A COMPARISON OF FISH AND EPIBENTHIC ASSEMBLAGES

ON ARTIFICIAL REEFS WITH AND WITHOUT

COPPER-BASED ANTI-FOULING PAINT

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Dianna Rose Miller

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A COMPARISON OF FISH AND EPIBENTHIC ASSEMBLAGES ON ARTIFICIAL REEFS WITH AND WITHOUT COPPER-BASED ANTI-FOULING PAINT

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Dianna Rose Miller

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Date of Graduation

THESIS ABSTRACT

A COMPARISON OF FISH AND EPIBENTHIC ASSEMBLAGES ON ARTIFICIAL REEFS WITH AND WITHOUT COPPER-BASED ANTI-FOULING PAINT

Dianna Rose Miller

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Artificial reefs attract fish, but whether or not actual production occurs remains unclear. To examine this question, fish and epibenthic assemblages were compared between reefs with and without copper-based anti-fouling paint treatment. Artificial reefs (n = 60) were constructed approximately 28 km south of Dauphin Island, Alabama, in the Hugh Swingle reef-building zone. Twenty reefs (n = 20) were constructed during October 2005 (Reef Set 1), and forty reefs (n = 40) were constructed during July 2006 (Reef Set 2). Each reef consisted of twelve concrete blocks (20 X 20 X 41 cm) with four break-away sample bricks arranged on a plywood base (1.48 m^2) that were placed on the bottom at 20 m depths. Half of the reefs (n = 30) were coated with copper-based anti-fouling paint and the other half (n = 30) were left unpainted. Reef Set 1 was surveyed 1 week, 2, 7, 10, and 14 months after deployment, and Reef Set 2 was surveyed

11 months after deployment. During each survey, two SCUBA divers visually estimated the abundance and size of all fish species. Break-away sample bricks were removed from reefs for later identification and measurement of epibenthic organisms.

Copper painted reefs showed significantly lower mean total epibenthos coverage, biomass, diversity, and richness compared to unpainted reefs. Epibenthic assemblages also showed significant patterns of succession over the duration of the study period and no "climax" was reached. Observed patterns in fish recruitment were correlated with epibenthic assemblages on artificial reefs. Mean total fish abundance, diversity, and richness were significantly greater on unpainted compare to painted reefs. Red snapper, *Lutjanus campechanus* (Poey); wrasse, *Halichoeres* spp., (Rüppell); bank sea bass, *Centropristis ocyurus* (Jordan & Evermann); rock sea bass, *Centropristis philadelphica* (L.); blenny, Blenniidae spp.; and Atlantic spadefish, *Chaetodipterus faber* (Broussonet), showed significantly higher abundances on unpainted versus painted reefs. Additionally, fish assemblages showed significant seasonal patterns with time. This study showed that epibenthic assemblages affected recruitment of fishes to artificial reefs. Since these epibenthos are known food items for many reef fishes, our findings support the contention that artificial reefs result in increased fish production, not simply attraction.

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INTRODUCTION

Artificial structures in the sea have long been recognized for their ability to attract and concentrate dispersed fish from surrounding waters and fishers have used this knowledge worldwide in the construction of artificial reefs. Artificial reefs are quickly colonized by fish and epibenthic organisms, turning barren, unproductive substrate into highly productive environments (Stone, Pratt, Parker & Davis 1979). In time, artificial reefs may show similar fish densities or species compositions to those of natural reefs (Talbot, Russell & Anderson 1978; Stone *et al.* 1979; Bortone, Martin & Bundrick 1994; Carr & Hixon 1997). Artificial reefs also have proven useful for experimental investigations since they are easy to construct and manipulate, and because reef size and complexity can be standardized for replication (Gratwicke & Speight 2005).

Artificial reefs provide shelter from predation, sites for orientation and breeding, and serve as substrate for epibenthic assemblages that may provide a new forage base for fishes (Hueckel & Buckley 1987; DeMartini, Barnett, Johnson & Ambrose 1994; Steele 1999; Szedlmayer & Lee 2004). Reef colonization typically is rapid, with many fish present before food resources have had time to develop (Hueckel & Stayton 1982; Shulman 1984; Bohnsack, Harper, McClellan & Hulsbeck 1994). This suggests that artificial reefs initially provide shelter, and many studies have shown a positive correlation between refuge availability and juvenile fish survival or abundance (Shulman 1984, 1985; Hixon & Beets 1989, 1993; Caley & St John 1996; Steele 1999; Lingo & Szedlmayer 2006; Piko & Szedlmayer 2007). For example, Hixon and Beets (1993) found higher reef fish abundance on artificial reefs with holes compared to reefs without holes. In addition to their function as a predator refuge, artificial reefs may provide food resources that are important for fish recruits (Buckley & Hueckel 1985; Relini, Relini, Torchia & De Angelis 2002; Szedlmayer & Lee 2004). Studies have suggested that fish become more abundant with the development of epibenthic assemblages on artificial reefs (Buckley & Hueckel 1985; Hueckel & Buckley 1987). Hueckel and Buckley (1987) found that fish became more abundant on artificial reefs in Puget Sound, Washington, as epibenthic assemblages progressed from barnacles to algal mats containing shrimp and crab prey.

Food resources develop over time as algae, invertebrates, and fish colonize artificial reefs. The development of epibenthic assemblages is a highly variable process that depends on substrate type and complexity, time since deployment, environmental variables, competition, and grazing pressure (Osman 1977; Hixon & Brostoff 1985). Pioneer species such as algae, barnacles, and serpulid worms are typically among the first colonizers on artificial reefs (Fager 1971; Ardizzone, Gravina & Belluscio 1989; Relini, Zamboni, Tixi & Torchia 1994; Boaventura, Moura, Leitão, Carvalho, Cúrdia, Pereira, Cancela da Fonseca, Neves dos Santos & Costa Monteiro 2006). Although initial colonization is rapid, slower colonizing taxa continue to settle, gradually replacing early colonizers (Ardizzone *et al.* 1989; Wendt, Knott & Van Dolah 1989). Epibenthic assemblages on artificial reefs may through time, converge towards that of natural reefs, but more often they appear to differ, and functional relations between natural and artificial reef assemblages remain unclear (Hixon & Brostoff 1985; Wendt *et al.* 1989; Perkol-Finkel & Benayahu 2007).

Many studies have shown that reef fishes can obtain substantial food resources from artificial reefs (Hueckel & Stayton 1982; Hueckel & Buckley 1987; Vose 1990; Vose & Nelson 1994; Relini *et al.* 2002; Ouzts & Szedlmayer 2003; Szedlmayer & Lee 2004). For example, Szedlmayer and Lee (2004) showed that red snapper, *Lutjanus campechanus* (Poey), fed on increasing amounts of reef-associated fish prey as they moved from open sand to artificial reef habitats. Gray triggerfish, *Balistes capriscus* (Gmelin), also forage on artificial reefs, consuming a variety of epibenthic invertebrates including barnacles and bivalves (Vose 1990; Vose & Nelson 1994; Szedlmayer & Blitch in prep). In a study in the Mediterranean Sea, three of the four fish species examined fed on reef-associated prey, and 91% of the prey items consumed by annular seabream, *Diplodus annularis* (L.), were exclusive to artificial reefs (Relini *et al.* 2002). Hueckel and Stayton (1982) found that the contribution of reef-associated prey to the diets of reef fishes depended on both fish species and size. Medium and large striped seaperch, *Embiotoca lateralis* (Agassiz), and quillback rockfish, *Sebastes maliger* (Jordan & Gilbert), fed mostly on artificial reefs, whereas small fish foraged in the nearby sand (Hueckel & Stayton 1982).

In contrast, other studies have suggested fish depend little on food resources from artificial reefs (Randall 1963; Shulman 1984; Lindquist, Cahoon, Clavijo, Posey, Bolden, Pike, Burk & Cardullo 1994; Ibrahim, Ambak, Shamsudin & Samsudin 1996; Nelson & Bortone 1996). Nelson and Bortone (1996) showed that many commercially important reef-associated fishes in the northern Gulf of Mexico fed on fishes, crabs, squids, polychaetes, and shrimps that were obtained from surrounding sandy habitat. Examination of stomach content showed that fishes associated with fish aggregating devices (FADs) did not consume attached organisms (Ibrahim *et al.* 1996), and fish associated with artificial habitat in St. John, Virgin Islands foraged in adjacent seagrass beds rather than on reef prey (Randall 1963).

It is clear that artificial reefs attract fish, but whether or not they lead to increased fish production remains unclear (Bohnsack & Sutherland 1985; Alevizon & Gorham 1989; Bohnsack 1989; Polovina 1989; Polovina & Sakai 1989; Bohnsack *et al.* 1994; DeMartini *et al.* 1994). Polovina (1989) suggested that artificial reefs may attract fish to known locations where they are easily harvested, potentially decreasing overall fish biomass. Polovina and Sakai (1989) used time series catch and effort data to show that flatfish catches near Shimamaki, Japan were related to attraction to artificial reefs, not enhanced fish production. Bohnsack (1989) suggested that artificial habitats function as nothing more than fish attractors when natural food and shelter resources are plentiful and fish abundance is limited by something else, like recruitment or exploitation. However, in areas lacking natural reef habitat, artificial reefs may increase fish carrying capacity by providing critical food and shelter resources, and thereby enhancing fish production.

Nearly all studies on artificial reefs have focused on fishery ecology while disregarding the development of epibenthic assemblages (Relini *et al.* 1994; Svane & Petersen 2001), furthermore, the few studies that have examined both fish and epibenthic assemblages involved variable reef complexity or poor reef replication (Buckley & Hueckel 1985; Hueckel & Buckley 1987; Relini *et al.* 2002). Under all circumstances, newly deployed artificial reefs are sources of new substrate for the settlement and recruitment of epibenthic species (Svane & Petersen 2001). Since epibenthos are important in the diets of many reef fishes, the successive development of epibenthic assemblages on artificial reefs should be studied together with fish recruitment. In addition to biological descriptions, the physical environment should be defined, and moreover, studies should aim to standardize reef complexity and provide independent sampling with replication in both time and space (Underwood 1996; Underwood, Chapman & Connell 2000).

In this study, we examined the effects of epibenthic assemblages (i.e. mobile and sessile organisms associated with hard substrate surfaces) on the recruitment of reef fishes to artificial habitats. The null hypothesis is that epibenthos development does not affect reef fish assemblages, and we tested this hypothesis by comparing fish assemblages on reefs without versus those with epibenthos. To make this comparison, copper-based paint was used to inhibit the development of epibenthos on half of the artificial habitats. Copper-based paints were originally developed to prevent the growth of epibenthic “fouling” on boat hulls, since copper is toxic to newly-settled invertebrates. Several studies have used copper anti-fouling paints to manipulate the development of epibenthic assemblages (Bosman & Hockey 1988; Farrell 1988), but only one study has examined its effect on reef fish recruitment (Redman & Szedlmayer in review). The objective of this study was to compare fish assemblages on reefs with and without epibenthos, and to describe both fish and epibenthos assemblages.

MATERIALS AND METHODS

Laboratory Experiment: Fish Avoidance Behavior of Copper

In the laboratory, we tested potential fish avoidance behavior of painted reefs due to copper toxicity. Two common species of reef fish, red snapper, *Lutjanus campechanus* (Poey), and gray triggerfish, *Balistes capriscus* (Gmelin), were placed in a 1200 L circular tank, which was part of a 14 080 L recirculating seawater system. The experimental tank contained two painted blocks on one side of the tank and two unpainted blocks on the opposite side. For each trial, 6 *L. campechanus*, 6 *B. capriscus*, or 3 *L. campechanus* and 3 *B. capriscus* were placed in the experimental tank and their behaviors were recorded for 1 h with a video camcorder (TR101 Hi-8, Sony) mounted above the tank. We completed 11 trials with 66 fish. Video tapes were reviewed with Image Pro-Plus 4.5 software and fish positions recorded in relation to the painted and unpainted blocks.

Field Experiment: Painted versus Unpainted Artificial Reefs

Study Site

The north-central Gulf of Mexico is primarily flat mud and sand with little vertical relief (Ludwick 1964; Parker, Colby & Willis 1983; Schroeder, Shultz, Fleischer, Briggs & Dindo 1987). Parker *et al.* (1983) found that the offshore habitat between Pensacola, Florida and Pass Cavallo, Texas was 69% mud, 27% sand/shell and only 3% natural reef. These few natural reefs support diverse assemblages of fish, including Serranids, Lutjanids, Labrids, and Sciaenids, and also invertebrates, including sponges, ahermatypic corals, and gorgonians (Smith 1976; Dennis & Bright 1988; Gittings, Bright, Schroeder, Sager, Laswell & Rezak 1992). In addition to these natural reefs, over 15 000 artificial reefs have been deployed in the Hugh Swingle reef-building zone in Alabama waters, and these reefs probably increase hard substrate habitat for fish and epibenthic assemblages (Minton & Heath 1998).

