for 57% of the dissimilarity between RS and REF. In contrast, the most influential slow-growing, 'climax' taxa, the hard coral *Porites astreoides* and crustose coralline algae (CCA), contribute together a total of only 8.5% of the dissimilarity.

Abundance of major taxa (groups with >10% cover plus hard corals) is shown in Fig. 3. RS assemblages were generally dominated by cyanobacterial as well as standard sparse turf and crustose coralline algae, while REF assemblages generally lacked cyanobacterial turf, but hosted greater components of *Dictyota* spp. and other upright macroalgae. The only groups that showed a consistent pattern in abundance between RS and REF substrates across all 4 sites were cyanobacterial turf (greater on RS substrates), *Dictyota* spp. (greater on REF substrates), and 'other invertebrates' (not including hard corals, greater on REF). Slower-growing plant and animal groups, such as CCA and hard corals, showed inconsistent patterns of abundance between sites, though, for hard corals, older sites appeared to have similar hard coral cover between substrate types, while newer sites showed less coral cover on RS than on REF substrates.

Larval settlement assays

Larvae of all 3 coral species showed significant variation among treatments in the main-effect ANOVAs.

Table 2. Analysis of species contribution to dissimilarity between restoration structure (RS) and reference (REF) substrate assemblages (SIMPER analysis in PRIMER-E, V.6). Average dissimilarity between these groups was 46%. CCA: crustose coralline algae

Species	RS av. abund.	REF av. abund.	Av. diss.	Diss./SD	Contrib. (%)	Cum. (%)
Turf/bare (<2 mm)	32.11	31.16	8.33	1.35	18.24	18.24
Cyano. turf	16.79	1.26	7.00	1.20	15.32	33.56
<i>Dictyota</i> spp.	9.11	19.00	6.08	1.57	13.32	46.89
<i>Palythoa caribaeorum</i>	0.32	6.89	4.54	0.94	9.95	56.84
CCA	9.26	10.74	2.88	1.38	6.3	63.13
<i>Halimeda</i> spp.	2.42	7.89	2.80	0.92	6.13	69.27
Turf (>2 mm)	9.42	5.26	2.37	0.58	5.19	74.46
<i>Peyssonnelia</i>	5.05	0.89	2.00	1.13	4.38	78.84
Other cyanobacteria	2.63	0.63	1.21	0.76	2.64	81.48
<i>Porites astreoides</i>	1.53	2.21	0.99	0.77	2.16	83.64
<i>Pseudopterogorgia</i> spp.	1.74	2.16	0.96	1.08	2.11	85.75
<i>Gorgonia ventalina</i>	0.74	1.37	0.78	0.74	1.71	87.46
Rubble	0.58	1.63	0.68	0.38	1.49	88.95
<i>Lobophora variegata</i>	2.53	0.84	0.66	0.36	1.44	90.39