Experimental Design

Artificial reefs (n = 100) were constructed 28 km south of Dauphin Island, Alabama, in the Hugh Swingle reef-building zone (Fig. 1). Forty reefs (n = 40) were initially constructed from 11 to 25 August 2005, however these reefs were immediately destroyed by Hurricane Katrina. Twenty new reefs (n = 20) were constructed on 10 and 12 October 2005 (Reef Set 1), and forty additional reefs (n = 40) were constructed from 18 to 26 July 2006 (Reef Set 2), for a total of 60 reefs (n = 60). Each reef consisted of twelve concrete blocks (20 X 20 X 41 cm with two 14 X 14 cm holes) arranged on a plywood base (1.48 m^2) that were placed on the bottom at 20 m depths (Fig. 2). Fitzhardinge and Baily-Brock (1989) recommended concrete for artificial reef construction because it is durable in seawater and supports diverse epibenthic assemblages compared to other substrates such as tires and metal, which are poor substrates for epibenthos development. Half of the reefs (*n* = 30) were coated with copper-based anti-fouling paint (34% copper, 214-7070, Ameron International) and the other half were left unpainted. Reefs were deployed in transects of 10 reefs each, alternating between painted and unpainted reefs spaced at 30 m intervals. Concrete blocks were arranged by two SCUBA divers and secured to the plywood base using 1.2 m plastic cable ties. Additionally, each reef had four small "break-away" concrete bricks (9 X 6 X 20 cm) placed on the larger blocks and secured with 30 cm cable ties (Nelson, Savercool, Neth & Rodda 1994; Fig. 2). Reefs were anchored in place with a 1.5 m nylon rope tied to a 1.2 m metal ground anchor embedded in the substrate. Reefs also were labeled with numbered metal or plastic tags for diver identification.

Reef Surveys

Reef Set 1 (*n* = 20) was initially surveyed 1 week after construction, on 20 October 2005. Reef Set 1 was then repeatedly surveyed, through December 2006 at 2, 7, 10, and 14 months after deployment. Reef Set 2 (*n* = 40) was surveyed once, 11 months after deployment, in June 2007. During each survey, two SCUBA divers used discrete group census methods to identify fish species, abundance, and size class (length in 2.5 cm intervals; Greene & Alevizon, 1989). Since reefs were small (1.48 m^2), all fish were counted. Reefs also were video recorded to confirm species identification and record rare or unknown species for later identification. Break-away sample bricks were removed from reefs, with one brick collected per reef on each survey. Bricks were placed in cloth sample bags (25 X 43 cm, #5250, Hubco Protexo) and preserved in alcohol-based preservative (NOTOXhisto fixative, Scientific Device Laboratory) for later analysis of epibenthic assemblages. Water samples were collected from the seawater directly surrounding each reef for measurement of copper levels. Salinity (ppt), temperature (°C), and dissolved oxygen (ppm) were recorded on each survey with a YSI 6920 meter.

Epibenthos Analysis

All epibenthic organisms on the top surface of each break-away brick were counted, measured, and identified to the lowest possible taxon. The side surfaces of the bricks were not analyzed since epibenthic organisms on the sides were frequently damaged during brick removal. The top of each brick was photographed with a digital camera (PowerShot A530, Canon). Photographs were size calibrated and analyzed with Image Pro-Plus 4.5 software to measure and record the surface area coverage (mm^2) of each individual organism. Coverage was reported relative to the brick area as cm^2 100 cm^{-2}. Both mobile and sessile epibenthic organisms were measured as coverage. In some cases, individuals overlapped so that total epibenthos coverage per brick may be greater than the total brick area (i.e. percent coverage per brick may be > 100%). Coverages of colonial or encrusting species [e.g. sabellid worms, Sabellidae (Malmgren); sea mat bryozoan, *Membranipora tenuis* (Desor); bugula bryozoans, *Bugula neritina* (L.); sponges, Demospongiae (Sollas)] were measured in clusters, since it was impossible to distinguish individual organisms. Brick sample bags contained many mobile epibenthic organisms, and additional sessile epibenthic organisms which had fallen off the bricks. To count and measure these organisms, bag contents were sieved through a 500 μm sieve to remove sand, mud, and any microbenthos that were present. These organisms were counted, photographed, measured with Image Pro-Plus software, and identified to the lowest possible taxon.

Following measurement of epibenthos coverage, all organisms were scraped from the top of each brick. These scraped epibenthos samples, and the organisms from the corresponding sample bags were then dried in a drying oven at 60°C until dry. Samples were weighed to the nearest 0.01 gram and weight was reported as DW (dry weight) g 100 cm^{-2}.

Statistical Analysis

Fish and epibenthos assemblages were compared with the Shannon-Weiner diversity index,

$$H' = \sum - p_i \ln (p_i)$$

where p_i is the proportion of the total count of the i^{th} species, richness or the total number of species present in the sample, and evenness,

$$J = H' / H'max$$

where H′max is the maximum possible value for H′ if all species were equally abundant

(Magurran 1988).

Patterns in fish and epibenthic assemblages between reef types and survey periods were compared using non-parametric multidimensional scaling (MDS; Szedlmayer & Able 1996; Lingo & Szedlmayer 2006). Fish and epibenthos abundance data were square root transformed to reduce the weight of highly abundant species (Field, Clarke & Warwick 1982). Bray-Curtis similarity coefficients were calculated,

$$S_{jk} = 1 - \{ \sum | Y_{ij} - Y_{ik} | / \sum (Y_{ij} + Y_{ik}) \}$$

where Y_{ij} is the score for the i^{th} species in the j^{th} sample, Y_{ik} is the score for the i^{th} species in the k^{th} sample, and S_{jk} is the similarity between the j^{th} and k^{th} samples based on all species (Field *et al.* 1982). These coefficients were calculated among individual reefs and mapped as MDS ordination plots by survey. Analysis of similarities (ANOSIM) was also used to compare fish and epibenthic assemblages between reef types (Clarke & Warwick 2001).

Reef Set 1 was surveyed multiple times, and repeated measures analysis of variance (rmANOVA) was used to compare mean abundance (m^{-2}) of dominant fish species (>1% of the total abundance), mean total abundance (m^{-2}), mean coverage (cm^2 $100\ cm^{-2}$) of dominant epibenthic species (>1% of the total coverage), mean total coverage (cm^2 $100\ cm^{-2}$), and mean epibenthos biomass (DW g $100\ cm^{-2}$) between reef types over all survey periods. Community variables (H′, S, J) for fish and epibenthos were also compared between reef types with rmANOVA. Stepwise multiple regression was used to analyze relations among water temperature, salinity, dissolved oxygen, and mean total fish abundance and epibenthos coverage. Reef Set 2 was surveyed once, and analysis of variance (ANOVA) was used to compare mean abundance (m^{-2}) of dominant fish species, mean total abundance (m^{-2}), mean coverage (cm^2 100 cm^{-2}) of dominant epibenthic species, mean total coverage (cm^2 100 cm^{-2}), mean epibenthos biomass (DW g 100 cm^{-2}), and community variables (H′, S, J) for fish and epibenthos between reef types. Tests were considered significant at $\alpha < 0.10$. When significant differences were detected, Student-Newman-Keuls test was used to determine specific differences.

RESULTS

Laboratory Experiment: Fish Avoidance Behavior of Copper

Video from the avoidance behavior experiment was reviewed and fish positions were compared between block types. Fish showed significant ($P < 0.01$) preference for painted compared to unpainted block types.

Field Experiment: Painted versus Unpainted Artificial Reefs

During reef surveys, water samples were collected from all reefs and tested for the presence of copper. Copper was detected in seawater from painted reefs (mean $\pm$ SE = 0.27 ± 0.1 ppm) for the first survey (October 2005) of Reef Set 1. No detectable copper levels were found for any survey after the first week.

Reef Set 1

Fish

Reef Set 1 ($n = 20$) was surveyed five times, for a total of 100 surveys. Individuals from 33 different fish species were observed, with 1307 individuals on unpainted reefs and 963 individuals on painted reefs. Mean total abundance showed a significant ($P < 0.01$) interaction between reef type and survey period (Appendix 1). In

August 2006, mean total abundance (m^{-2}) was significantly ($P < 0.05$) greater for unpainted versus painted reefs (Fig. 3). Dominant species included red snapper, *Lutjanus campechanus* (Poey); wrasse, *Halichoeres* spp., (Rüppell); tomtate, *Haemulon aurolineatum* (Cuvier); gray triggerfish, *B. capriscus* (Gmelin); lane snapper, *Lutjanus synagris* (L.); sand perch, *Diplectrum* spp., (Holbrook); cocoa damselfish, *Stegastes variabilis* (Castelnau); pigfish, *Orthopristis chrysoptera* (L.); bank sea bass, *Centropristis ocyurus* (Jordan & Evermann); blenny, Blenniidae; rock sea bass, *Centropristis philadelphica* (L.); greater amberjack, *Seriola dumerili* (Risso); and Atlantic spadefish, *Chaetodipterus faber* (Broussonet; Table 1). These 13 species were each >1% of the total abundance and together accounted for 95.2% of all the fish observed during the study period. The remaining 20 species made up 4.8% of all observed fish (Appendix 2).

Lutjanus campechanus ($P = 0.088$), *Halichoeres* spp., ($P < 0.05$), Blenniidae ($P < 0.05$), and *C. faber* ($P = 0.09$) were significantly more abundant on unpainted compared to painted reefs (Fig. 4, Appendix 1). No significant abundance differences were detected between reef types for the other common fish species (Table 1). The abundances of *Halichoeres* spp., Blenniidae, and *C. faber* showed significant interaction between reef type and survey period ($P < 0.05$). Significantly higher abundances were detected for *Halichoeres* spp., and Blenniidae in August 2006, and *C. faber* December 2005 on unpainted compared to painted reefs (Fig. 5). Overall, there was little difference in mean total fish length (mm) between reef types for dominant fish species, with the exception of *Halichoeres* spp. and *B. capriscus* with larger fish found on unpainted versus painted reefs (Fig. 6). Additionally, mean total length (mm) of *L. campechanus*, *L. synagris*, and *B. capriscus* decreased in December 2006 (Fig. 6).

Water temperature ranged from 17.1 to 27.9 °C, and was significantly correlated ($P < 0.01$) with mean total fish abundance, reflecting seasonal changes. In contrast, dissolved oxygen (ppm) and salinity (ppt) were negatively correlated ($P < 0.01$) with fish abundance. However, dissolved oxygen ranged from 4.8 to 7.8 ppm and salinity ranged from 33.3 to 35.4 ppt, and since these conditions are well within the range of tolerance for most marine organisms, they probably had little biological effect on fish assemblages (Table 2). Visual inspection of the MDS plot of Bray-Curtis similarities showed separation by reef type for surveys in December 2005 and August 2006 (Fig. 7). These separations were significant ($P < 0.05$) based on analysis of similarities (ANOSIM; Fig. 7). Mean fish richness ($P < 0.05$) was significantly greater on unpainted versus painted reefs, while mean fish evenness ($P < 0.05$) was significantly greater on painted versus unpainted reefs for Reef Set 1 (Table 3). A significant interaction ($P < 0.05$) was detected for mean diversity between reef type and survey period. Significant differences ($P < 0.01$) were detected for all community variables among survey periods (Table 3).

Most of the dominant reef fishes found on artificial reefs in this study are known to feed on epibenthic organisms found on reef habitats (Table 4). Common epibenthic organisms consumed by reef fishes include crabs, shrimp, gastropods, and polychaetes.

Epibenthos

Epibenthos samples ($n = 74$) were collected in December 2005, May 2006, August 2006, and December 2006. A total of 35 epibenthic species were identified, covering a total area of 5412 cm^2 on unpainted bricks and 2155 cm^2 on painted bricks for Reef Set 1. Mean total coverage and mean total biomass showed significant ($P < 0.01$) interactions between reef type and survey period. Mean total coverage (cm^2 100 cm^{-2}) and mean total biomass (DW g 100 cm^{-2}) were significantly ($P < 0.05$) greater for unpainted versus painted bricks in May, August, and December 2006 (Figs 8 and 9). Mean total biomass (DW g 100 cm^{-2}) was 78% greater in December 2005, 85% greater in May 2006, 78% greater in August 2006, and 47% greater in December 2006 on unpainted compared to painted reefs (Fig. 9). Barnacles, *Balanus* spp., (Da Costa), covered the greatest area, followed by bugula bryozoans, *Bugula neritina* (L.); sabellid worms, Sabellidae (Malmgren); purse oysters, *Isognomon* spp., (Lightfoot); sponges, Demospongiae (Sollas); mud crabs, *Panopeus* spp., (Edwards); and sea mat bryozoans, *Membranipora tenuis* (Desor; Table 5). These seven species each covered >1% of the total coverage and together accounted for 93.1% of the total coverage on bricks from Reef Set 1. The remaining 28 species made up 6.9% of the total coverage (Appendix 3).

Balanus spp., ($P < 0.01$), *Isognomon* spp., ($P < 0.01$), Demospongiae ($P < 0.01$), *Panopeus* spp., ($P < 0.01$), and *M. tenuis* ($P < 0.05$) had significantly greater coverage on unpainted compared to painted bricks (Fig. 10). No significant coverage differences were detected between reef types for the other dominant epibenthic species (Table 5). The coverages of *Balanus* spp., *Isognomon* spp., Demospongiae, *Panopeus* spp., and *M. tenuis* were significantly affected by the interaction between reef type and survey period ($P < 0.05$). Greater coverages on unpainted compared to painted bricks were detected for

Balanus spp., in May and August 2006, *Isognomon* spp., and *Panopeus* spp., in May, August, and December 2006, Demospongiae in August and December 2006, and *M. tenuis* in December 2006 (Fig. 11).