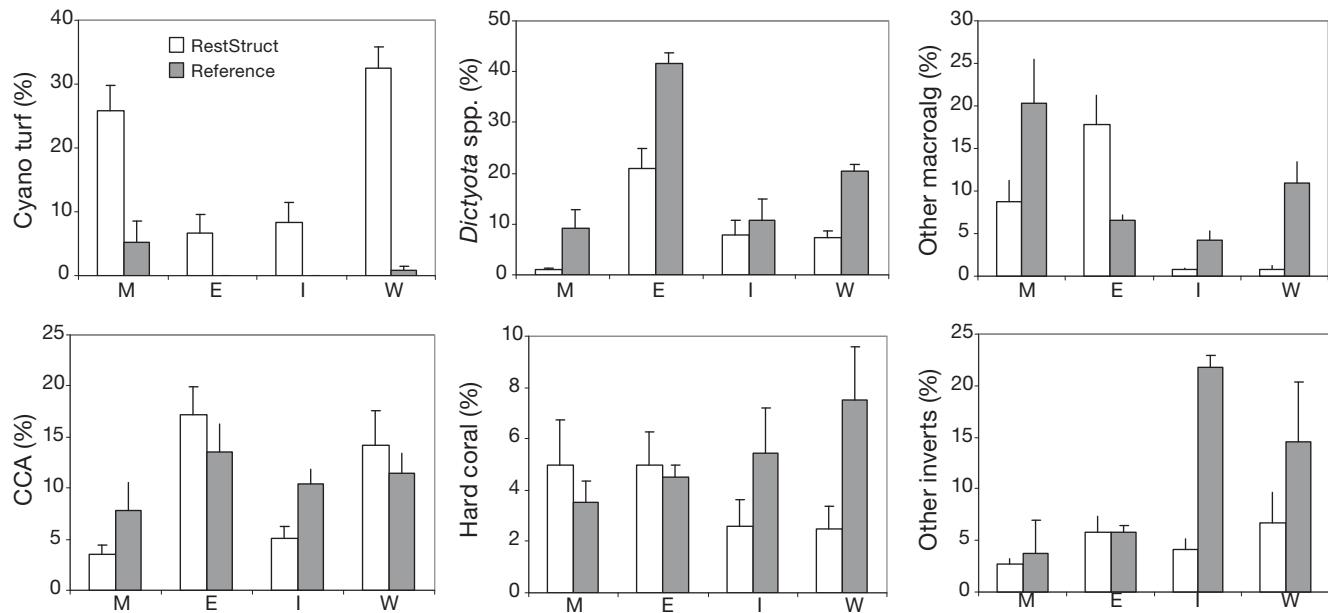


Fig. 3. Mean percent cover (± 1 SE) of dominant benthic groups on restoration structures and reference substrates at 4 reef restoration sites (W: Wellwood; M: Maitland; E: Elpis; I: Iselin) in the Florida Keys National Marine Sanctuary. Site characteristics are given in Table 1. CCA: crustose coralline algae; Cyano turf: thick filamentous turf dominated by cyanobacteria (putatively *Dichothrix utahensis*). Other macroalg: mostly *Halimeda* spp. and *Lobophora variegata*; Other inverts: *Palythoa caribaeorum*, sponges, and various gorgonian soft corals. Note that sites are in order of decreasing age on the x-axes, and that scale on the y-axes varies by taxon

For *Montastraea faveolata*, WREF and MRS exudates significantly inhibited settlement ($p < 0.001$, Holm-Sidak post hoc comparison with seawater control; Fig. 4), while WRS and MREF exudates did not. For *Acropora palmata* and *Diploria strigosa*, both the exudates tested (WRS and WREF) significantly deterred settlement compared to the seawater control ($p < 0.001$, Dunn's non-parametric and Holm-Sidak parametric post hoc comparisons, respectively; Fig. 4). WREF exudates elicited the lowest settlement rates for all 3 species (Fig. 4), while MREF exudates were not deterrent to *M. faveolata*, the only species for which it was tested. *A. palmata* displayed a particular sensitivity to WREF exudates. No live *A. palmata* larvae were observed at the end of the experiment, while the other 2 species had $>60\%$ re-sighting of larvae (settled plus unattached) following this treatment.

DISCUSSION

Benthic assemblages

In the field of ecological restoration in general (e.g. Alexander & Allan 2007) and reef restoration in particular (Miller 2002), the adage of 'build it and they will come' (and presumably fulfill their ecological function) is rarely effectively tested. The presumption is that the stabilization of damaged reef substrates and enhance-

ment of 3-dimensional habitat structure (with appropriate configuration and materials) will provide for the accelerated trajectory toward convergence with the reference or target community. In ecosystems dominated by large, long-lived organisms such as reef corals or trees, this trajectory may be expected to be slow but progressive (Dobson et al. 1997).

If successional processes on RS were advancing toward convergence, we would predict that older sites would display greater similarity between RS and REF than younger sites and that long-lived, slow-growing taxa such as hard corals and CCA would strongly influence the overall differences in assemblage structure. However, neither of these conditions was observed. Cluster analysis indicated that, within sites, the 2 older sites (Maitland and Elpis) had approximately 40 and 50% similarity, respectively, between the bulk of their RS and REF samples, while the middle-aged Iselin showed the greatest convergence between RS and REF samples (i.e. interspersion of samples within a single cluster and overall similarity $>60\%$; Fig. 2A). These patterns of similarity appear to align more closely with geographic or depth effects, rather than age (Table 1). In addition, slow-growing CCA and hard corals did not show a consistent pattern of abundance between RS and REF sites (Fig. 3), and SIMPER analysis indicated that both taxa had less influence on community differences than did groups with faster growth rates such as cyanobacterial turfs, *Dictyota* sp., or the encrusting

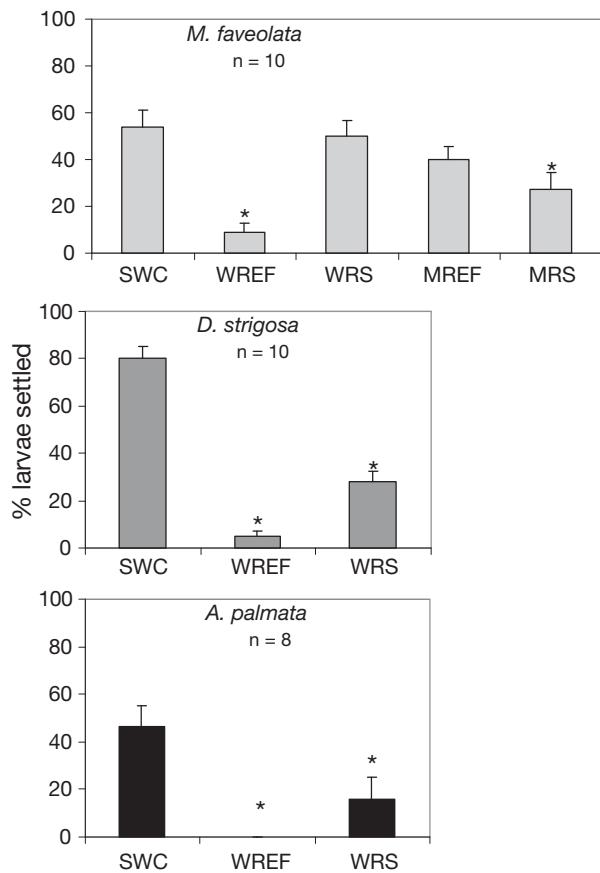


Fig. 4. *Montastraea faveolata*, *Diploria strigosa*, *Acropora palmata*. Mean (+1 SE) percent of larvae successfully settled in algal exudates from different reefs (WREF: Wellwood reference; WRS: Wellwood restoration structure; MREF: Maitland reference; MRS: Maitland restoration structure) and in the seawater control (SWC). Only *M. faveolata* was tested in exudates from the Maitland site. *M. faveolata* and *D. strigosa* replicates contained 10 larvae each, and *A. palmata* replicates contained 8 larvae each. Asterisks above individual bars indicate a significant difference from respective SWC ($p < 0.05$) as determined from Holm-Sidak (parametric, for *M. faveolata* and *D. strigosa*) or from Dunn's (non-parametric, for *A. palmata*) post hoc comparisons versus control

zoanthid *Palythoa caribaeorum* (Table 2). Hard coral cover was higher on the older RS (Maitland and Elpis, ~5%) than on the younger sites (Wellwood and Iselin, <3%; Fig. 1), but was almost entirely dominated by brooding *Porites astreoides*. Overall, the lack of similarity between RS and REF assemblages, lack of relationship of community structure with age, and lack of consistent differences in long-lived or slow-growing organisms all suggest that these RS assemblages are not proceeding in a trajectory of convergence with their respective REF sites. In a similar fashion, investigations in coastal wetland restoration have challenged the general notion of progressive trajectories in either ecosystem structure or function (e.g. Zedler & Callaway 1999).