Dissolved oxygen (ppm) was significantly negatively correlated ($P < 0.01$) with total epibenthos coverage, but probably had little biological effect on these epibenthic assemblages (Table 2). Visual inspection of the MDS plot of Bray-Curtis similarities showed separation by reef type for all surveys (Fig. 12). These separations were significant ($P < 0.01$) based on ANOSIM (Fig. 12). Mean epibenthos diversity ($P < 0.01$) and richness ($P < 0.01$) were significantly greater on unpainted versus painted reefs, while evenness ($P < 0.01$) was significantly greater on painted versus unpainted reefs for Reef Set 1 (Table 6). Significant differences were detected for all community variables among survey periods ($P < 0.01$; Table 6). In addition, all community variables were significantly affected by the interaction between reef type and survey period ($P < 0.01$).

Reef Set 2

Fish

Reef Set 2 ($n = 40$) was surveyed once, from 6 to 11 June 2007. Individuals from 18 different fish species were observed, with 566 individuals on unpainted reefs and 610 individuals on painted reefs. No significant differences were detected for mean total abundance (m^{-2}) between reef types ($P = 0.73$). *Lutjanus campechanus* was the most abundant species, followed by *C. philadelphica*, *B. capriscus*, *O. chrysoptera, L.*

synagris, whitespotted soapfish, *Rypticus maculatus* (Holbrook); *C. ocyurus, Diplectrum* spp., and *H. aurolineatum* (Table 7). These 9 species were each >1% of the total abundance and together accounted for 97.4% of all the fish observed during the study period. The remaining 9 species made up 2.6% of all observed fish (Appendix 4).

Centropristis philadelphica ($P < 0.01$) and *C. ocyurus* ($P = 0.02$) were significantly more abundant on unpainted versus painted reefs for Reef Set 2, however, *B. capriscus* ($P = 0.01$) were significantly more abundant on painted versus unpainted reefs (Fig. 13). No significant differences were detected for community variables between reef types (diversity $P = 0.31$, richness $P = 0.73$, evenness $P = 0.\ 10$; Table 8). Visual inspection of the MDS plot of Bray-Curtis similarities showed separation by reef type, and separation was significant ($P < 0.01$) based on ANOSIM (Fig 14).

Epibenthos

For Reef Set 2, sample bricks ($n = 40$) were collected from each reef. A total of 43 different epibenthic species were identified, covering a total area of 2722 cm^2 on unpainted bricks and 320 cm^2 on painted bricks. Many large, empty *Balanus* shells were observed on bricks from Reef Set 2, so "dead *Balanus* spp." were counted as a separate category. Mean total coverage (cm^2 100 cm^{-2}) and biomass (DW g 100 cm^{-2}) were significantly ($P < 0.01$) greater for unpainted versus painted bricks (Fig. 15). Mean total biomass (DW g 100 cm^{-2}) was 89% greater on unpainted compared to painted reefs (Fig. 15). Demospongiae covered the greatest area, followed by Sabellidae, tubular bryozoans, Gymnolaemata; dead *Balanus* spp., *M. tenuis*, (living) *Balanus* spp., *Panopeus* spp., urchins, Echinometridae (Gray); *B. neritina*, algae, Chlorophyta; well-ribbed dovesnails, *Anachis lafresnayi* (Fischer & Bernardi); Florida dovesnails, *Costoanachis floridana* (Rehder); gray pygmy venus, *Timoclea grus* (Holmes); and *Isognomon* spp., (Table 9). These 14 species each covered >1% of the total coverage and together accounted for 95.6% of the total coverage on bricks from Reef Set 2. The remaining 29 species made up 4.4% of the total coverage (Appendix 5).

Demospongiae ($P < 0.01$), Sabellidae ($P < 0.01$), Gymnolaemata ($P < 0.05$), dead *Balanus* spp., ($P < 0.01$), *M. tenuis* ($P = 0.01$), *Panopeus* spp., ($P < 0.01$), Echinometridae ($P < 0.05$), *A. lafresnayi* ($P < 0.01$), *C. floridana* ($P < 0.01$), and *T. grus* ($P < 0.01$) had significantly greater coverages on unpainted bricks versus painted bricks, while (living) *Balanus* spp., ($P < 0.01$) had significantly greater coverage on painted versus unpainted bricks (Fig. 16). Mean epibenthos diversity ($P < 0.01$) and richness ($P < 0.01$) were significantly greater on unpainted versus painted reefs (Table 10). No significant differences were detected for mean epibenthos evenness ($P = 0.75$) between reef types. Visual inspection of the MDS plot of Bray-Curtis similarities showed separation by reef type, and separation was significant ($P < 0.01$) based on ANOSIM (Fig. 17).

DISCUSSION

Epibenthos development

Mean total epibenthos coverage, biomass, diversity, and richness were significantly greater on unpainted versus painted reefs. These findings are consistent with past studies that found lower epibenthos coverage on copper-painted surfaces (Lee & Trott 1973; Redman & Szedlmayer in review). Time since reef deployment also affected recruitment of epibenthic species, with significant increases in mean epibenthos diversity and richness over time. On painted reefs in Reef Set 1, mean total epibenthos coverage and biomass showed an increasing trend for the duration of the study period as the copper paint became less effective with time. After 1 to 3 years submersion, copper release rates decline to levels that are not sufficient to prevent epibenthos recruitment.

Epibenthos Succession

The concept of succession in the marine environment implies a series of predicable and successive replacements of individuals as the amount of open space changes due to growth, competition, and predation (Dayton 1971; Sousa 1985). Many studies have observed succession patterns in epibenthic assemblages on artificial habitats, without a dominating final "climax" (Ardizzone *et al.* 1989; Relini *et al.* 1994; Butler &

Connolly 1999). In this study, succession patterns in epibenthic assemblages were observed on artificial reefs. Early colonizers included *Balanus* spp., common jingle, *Anomia simplex* (D'Orbigny); serpulid worms, Serpulidae (Johnston); and Sabellidae. Other studies also found barnacles and serpulid worms among the earliest colonizers on artificial reefs (Ardizzone *et al.* 1989, Relini *et al.* 1994; Boaventura *et al.* 2006). Over time, coverage of slower growing, encrusting or colonial organisms, including *Isognomon* spp., Demospongiae, *B. neritina*, and *M. tenuis*, and mobile invertebrates, including *Panopeus* spp., *A. lafresnayi*, *C. floridana*, and shrimp, Alpheoidea (Rafinesque); increased on artificial reefs. Mean total coverage showed no significant increases over the last three surveys, however, relative coverages of the various species continued to change. This suggests that a stable "climax" was not reached and that further changes in the coverages of the various epibenthic species would occur with time. Relini *et al.* (1994) studied epibenthic assemblages on artificial reefs in the northwestern Mediterranean and found that after five years submersion no climax had been reached, and coverage of sponges and large algae continued to increase. In this study, epibenthic algae was rare on artificial reefs, but this was probably not related to fish grazing since few of the dominant reef fishes were herbivores. The lack of algae may have been related to grazing activity of epibenthic organisms or lack of light, but further study is needed.

A wide variety of epibenthic organisms colonized both painted and unpainted reefs. However, epibenthic assemblages on the artificial reefs in the present study showed little similarity to that of nearby natural reefs. Notably absent were the large gorgonians and ahermatypic corals common on natural reefs in the northern Gulf of Mexico (Gittings *et al.* 1992). However, a few corals [e.g. northern star coral, *Astrangia poculata* (Ellis & Solander); tube coral, *Cladocora arbuscula* (Lesueur)] were found on Reef Set 2, and perhaps recruitment of these species would have increased with time. Bailey-Brock (1989) also reported that corals were slow to recruit to an artificial reef in Hawaii, however, coral densities increased with time.

Fish Recruitment

Epibenthos may affect fish assemblages on artificial reefs (Buckley & Hueckel 1985; Hueckel & Buckley 1987; Relini *et al.* 2002), and in this study, significant differences in fish assemblages were found between painted and unpainted reef types. Mean total fish abundance and the abundances of *L. campechanus*, *Halichoeres* spp., Blenniidae, and *C. faber* were significantly greater on unpainted versus painted reefs for Reef Set 1, and the abundances of *C. philadelphica*, and *C. ocyurus* were significantly greater on unpainted versus painted reefs for Reef Set 2. These reef fish species are known to feed on reef prey types, and thus, the greater epibenthic assemblages on unpainted reefs provided greater food resources (Randall 1967; Ross, Pavela & Chittenden 1989; Bullock & Smith 1991; Clifton & Motta 1998; Szedlmayer & Lee 2004). Additionally, *B. capriscus* and *Halichoeres* spp. were larger on unpainted compared to painted reefs for Reef Set 1, which may have been related to increased epibenthic prey. On Reef Set 1, specific preference for unpainted reefs was detected for *Halichoeres* spp., and Blenniidae in August 2006, and for *C. faber* in December 2005.

This suggested that time since reef deployment also affected recruitment of fish species. Initial recruitment of reef fishes on newly deployed artificial reefs occurs before epibenthic assemblages have developed. However, epibenthos coverage increases with time, and may eventually affect reef fish abundance by providing a new forage base. Hueckel and Buckley (1987) found that fish became more abundant on artificial reefs in Puget Sound, Washington, as epibenthic shrimp and crab prey items increased. In this study, mean total epibenthos coverage peaked in August 2006, and may have affected the abundances of *Halichoeres* spp., and Blenniidae, which were also significantly greater in August 2006 compared to the other surveys. Diet studies have shown that fish may obtain substantial food resources from artificial reefs (Hueckel & Stayton 1982; Hueckel & Buckley 1987; Vose 1990; Vose & Nelson 1994; Relini *et al.* 2002; Ouzts & Szedlmayer 2003; Szedlmayer & Lee 2004), and in this study, *Halichoeres* spp., and Blenniidae may have consumed epibenthos on artificial reefs. Randall (1967) found that Blenniidae fed primarily on algae and detritus, and *Halichoeres* spp., fed on crabs, gastropods, shrimps, and polychaetes. These prey types were present on reefs in this study and may have provided a forage base for these species. Additionally, Topolski and Szedlmayer (2004) found that abundances of Blenniidae on artificial structures in the northcentral Gulf of Mexico were positively related to barnacles, and that Blenniidae used empty barnacle shells as shelter. In this study, Blenniidae abundance may have been related to coverage of *Balanus* barnacles on artificial reefs, which also peaked in August.

Seasonality of Fish Abundance

In this study, seasonal changes in fish assemblages were observed on Reef Set 1. Mean total fish abundance, and mean fish diversity and richness showed significant increases across surveys, peaked in August 2006, then declined by December 2006. Other studies have also observed declines in fish abundance in the winter (Bohnsack *et al.* 1994; Redman & Szedlmayer in review). This decline in fish abundance may be related to declines in epibenthos that occur during winter, causing fish to seek other foraging habitats. Osman (1977) found that settlement and growth of epibenthos declines to a minimum in the winter. In this study, mean epibenthos diversity and richness showed significant declines between August and December 2006, although no significant declines in mean total epibenthos coverage or biomass were found. Mean total fish abundance peaked in late summer, and water temperature was a significant predictor of total abundance. Increased fish abundance in summer was in part due to the seasonal appearance of juvenile tropical species including *Halichoeres* spp., *S. variabilis*, and Blenniidae. Mean abundance of these three species showed significant peaks in August 2006, with significantly less fish observed in other months. Smith (1976) also observed warm-water seasonal increases in numbers of species and individuals for tropical fish species, including *Halichoeres* spp., on reefs in the northeastern Gulf of Mexico. Additionally, the peak in mean total fish abundance in August 2006 may have been related to the seasonal settlement of many reef fishes, including *L. campechanus* and *B.*

capriscus. Szedlmayer and Lee (2004) reported *L. campechanus* moving to structured habitat in early September, and Simmons and Szedlmayer (in prep) reported that *B. capriscus* on artificial reefs were smallest in the fall compared to the other sampling months, suggesting this species may settle onto reefs at that time. In this study, mean total length of several fish species, including *L. campechanus*, *B. capriscus*, and *L. synagris* decreased in December 2006, probably due to the seasonal settlement of new recruits. Season had a significant affect on the abundances of many fish species, however *Diplectrum* spp., were initially the dominant species on Reef Set 1, but showed no significant changes in abundance across survey periods. This suggested that the abundance of this species was not significantly affected by the presence of artificial reefs. Similarly, Bullock and Smith (1991) found that *Diplectrum* spp., were most commonly associated with mud-silt, or sandy substrates.