The finding of significant differences between RS and REF substrates in benthic assemblage structure begs the question of cause. McClanahan (1997) reports that macroalgal primary succession on Kenyan reefs results in a climax community reached in 120 d, generally dominated by canopy-forming brown algae under a herbivory regime dominated by fish grazing (as in the Florida Keys, where minimal recovery of the key-stone grazing sea urchin *Diadema antillarum* [Chiapponi et al. 2002] yields low urchin grazing pressure). Turf-dominated climax communities were reported to develop within 50 d in conditions of intense urchin grazing or in damselfish territories (McClanahan 1997), neither of which were the case for the cyanobacterial/turf-dominated RS assemblages in the current study. Providing habitat structure that encourages grazing by fishes is an explicit design consideration for some designed reef restoration structures (e.g. Moore & Erdmann 2002). The Wellwood RS includes actual 'caves' within the RS modules for fish shelter (Hudson et al. 2007). Data on actual development of RS and REF fish assemblages at these sites is forthcoming, and potential differences in grazing regime cannot be evaluated at this time.

Meanwhile, the artificial substrate itself may influence the colonization and development of benthic assemblages. Slight substitution in restoration structure materials (e.g. clam shells for oyster shells) has been shown to significantly affect recruitment success of reef-building organisms (Nestlerode et al. 2007). Unlike many artificial reefs where major differences in community structure have been documented even over long time frames (e.g. Moschella et al. 2005, Perkol-Finkel & Benayahu 2005, Perkol-Finkel et al. 2005), the RS in the current study were specifically designed to mimic natural reefs in both material (primarily locally quarried limestone (<http://sanctuaries.noaa.gov/special/columbus/project.html>) and architectural structure (see Fig. 1). Microtopographic differences in the quarried rock versus natural reef surfaces might be influential in algal colonization processes. Alternatively, though the quarried carbonate material originated from local reefal deposits, it is possible that diagenetic processes may have resulted in some physico-chemical alterations that could affect algal development. For example, direct leaching of phosphate to some degree could be expected to enhance (N-fixing) cyanobacterial production. Similarly, it is known that nutrient regeneration from reef sediments, interstitial spaces in the reef, or by endolithic organisms can be an important source of nutrients, particularly dissolved inorganic nitrogen, to reef organisms (Entsch et al. 1983, Richter et al. 2001). It seems plausible that differences in endolithic or other cryptic communities due to concrete barrier lay-

ers or differing configuration of interstitial spaces within the RS could affect benthic nutrient supply (i.e. reduced N-availability) and, therefore, the development of benthic algal assemblages in favor of cyanobacteria. This scenario is partially illustrated in a study by Larkum (1988) who reported high rates of N-fixation due to preferential cyanobacterial colonization of new carbonate substrates (i.e. coral skeletons killed up to 9 mo previously by *Acanthaster* predation at One Tree Reef on Australia's Great Barrier Reef), which lacked eroded crevices or endolithic colonization relative to typical reef substrates. These hypotheses remain to be investigated, but highlight the potential importance of subtle aspects of ecosystem function that are easily overlooked in restoration design and evaluation.

Coral settlement

The presence of both macroalgae and cyanobacteria has been previously shown to deter settlement by coral larvae (Kuffner & Paul 2004, Kuffner et al. 2006). In our assays, settlement of *Diploria strigosa* and *Acropora palmata* larvae was significantly deterred by Wellwood RS exudates, while that of *Montastraea faveolata* was not (Fig. 4). Meanwhile, the Maitland (but not Wellwood) RS exudates were deterrent to *M. faveolata* larvae, though both Maitland and Wellwood RS assemblages were dominated by cyanobacterial (25 to 30% cover) and other algal turfs (~30 to 40% cover) with relatively low upright macroalgal cover (8 to 10%; see Fig. 3). Individual species composition within these broad morphological groups likely influences the degree of settlement deterrence of algal exudates (Walters et al. 1996, Kuffner et al. 2006) and may account for the site variation observed in the present study. Overall, it seems likely that the 'recruitment potential' of both types of reef (RS and REF) is compromised to some degree for the major reef-building coral species tested.

Another deterrent to the recruitment of coral larvae is sediment-binding in dense algal filamentous turfs (Birrell et al. 2005). The RS have noticeable thick sediment-binding turfs (including but not limited to the cyanobacterial turfs) that are not obvious on REF substrates. Cover on the Wellwood and Maitland RS is dominated by these groups, and turf heights of up to 15 or 20 mm, respectively, were observed (Miller & Valdivia unpubl. data). Though exudates of the cyanobacterial turfs from the RS were somewhat variable in their effect on settlement, the additional physical barrier represented by these thick turf/sediment mats to coral larval settlers is likely substantial, but remains to be tested.

Implications for reef restoration design and monitoring

The FKNMS has, since 2004, undertaken ongoing restoration monitoring efforts at all 4 of the current study sites. Monitoring parameters are limited to the integrity of the physical structure, and to the hard and soft coral recruit density and species composition. Results of these efforts show statistical convergence in recruitment rates of total scleractinians (predominantly the weedy brooders *Porites astreoides* and *Agaricia* spp.) at the Wellwood (4 yr after construction) and at the Maitland and Elpis (sampled 10 yr after construction) sites (Hudson et al. 2007, 2008a,b). *P. astreoides* has in fact gained up to 5% cover on the older RS, a level convergent with these REF reefs (Fig. 3). The general convergence of recruit densities (Hudson et al. 2008a,b) and the size frequencies of brooding corals have been reported and predicted, while successful recruitment and growth of reef-building spawning species are extremely low (Lirman & Miller 2003, Hudson et al. 2008a,b). In addition to *P. astreoides'* brooded larvae being immediately competent to settle, their greater recruitment success relative to spawning species may also be related to the duration and timing of larval release (April to June), as macroalgal abundances on reefs in the northern Florida reef tract are notably seasonal. Lirman & Biber (2000) report total macroalgae at minimal abundance in winter, gradually increasing to a maximum in July to August. *Halimeda* spp. and, to a lesser extent, *Dictyota* spp. show marked increases in biomass between May (peak settlement for *P. astreoides*) and August or September (settlement for broadcasting species assayed in the current study). Becerro et al. (2006) also suggested that temporal variation in cyanobacterial standing stock may influence the settlement success of mass-spawning corals in Guam.

Considering more proactive strategies (Rinkevich 2005), as well as re-evaluating basic design (e.g. materials or configuration of artificial structure), may benefit future restoration projects. For example, the concept of 'coral gardening' has been advocated by various authors (Epstein et al. 2003, Kaufman 2006), to include both active culture and transplant of coral colonies, as well as active enhancements of grazing or other ecological processes. Indeed, *Acropora cervicornis* fragments that were transplanted to 1 module at the Wellwood site have thrived and have yielded a small island of high coral cover within 4 yr (Miller pers. obs.). Recent advances in culture capacity and rescued 'caches' of coral material in the southern Florida region have increased interest in coral restocking. Such interest has raised additional management concerns, such as diluting potential small-scale genetic adaptation

(Baums 2008) or the potential for introduction of harmful microbes to the natural reef environment, requiring directed research for accurate risk assessment.