Copper paint treatment

A potential problem of this study was that copper toxicity may inhibit fish recruitment. However, following submersion, painted surfaces soon become covered with a thin bio-film that slows the release of copper to low levels (8-22 $\mu g\ cm^{-2}\ day^{-1}$), while still preventing epibenthos development (Dempsey 1981; Valkirs, Seligman, Haslbeck & Caso 2003). Additionally, the constant water flow in the open Gulf of Mexico prevents accumulation of copper in the surrounding seawater. Water samples were collected from the seawater directly surrounding the reefs and tested for copper. Copper was detected at very low concentrations (< 1 ppm) on painted reefs one week after deployment, but was not detected on any reefs on subsequent surveys of Reef Set 1, or on Reef Set 2. Additionally, fish in the laboratory experiment showed no avoidance behavior of copper-painted blocks. Instead, fish showed preference for the copper-painted blocks, which may have been related to color, but further study is needed. Therefore, any differences in fish abundance between reef types were not related to copper toxicity, but rather the differences in epibenthos assemblages between reef types.

Treatment Effects

Copper paint was useful for preventing epibenthos development on artificial reefs, however, an unpredicted consequence of this treatment was differential degradation of reefs with time. Lee and Trott (1973) found that copper-based paints prevented fouling on woody substrates compared to wood without copper paint treatment. In this study, painted reefs were constructed on painted plywood bases, while the wood was not painted for unpainted reefs. With time, fouling organisms on the unpainted plywood bases caused greater structural degradation of unpainted reefs compared to that of painted reefs. Wooden reef bases became soft and broke apart, allowing concrete blocks to separate from the main reef and become partially buried in the surrounding substrate. This effect was mild towards the end of the study for Reef Set 1, but far more pronounced on unpainted reefs for Reef Set 2. The smaller profile of unpainted reefs in Reef Set 2 may have lead to the lower total fish abundance compared to painted reefs. Therefore, the significantly greater abundances of *C. philadelphica* and *C. ocyurus* on unpainted versus painted reefs for Reef Set 2 further support the contention that epibenthos assemblages have a significant affect on reef fish recruitment.

Differential Balanus Mortality between Reef Types

Analysis of the epibenthic assemblages on Reef Set 2 yielded unpredicted results. For Reef Set 2, dead *Balanus* spp., were abundant and were counted as a separate category. Although empty *Balanus* shells would not provide a forage base for fishes, nearly all of the empty shells contained *Panopeus* spp., or Alpheoidea. Thus, these empty shells may have affected reef fishes indirectly by providing microhabitat, and increasing abundances of other reef prey items. Coverage of dead *Balanus* was significantly greater on unpainted versus painted reefs, and conversely, painted reefs had significantly greater coverage of living *Balanus*. The increased *Balanus* mortality on unpainted reefs was probably due to interspecific interactions (e.g. predation, competition) within the epibenthic assemblage. Several large epibenthic species [e.g. Echinometridae; Florida rocksnails, *Stramonita haemastoma* (L.)] unique to unpainted reefs were found in relatively high concentrations, and these species may have directly or indirectly caused *Balanus* mortality. Relini *et al.* (1994) found that large urchins on artificial reefs in the Mediterranean cleared reef surfaces of epibenthic organisms, and only large barnacles and oysters were able to withstand this grazing activity. Differences in *Balanus* coverage between reef types may have affected reef fishes for Reef Set 2. Diet studies have shown that *B. capriscus* forage on artificial reefs, consuming a variety of epibenthic invertebrates including *Balanus* spp., (Vose 1990; Vose & Nelson 1994; Szedlmayer & Blitch in prep). *Balistes capriscus* were significantly more abundant on painted versus unpainted reefs for Reef Set 2, and this may have been related to differential *Balanus* mortality between reef types.

Conclusions

Copper paint treatment resulted in significantly greater mean total epibenthos coverage, biomass, diversity, and richness on unpainted versus painted reefs. These patterns in epibenthic assemblages resulted in increased mean total fish abundance and increased abundances of six fish species on unpainted compared to painted reefs. Clearly artificial reefs attract fishes, however, the question is whether or not they produce new fish biomass. In this study, patterns in fish recruitment suggested that artificial reefs provide a new forage base for reef fishes, serving as more than just simple attractors and increasing fish production. Future researchers should attempt to quantify fish diets, and compare diets of fish on unpainted reefs with that of fish on painted reefs. In addition, obtaining fish biomass estimates for both painted and unpainted reefs types may provide greater insights on the production value of artificial reefs.

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TABLES

Table 1. Mean total fish abundance (m^{-2}), percent, and mean fish abundance (m^{-2}) for species >1% of the total abundance, by reef type and survey period for Reef Set 1. Significant differences ($\alpha < 0.10$) are shown by different letters for comparison between reef types (U = unpainted, P = painted) and across survey periods.

	Mean	%	Type		Survey				
Species			U	P	Oct 2005	Dec 2005	May 2006	Aug 2006	Dec 2006
Total	15.3	100	17.6a	13.0b	2.0a	8.6b	15.3c	36.8d	14.1c
L. campechanus (Poey)	5.8	38.0	6.6a	5.1b	0.2a	4.8b	7.2c	8.7c	8.2c
Halichoeres spp (Rüppell)	1.9	12.6	2.9a	1.0b	0.0a	0.0a	0.0a	9.6b	0.0a
H. aurolineatum (Cuvier)	1.9	12.6	2.0a	1.8a	0.0a	0.0a	2.5b	6.9c	0.2a

(continued)

Table 1, continued.

Species	Mean	%	Type		Survey				
			U	P	Oct 2005	Dec 2005	May 2006	Aug 2006	Dec 2006
B. capriscus (Gmelin)	1.2	7.5	1.0a	1.3a	0.1a	0.5ab	1.0b	1.2b	3.0c
L. synagris (L.)	0.8	5.2	0.8a	0.8a	0.5a	0.5a	1.1b	1.9c	0.1a
Diplectrum spp. (Holbrook)	0.7	4.5	0.7a	0.7a	0.8a	0.6a	0.6a	0.7a	0.6a
S. variabilis (Castelnau)	0.5	3.3	0.6a	0.4a	0.0a	0.0a	0.0a	2.3b	0.3a
O. chrysoptera (L.)	0.4	2.9	0.5a	0.4a	0.1a	0.7b	0.8b	0.2a	0.4ab
C. ocyurus (Jordan & Evermann)	0.4	2.3	0.4a	0.3a	0.0a	0.1a	0.7b	0.8b	0.2a

(continued)

Table 1, continued.

Species	Mean	%	Type		Survey				
			U	P	Oct 2005	Dec 2005	May 2006	Aug 2006	Dec 2006
Blenniidae	0.3	2.1	0.5a	0.1b	0.0a	0.0a	0.4a	1.1b	0.0a
C. philadelphica (L.)	0.3	1.6	0.3a	0.2a	0.0a	0.0a	0.5b	0.4b	0.3ab
S. dumerili (Risso)	0.2	1.6	0.3a	0.1a	0.0a	0.0a	0.0a	1.2a	0.0a
C. faber (Broussonet)	0.2	1.0	0.2a	0.1b	0.0a	0.6b	0.1a	0.0a	0.1a

Table 2. Stepwise multiple regression of mean total fish abundance (m^{-2}) with temperature (°C), salinity (ppt), and dissolved oxygen (ppm), and mean total epibenthos coverage (cm^2 $100\ cm^{-2}$) with dissolved oxygen (ppm). Significance ($\alpha < 0.01$) is shown by an asterisk.

Fish

Variable	Estimate	SE	SS	F	Pr > F
Intercept	-1673.6	155.0	17674	116.6	< 0.01*
Temperature	12.6	1.0	24328	160.5	< 0.01*
Salinity	35.9	3.5	15744	103.9	< 0.01*
DO	30.1	2.6	20042	132.3	< 0.01*

Epibenthos

Intercept	31993.0	5868.9	1787376730	29.7	< 0.01*
DO	-3397.9	905.3	847384644	14.1	< 0.01*

Table 3. Mean fish diversity (H′), richness (S), and evenness (J) for Reef Set 1, by reef type and survey period. Significant differences (α < 0.10) are shown by different letters for comparison between reef types (U = unpainted, P = painted) and across survey periods.

Community variable	Type		Survey				
	U	P	Oct 2005	Dec 2005	May 2006	Aug 2006	Dec 2006
H′	1.2a	1.2a	0.6a	1.1b	1.4c	1.7d	1.1b
S	5.8a	5.1b	2.1a	4.3b	6.5c	9.0d	5.2b
J	0.77a	0.81b	0.93a	0.77b	0.78b	0.77b	0.71b

Table 4. Common prey items and prey habitat types for dominant fish species on artificial reefs.

Species	Prey items	Prey habitat	Source
L. campechanus (Poey)	fishes, squid, shrimp, crabs	reef, sand, pelagic	Szedlmayer & Lee 2004
Halichoeres spp. (Rüppell)	crabs, shrimp, gastropods	reef, sand	Randall 1967; Clifton & Motta 1998
H. aurolineatum (Cuvier)	shrimp, polychaetes	reef, sand	Randall 1967
B. capriscus (Gmelin)	barnacles, bivalves	reef, sand	Vose & Nelson 1994; Szedlmayer & Blitch in prep
L. synagris (L.)	crabs, shrimp, fishes	reef, sand, pelagic	Randall 1967; Franks & Vanderkooy 2000
Diplectrum spp. (Holbrook)	crustaceans, polychaetes	sand, pelagic	Bortone, Rebenak & Siegel 1981
S. variabilis (Castelnau)	algae, polychaetes	reef	Randall 1967
O. chrysoptera (L.)	shrimp, polychaetes	reef, sand	Howe 2001
C. ocyurus (Jordan & Evermann)	crabs, shrimp	reef, sand	Bullock & Smith 1991
Blenniidae	algae, detritus, polychaetes	reef	Randall 1967
C. philadelphica (L.)	shrimp, crabs, fishes	reef, sand, pelagic	Ross, Pavela & Chittenden 1989
S. dumerili (Risso)	fishes	reef, pelagic	Randall 1967
C. faber (Broussonet)	sponges, salps, polychaetes	reef, pelagic	Randall 1967
R. maculatus (Holbrook)	shrimp, crabs	reef, sand	Bullock & Smith 1991

Table 5. Mean total epibenthos coverage (cm^2 100 cm^{-2}), percent, and mean epibenthos coverage (cm^2 100 cm^{-2}) for species >1% of the total coverage, by reef type and survey period for Reef Set 1. Significant differences (α <0.05) are shown by different letters for comparison between reef types (U = unpainted, P = painted) and across survey periods.

Species	Mean	%	Type		Survey			
			U	P	Dec 2005	May 2006	Aug 2006	Dec 2006
Total	56.8	100	81.3a	35.2b	2.0a	63.3b	69.6b	88.9c
Balanus spp. (Da Costa)	33.1	58.3	47.7a	18.6b	1.5a	40.5b	47.7c	39.0b
B. neritina (L.)	4.7	8.3	5.0a	4.4a	0.0a	0.0a	2.5a	17.6b
Sabellidae (Malmgren)	4.3	7.6	4.3a	4.3a	0.1a	12.6b	1.3a	2.3a

(continued)

Table 5, continued.

Species	Mean	%	Type		Survey			
			U	P	Dec 2005	May 2006	Aug 2006	Dec 2006
Isognomon spp. (Lightfoot)	3.6	6.3	6.5a	0.6b	0.1a	2.8b	4.8c	6.4c
Demospongiae (Sollas)	3.1	5.4	5.5a	0.6b	0.0a	0.0a	4.3b	8.3c
Panopeus spp. (Edwards)	3.0	5.3	4.5a	1.6b	0.0a	2.5b	3.3c	6.2d
M. tenuis (Desor)	1.1	1.9	2.0a	0.2b	0.0a	0.5a	0.7a	3.2b

Table 6. Mean epibenthos diversity (H′), richness (S), and evenness (J) for Reef Set 1, by reef type and survey period. Significant differences (α <0.10) are shown by different letters for comparison between reef types (U = unpainted, P = painted) and across survey periods.

	Type		Survey			
Community variable	U	P	Dec 2005	May 2006	Aug 2006	Dec 2006
H′	1.5a	1.1b	0.5a	1.5b	1.5b	1.8c
S	13.4a	7.8b	3.3a	10.4a	13.0b	15.3c
J	0.58a	0.65b	0.53a	0.65b	0.57a	0.67b

Table 7. Mean total fish abundance (m^{-2}), percent, and mean fish abundance (m^{-2}) for species >1% of the total abundance, by type for Reef Set 2. Significant differences ($\alpha < 0.05$) between reef types (U = unpainted, P = painted) are shown by different letters.

Species	Mean	%	Type	
			U	P
Total	19.9	100	19.1a	20.6a
L. campechanus (Poey)	12.5	62.8	11.3a	13.6a
C. philadelphica (L.)	2.6	13.0	3.4a	1.8b
B. capriscus (Gmelin)	1.3	6.6	0.9a	1.7b
O. chrysoptera (L.)	1.1	5.4	0.7a	1.4a
L. synagris (L.)	0.7	3.3	0.8a	0.5a
R. maculatus (Holbrook)	0.5	2.6	0.7a	0.4a
C. ocyurus (Jordan & Evermann)	0.3	1.3	0.4a	0.1b
Diplectrum spp. (Holbrook)	0.3	1.3	0.3a	0.2a
H. aurolineatum (Cuvier)	0.2	1.0	0.2a	0.2a

Table 8. Mean fish diversity (H′), richness (S), and evenness (J) for Reef Set 2. Significant differences ($\alpha < 0.05$) between reef types (U = unpainted, P = painted) are shown by different letters.