Ironically, it appears that coral assemblages on RS in the Florida Keys are more convergent to reference reefs than are benthic assemblages on the whole (i.e. full suite of plant and animal taxa). However, this must be attributed to the decline of coral cover and lack of recruitment of reef-building coral species in REF reefs, not to the high performance of the RS. Given the drastic decline in live coral cover in Florida Keys reefs in the past decade (from 11.9% in 1996 to 6.1% in 2006) (Callahan et al. 2007), it seems that a broader (i.e. community level) view is needed, both in evaluating past restoration projects and in planning appropriate actions and goals for future ones.

Acknowledgements. This work was supported by the NOAA Coral Reef Conservation Program and National Marine Sanctuary Program and conducted under Permit FKNMS-2006-026 (to A. Szmant). Mentoring and advice of A. Szmant enabled culture and experimentation with broadcasting coral larvae. Logistical support was provided by the Florida Keys National Marine Sanctuary and D. McClellan (NMFS/SEFSC). Field and laboratory assistance was provided by I. Baums, N. Polato, J. Zimmerman, T. Vardi, and A. Cedzo. Constructive review of the manuscript by T. Kellison and A. Chester is gratefully acknowledged.

LITERATURE CITED

- Alexander GG, Allan JD (2007) Ecological success in stream restoration: case studies from the midwestern United States. *Environ Manag* 40:245–255
- Baums IB (2008) A restoration genetics guide for coral reef conservation. *Mol Ecol* 17:2796–2811
- Becerro MA, Bonito V, Paul VJ (2006) Effects of monsoon-driven wave action on coral reefs of Guam and implications for coral recruitment. *Coral Reefs* 25:193–199
- Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Mar Pollut Bull* 51: 408–415
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2:e711
- Callahan M, Wheaton J, Beaver C, Brooke S and others (2007) Coral reef evaluation and monitoring project 2006, executive summary. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL
- Carbindale BJ, Palmer SA, Swan CM, Brooks S, Poff NL (2002) The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83:412–422
- Chiappone M, Swanson DW, Miller SL (2002) Density, spatial distribution and size structure of sea urchins in Florida Keys coral reef and hard-bottom habitats. *Mar Ecol Prog Ser* 235:117–126
- Clarke CK, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- Dobson AP, Bradshaw AD, Baker AJM (1997) Hopes for the future: restoration ecology and conservation biology. *Science* 277:515–522
- Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecol Monogr* 77:3–18
- Entsch B, Boto KG, Sim RG, Wellington JT (1983) Phosphorus and nitrogen in coral reef sediments. *Limnol Oceanogr* 28: 465–476
- Epstein N, Bak RPM, Rinkevich B (2003) Applying forest restoration principles to coral reef rehabilitation. *Aquat Conserv: Mar Freshw Ecosyst* 13:387–395
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Genin A, Dayton PK, Lonsdale PF, Spiess FN (1986) Corals on seamounts: evidence of current acceleration over deep-sea topography. *Nature* 322:59–61
- Gladfelter WB, Gladfelter EH (1978) Fish community structure as a function of habitat structure on West Indian patch reefs. *Rev Biol Trop* 26:65–84
- Grabowski JH, Powers SP (2004) Habitat complexity mitigates trophic transfer on oyster reefs. *Mar Ecol Prog Ser* 277:291–295
- Hobbs RJ, Norton DA (1996) Toward a conceptual framework for restoration ecology. *Restor Ecol* 4:93–110
- Hudson JH, Anderson J, Franklin EC, Schittone J, Stratton A (2007) M/V Wellwood coral reef restoration monitoring report, monitoring events 2004–2006. Marine Sanctuaries Conservation Series NMSP-07-02, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD
- Hudson JH, Schittone J, Anderson J, Franklin EC, Stratton A (2008a) M/V Alec Owen Maitland coral reef restoration monitoring report, monitoring events 2004–2007. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-08-01, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD
- Hudson JH, Schittone J, Anderson J, Franklin EC, Stratton A (2008b) M/V Elpis coral reef restoration monitoring report, monitoring events 2004–2007. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-08-03, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551
- Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Kaufman LS (2006) If you build it, will they come? Toward a concrete basis for coral reef gardening. In: Precht WF (ed) *Coral reef restoration handbook*. CRC Taylor and Francis, Boca Raton, FL, p 119–142
- Kuffner IB, Paul VJ (2004) Effects of the benthic cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs* 23:455–459
- Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser* 323: 107–117