	Type	
Community variable	U	P
H′	1.2a	1.1a
S	5.9a	6.0a
J	0.67a	0.61a

Table 9. Mean total epibenthos coverage (cm^2 100 cm^{-2}), percent, and mean epibenthos coverage (cm^2 100 cm^{-2}) for species >1% of the total coverage, by type for Reef Set 2. Significant differences ($\alpha < 0.05$) between reef types (U = unpainted, P = painted) are shown by different letters.

Species	Mean	%	Type	
			U	P
Total	42.3	100	75.6a	8.9b
Demospongiae (Sollas)	11.1	26.3	22.1a	0.0b
Sabellidae (Malmgren)	5.4	12.9	10.0a	0.9b
Gymnolaemata	5.4	12.8	10.2a	0.6b
dead *Balanus* spp. (Da Costa)	5.3	12.5	9.7a	0.8b
M. tenuis (Desor)	3.5	8.4	7.0a	0.1b
Balanus spp. (Da Costa)	2.0	4.6	0.1a	3.8b
Panopeus spp. (Edwards)	1.9	4.4	3.5a	0.2b
Echinometridae (Gray)	1.1	2.7	2.3a	0.0b

(continued)

Table 9, continued.

Species	Mean	%	Type	
			U	P
B. neritina (L.)	1.1	2.6	0.8a	1.4a
Chlorophyta	0.9	2.0	1.2a	0.5a
A. lafresnayi (Fischer & Bernardi)	0.8	1.9	1.5a	0.1b
C. floridana (Rehder)	0.7	1.7	1.1a	0.3b
T. grus (Holmes)	0.7	1.6	1.3a	0.0b
Isognomon spp. (Lightfoot)	0.5	1.1	0.9a	0.0a

Table 10. Mean epibenthos diversity (H′), richness (S), and evenness (J) for Reef Set 2. Significant differences ($\alpha < 0.05$) between reef types (U = unpainted, P = painted) are shown by different letters.

	Type	
Community variable	U	P
H′	2.2a	1.7b
S	18.4a	9.2b
J	0.77a	0.76a

FIGURES

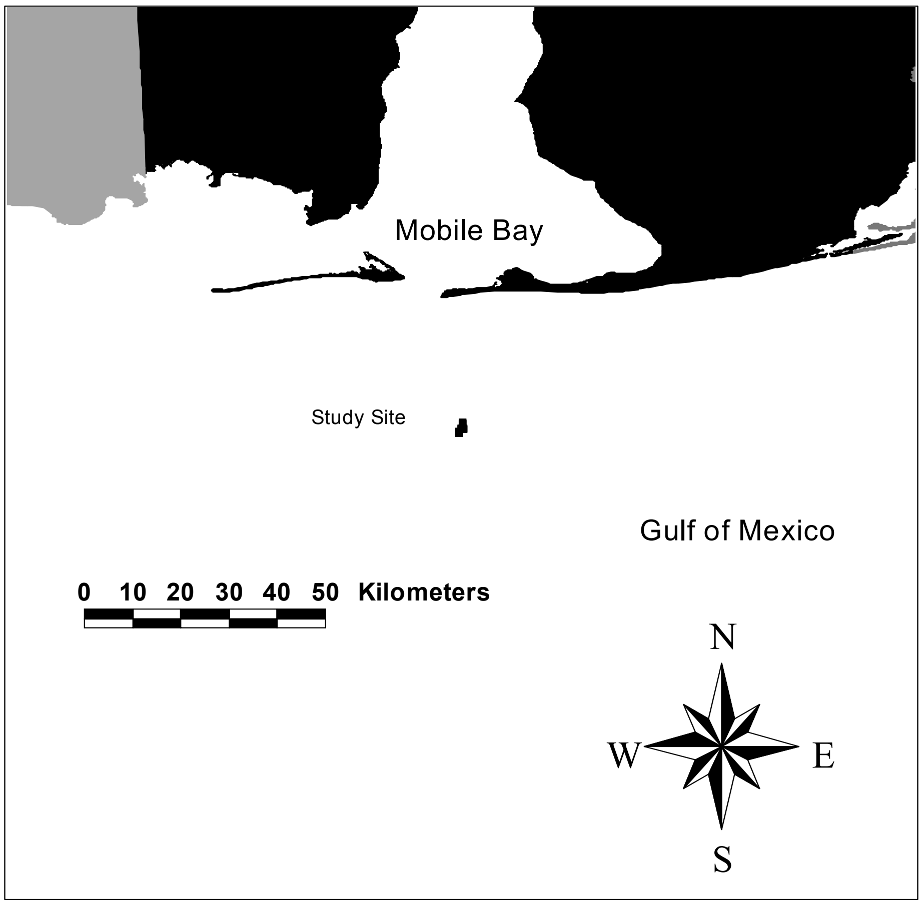

Fig. 1. Location of study sites in the north-central Gulf of Mexico

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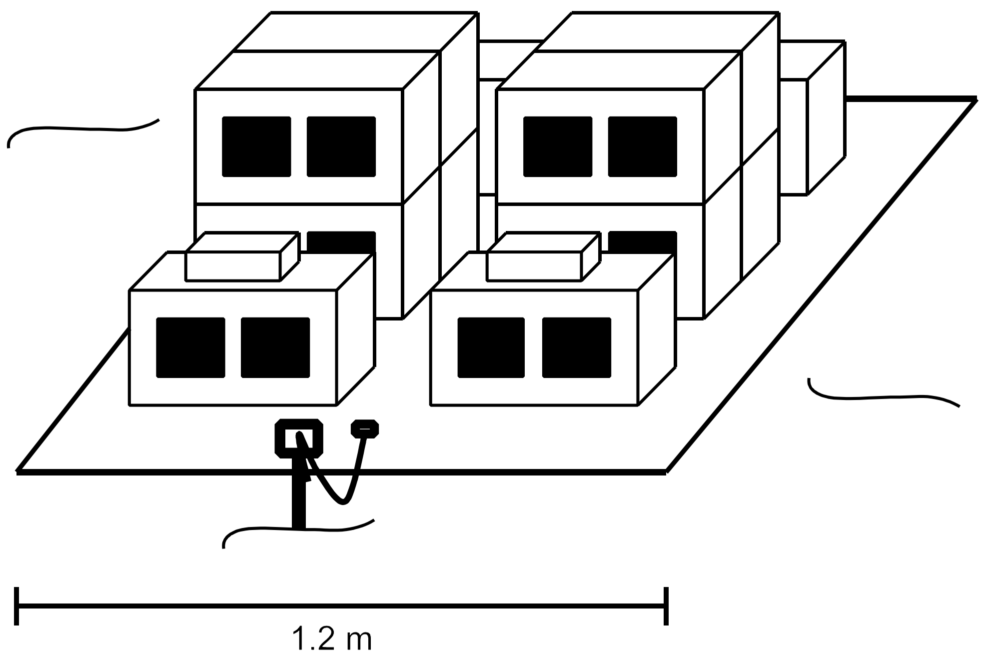

Fig. 2. Diagram of reef design showing the placement of 12 concrete blocks on the plywood base, and 4 small "break-away" bricks (2 hidden). The ground anchor secures the reef to the sand substrate.

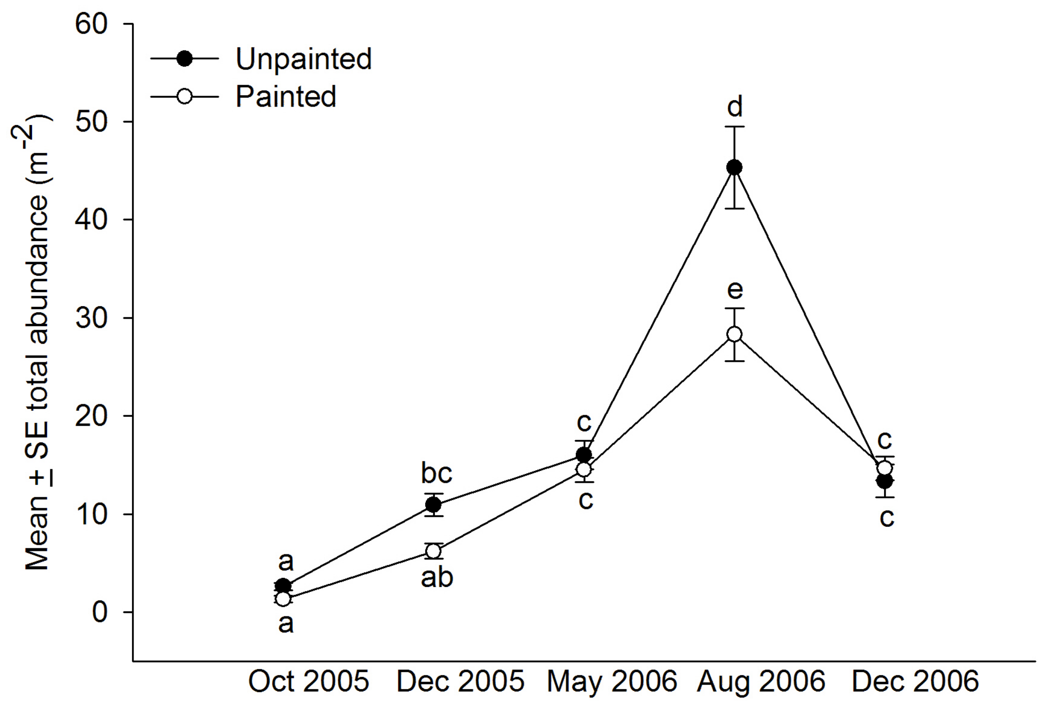

Fig. 3. Mean total fish abundance (m^{-2}) for Reef Set 1 by survey period and reef type. Significant differences ($\alpha < 0.05$) between survey periods and reef types are shown by different letters.

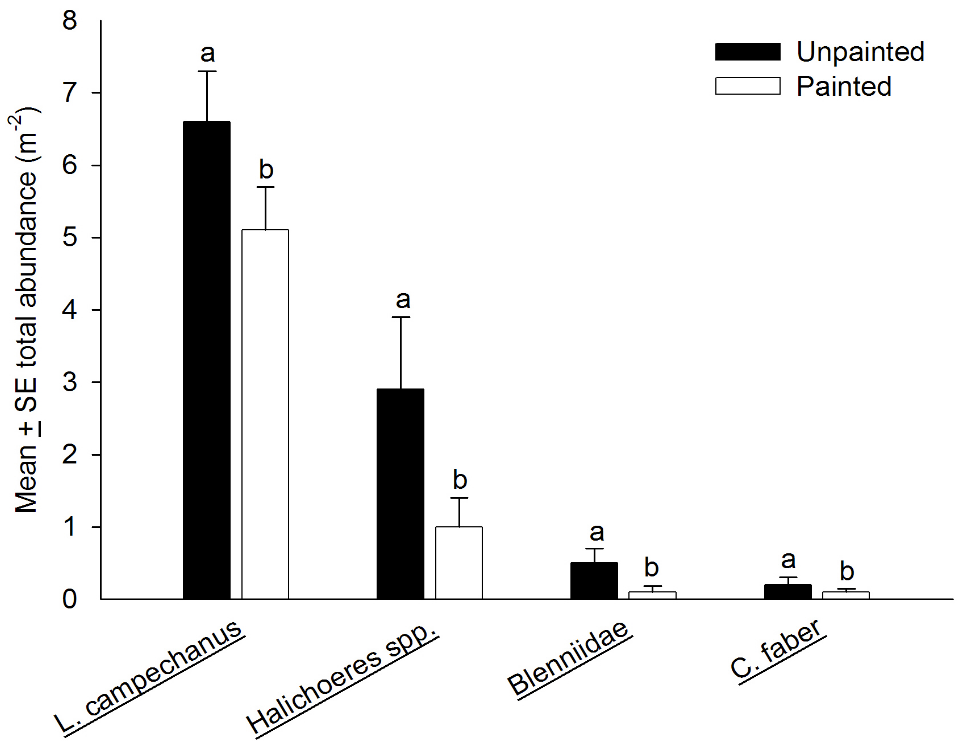

Fig. 4. Mean total fish abundance (m^{-2}) for dominant fish species with significant abundance differences for Reef Set 1 by reef type. Significant differences ($\alpha < 0.10$) between reef types are shown by different letters.

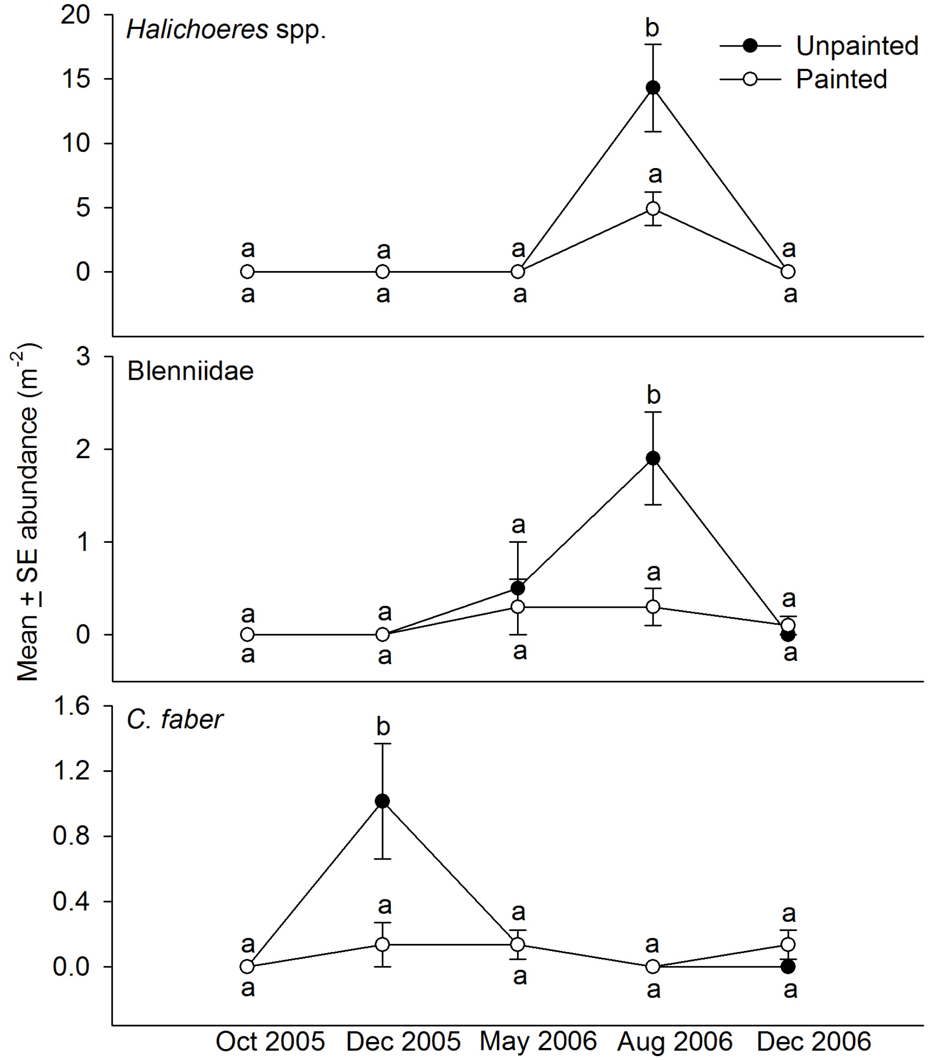

Fig. 5. Mean abundances (m^{-2}) of *Halichoeres* spp., Blenniidae, and *C. faber* for Reef Set 1 by survey period and reef type. Significant differences ($\alpha < 0.05$) between survey periods and reef types are shown by different letters.

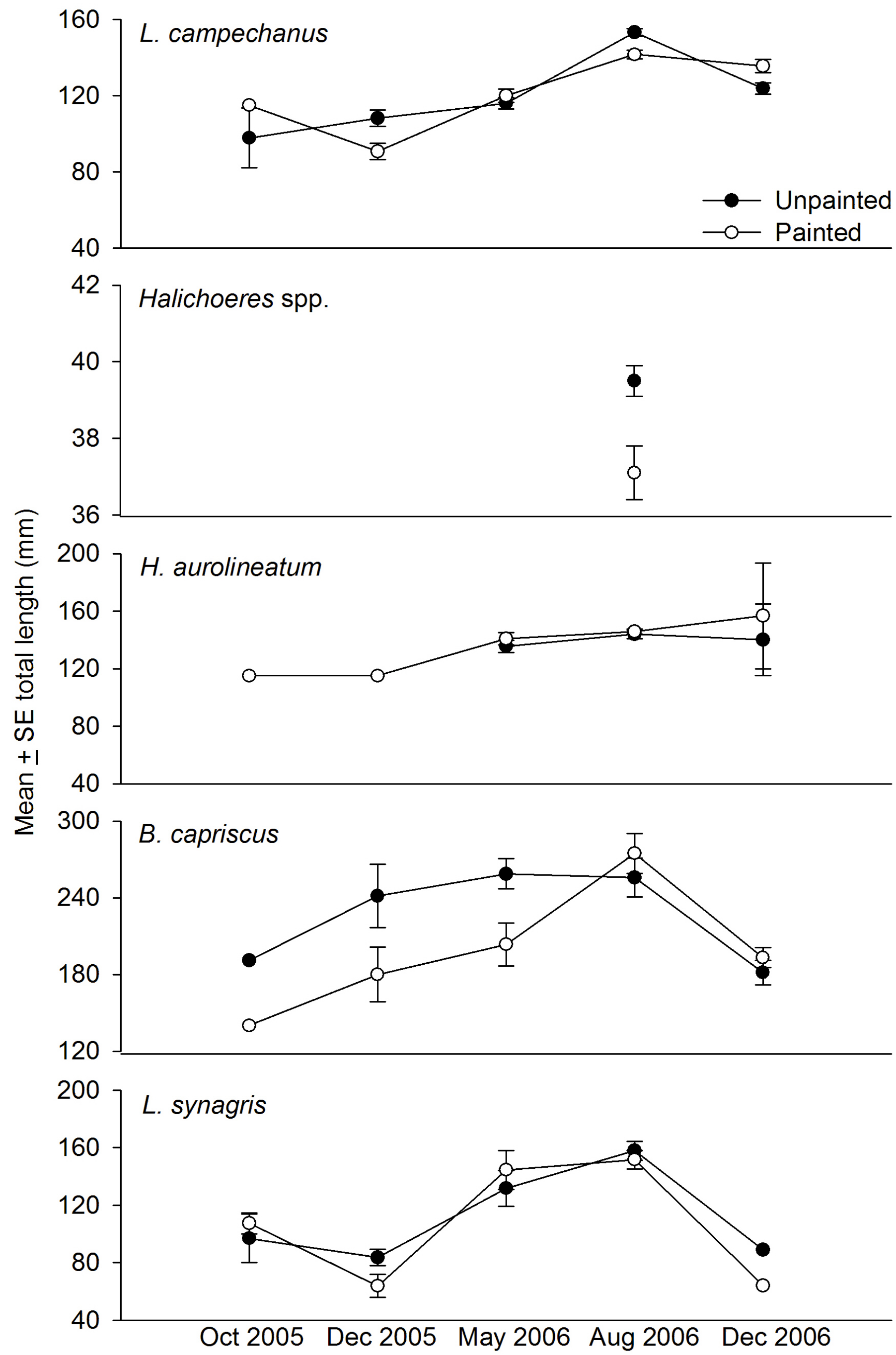

Fig. 6. Mean total length (mm) of *L. campechanus*, *Halichoeres* spp., *H. aurolineatum*, *B. capriscus*, and *L. synagris* by reef type and survey period for Reef Set 1.

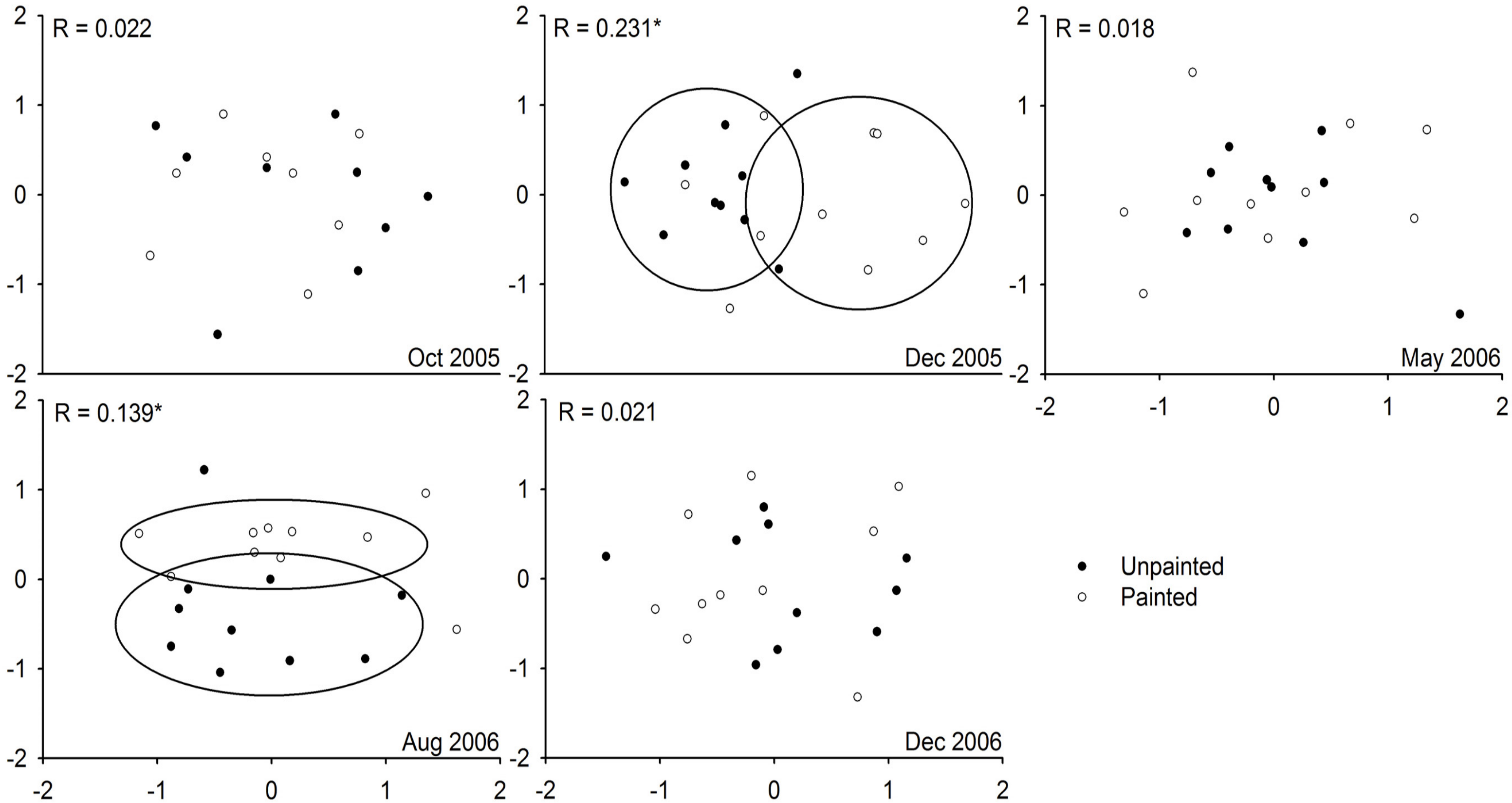

Fig. 7. Multidimensional scaling plots based on Bray-Curtis similarities for fish abundances by reef type and survey period for Reef Set 1. Significant differences (α < 0.05) between reef types are shown by asterisks, and circles drawn around clusters.

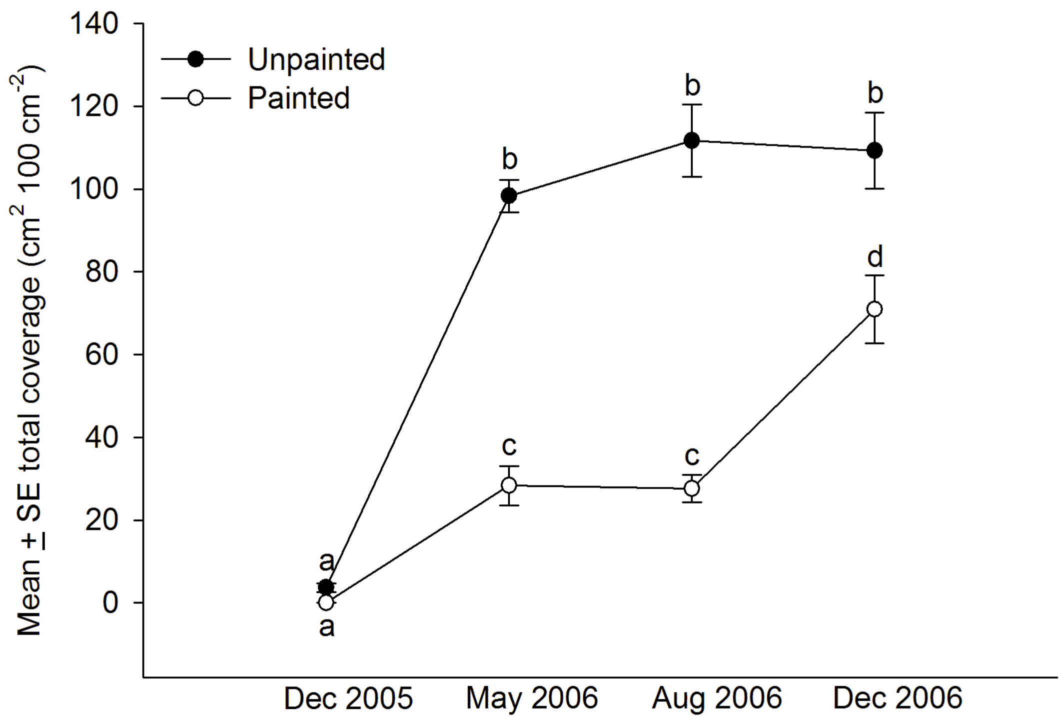

Fig. 8. Mean total epibenthos coverage (cm^2 100 cm^{-2}) for Reef Set 1 by survey period and reef type. Significant differences ($\alpha < 0.05$) between survey periods and reef types are shown by different letters.