- Larkum AWD (1988) High rates of nitrogen fixation on coral skeletons after predation by the crown of thorns starfish *Acanthaster planci*. Mar Biol 97:503–506
- Lee SC (2006) Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. Oikos 112: 442–447
- Lenihan HS (1999) Physical–biological coupling on oyster reefs: how habitat form influences individual performance. Ecol Monogr 69:251–275
- Lindahl U, Ohman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. Mar Pollut Bull 42:127–131
- Lirman D, Biber P (2000) Seasonal dynamics of macroalgal communities of the northern Florida reef tract. Bot Mar 43: 305–314
- Lirman D, Miller MW (2003) Modeling and monitoring tools to assess recovery status and convergence rates between restored and undisturbed coral reef habitats. Restor Ecol 11:448–456
- McClanahan TR (1997) Primary succession of coral reef algae: differing patterns on fished versus unfished reefs. J Exp Mar Biol Ecol 218:77–102
- Miller MW (2002) The importance of evaluation, experimentation, and ecological process in advancing reef restoration success. In: Proc 9th Int Coral Reef Symp, Vol 2. International Coral Reef Society, Bali, Indonesia, p 977–981
- Miller MW, Szmant AM (2006) Lessons learned from experimental key-species restoration. In: Precht WF (ed) Coral reef restoration handbook. CRC Taylor and Francis, Boca Raton, FL, p 219–234
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233
- Moore M, Erdmann M (2002) EcoReefs: a new tool for coral reef restoration. Conservation in Practice 3:41–44
- Moschella PS, Abbiati M, Airola P, Anderson JM and others (2005) Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. Coast Eng 52:1053–1071
- Nestlerode JA, Luckenbach MW, O'Beirn FX (2007) Settlement and survival of the oyster *Crassostrea virginica* on created oyster reef habitats in Chesapeake Bay. Restor Ecol 15:273–283
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH and others (2005) Are U.S. coral reefs on the slippery slope to slime? Science 307:1725–1726
- Paul VJ, Thacker RW, Banks K, Golubic S (2005) Benthic cyanobacterial bloom impacts the reefs of South Florida (Broward County, USA). Coral Reefs 24:693–697
- Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Mar Environ Res 59:79–99
- Perkol-Finkel S, Shashar N, Barneah O, Ben-David-Zaslow R and others (2005) Fouling reefal communities on artificial reefs: Does age matter? Biofouling 21:127–140
- Richter C, Wunsch M, Rasheed M, Koetter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726–730
- Rinkevich B (2005) Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. Environ Sci Technol 39:4333–4342
- Symons LC, Stratton A, Goodwin W (2006) Streamlined injury assessment and restoration planning in the U.S. National Marine Sanctuaries. In: Precht WF (ed) Coral reef restoration handbook. CRC Press, New York, p 167–192
- Thacker RW, Paul VJ (2001) Relationships between cyanobacterial abundance and environmental factors on the reef flats of Guam. Bull Mar Sci 69:497–508
- Walters LJ, Hadfield MG, Smith CM (1996) Waterborne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. Mar Biol 126:383–393
- Wilkinson CL, Souter D (eds) (2008) Status of Caribbean coral reefs after bleaching and hurricanes in 2005. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville
- Zedler JB, Callaway JC (1999) Tracking wetland restoration: Do mitigation sites follow desired trajectories? Restor Ecol 7:69–73

Editorial responsibility: Laura Airola,
Ravenna, Italy

Submitted: September 24, 2008; *Accepted:* May 6, 2009
Proofs received from author(s): July 17, 2009