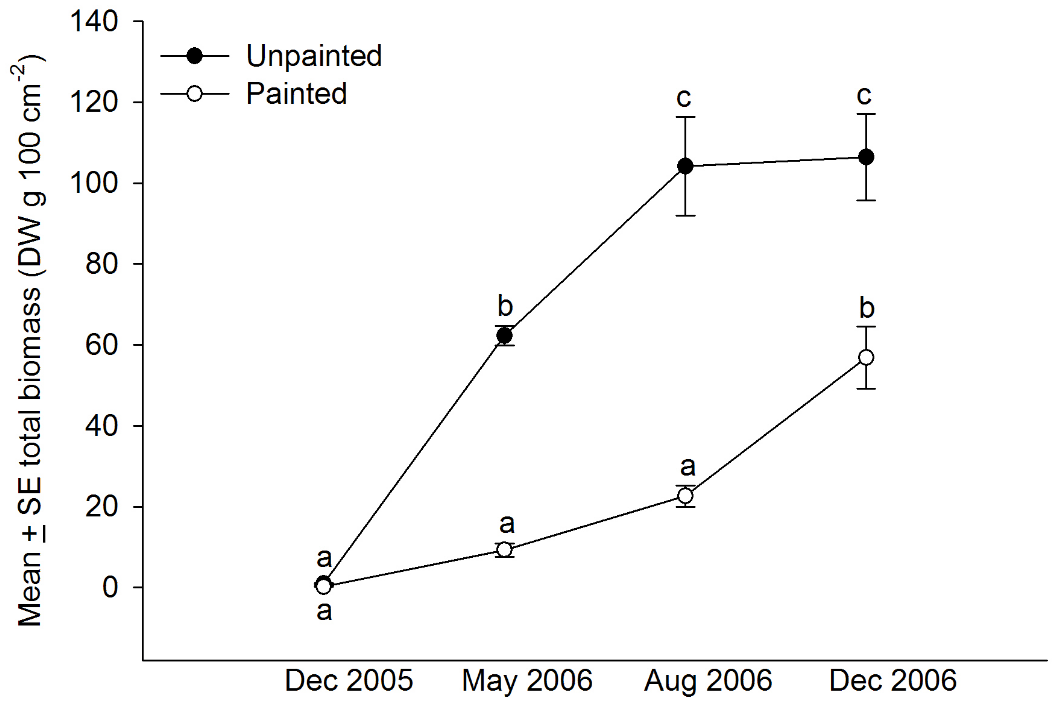

Fig. 9. Mean total epibenthos biomass (DW g 100 cm^{-2}) for Reef Set 1 by survey period and reef type. Significant differences ($\alpha < 0.05$) between survey periods and reef types are shown by different letters.

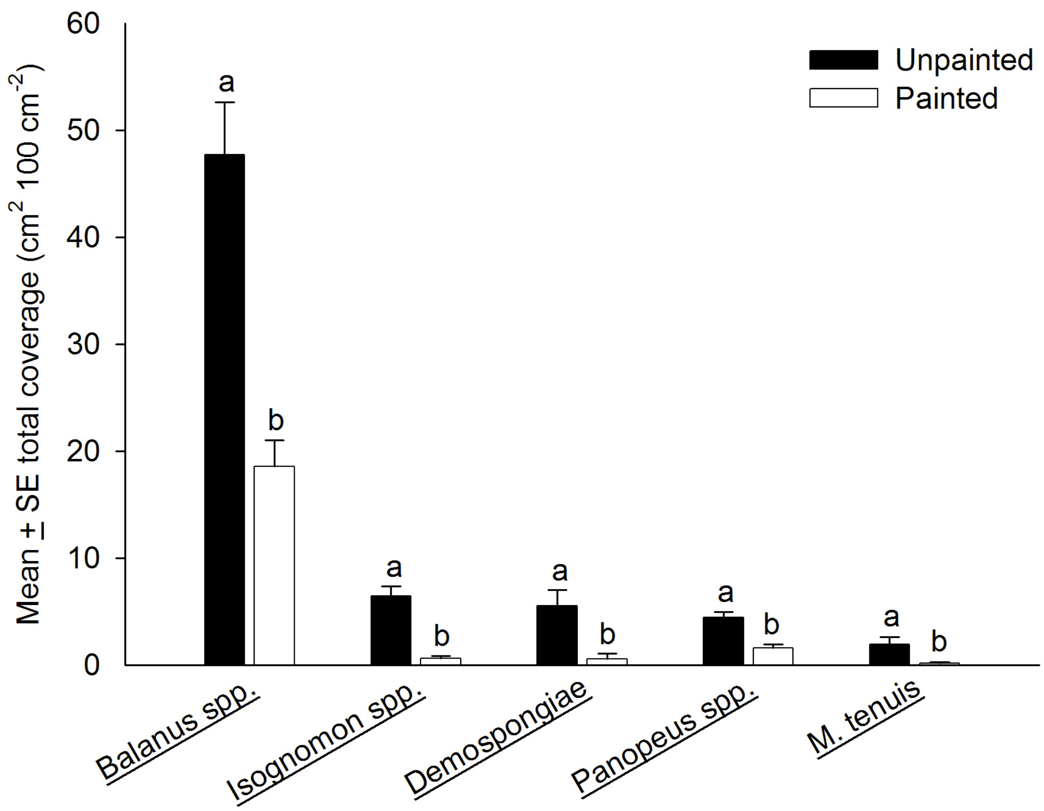

Fig. 10. Mean total epibenthos coverage (cm^2 100 cm^{-2}) of dominant epibenthic species with significant coverage differences for Reef Set 1 by reef type. Significant differences ($\alpha < 0.05$) between reef types are shown by different letters.

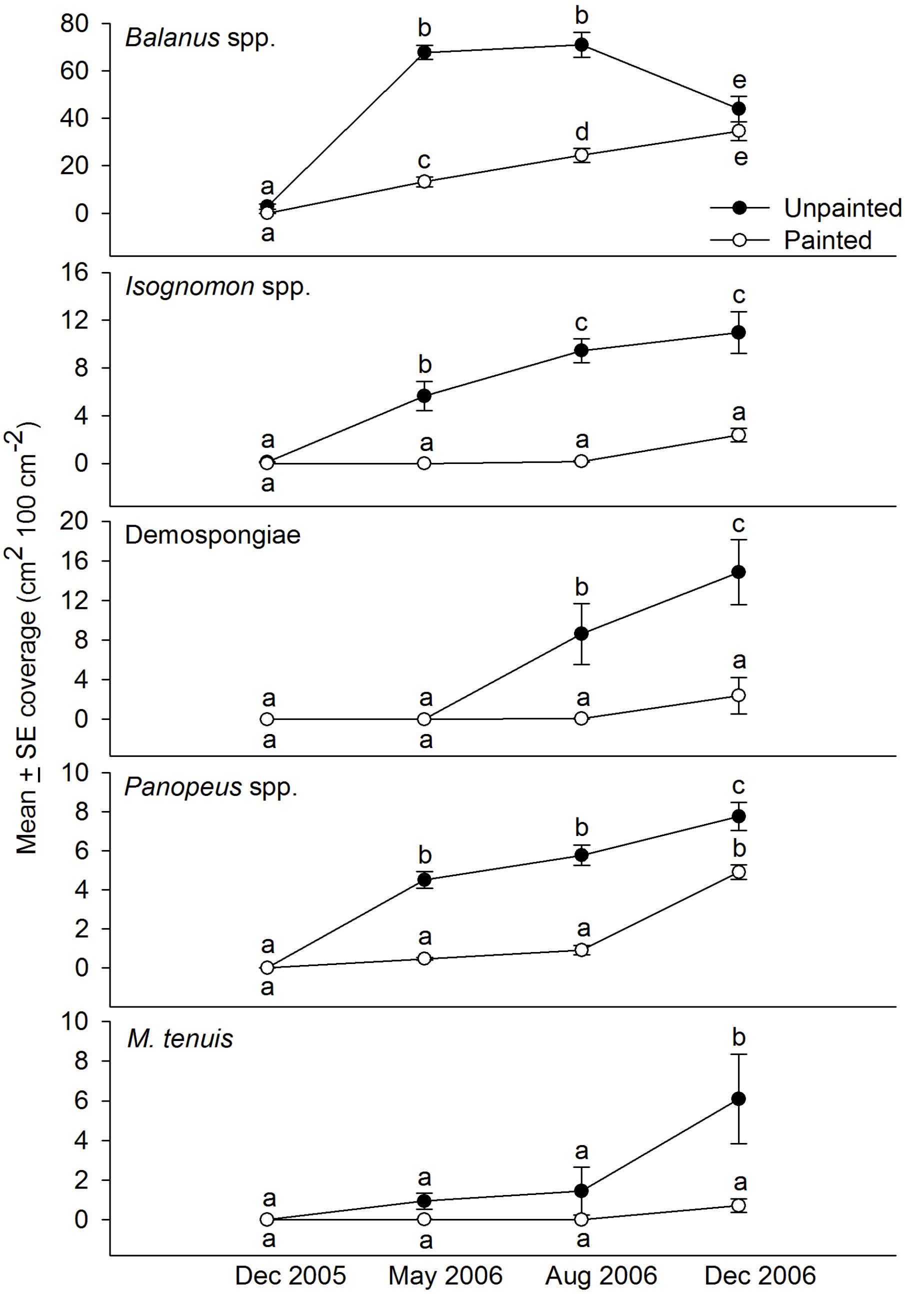

Fig. 11. Mean coverages (cm^2 100 cm^{-2}) of *Balanus* spp., *Isognomon* spp., Demospongiae, *Panopeus* spp., and *M. tenuis* for Reef Set 1 by survey period and reef type. Significant differences (α < 0.05) between survey periods and reef types are shown by different letters.

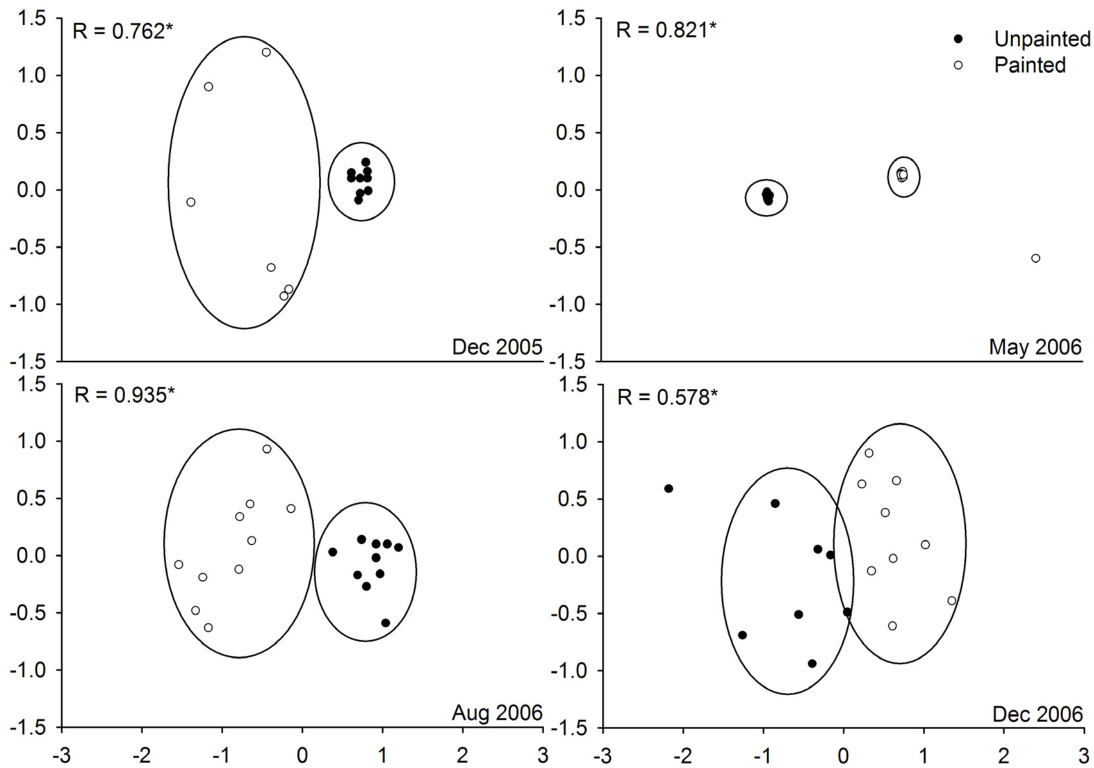

Fig. 12. Multidimensional scaling plots based on Bray-Curtis similarities for epibenthos abundances by reef type for individual surveys for Reef Set 1. Significant differences ($\alpha < 0.01$) between reef types are shown by asterisks, and circles drawn around clusters.

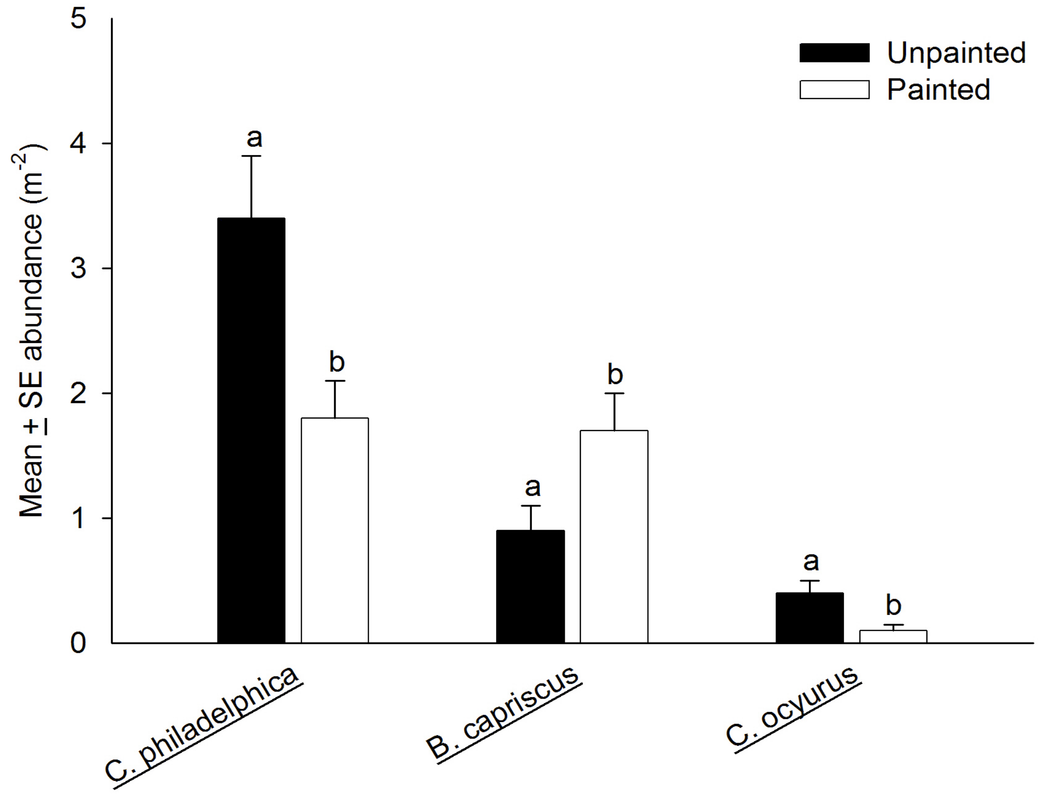

Fig. 13. Mean fish abundance (m^{-2}) for dominant fish species with significant abundance differences for Reef Set 2 by reef type. Significant differences ($\alpha < 0.05$) between reef types are shown by different letters.

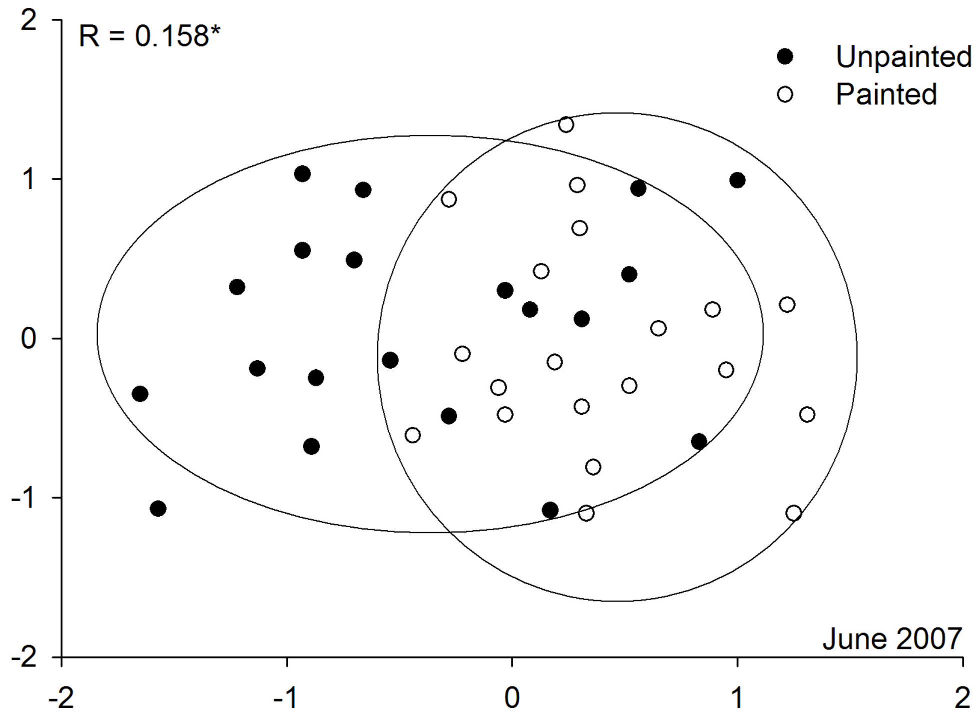

Fig. 14. Multidimensional scaling plot based on Bray-Curtis similarities for fish abundances by reef type for Reef Set 2. Significant differences ($\alpha < 0.01$) between reef types are shown by an asterisk, and circles drawn around clusters.

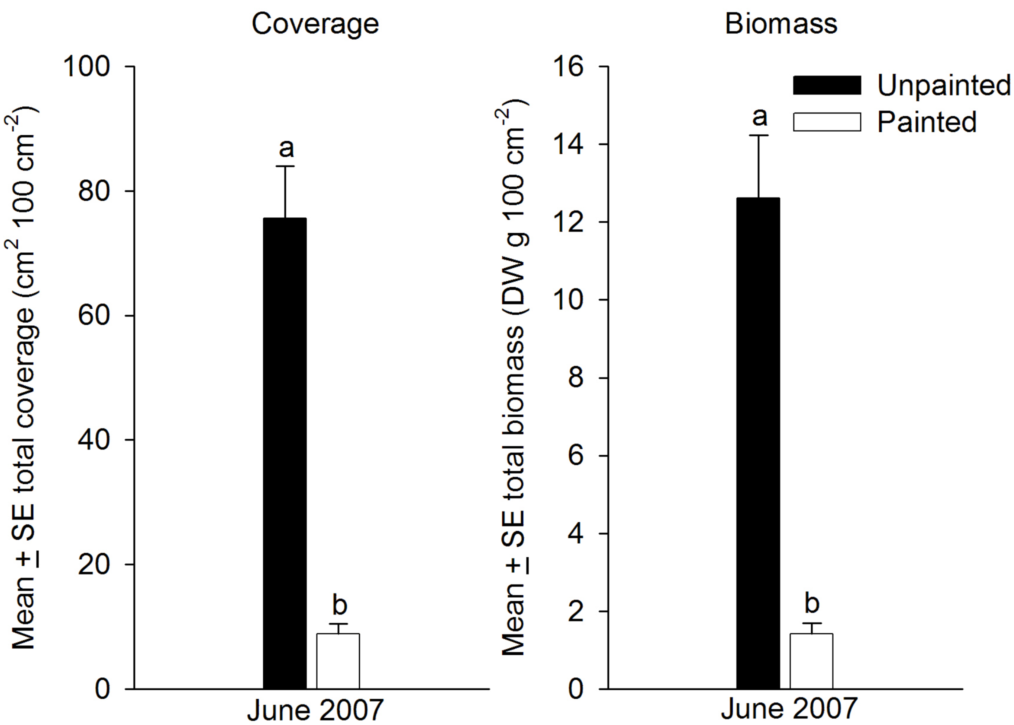

Fig. 15. Mean total epibenthos coverage (cm^2 100 cm^{-2}), and biomass (DW g 100 cm^{-2}) for Reef Set 2 by reef type. Significant differences ($\alpha < 0.01$) between reef types are shown by different letters.

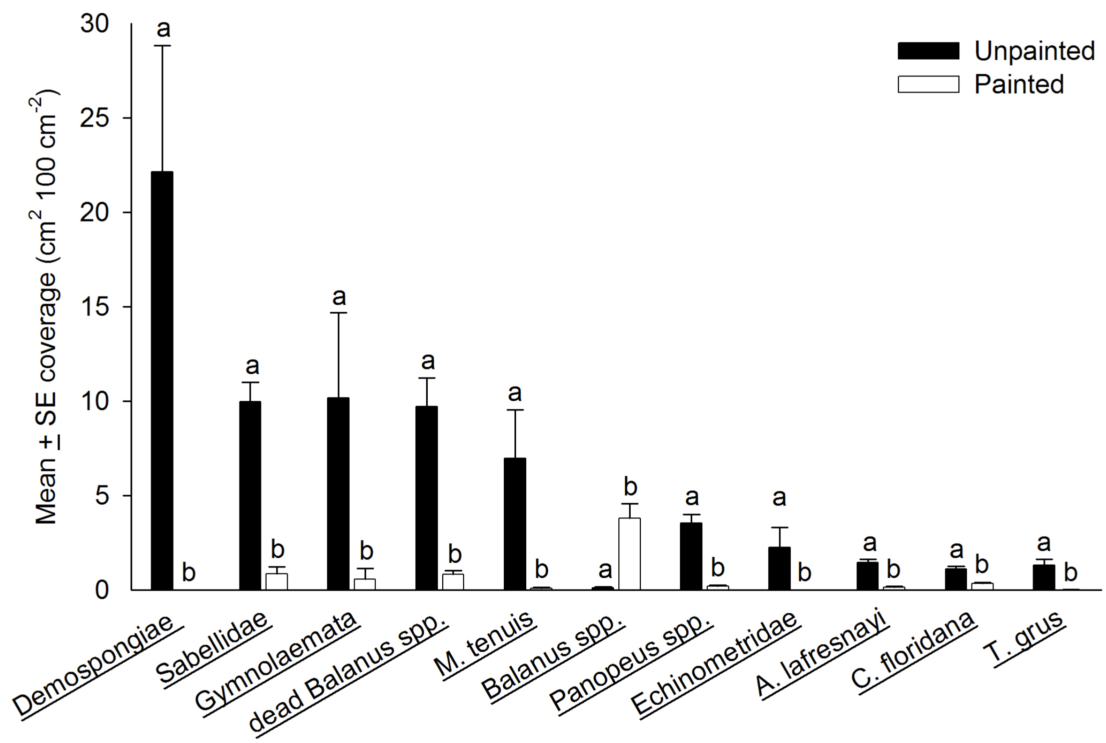

Fig. 16. Mean epibenthos coverage (cm^2 100 cm^{-2}) of dominant epibenthic species with significant coverage differences for Reef Set 2 by reef type. Significant differences ($\alpha < 0.05$) between reef types are shown by different letters.

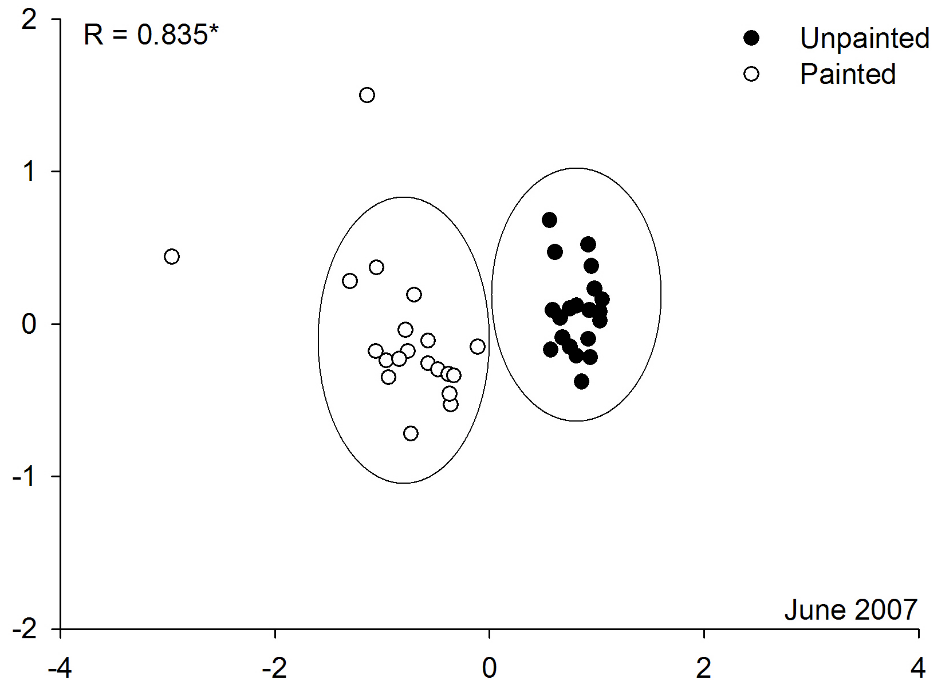

Fig. 17. Multidimensional scaling plot based on Bray-Curtis similarities for epibenthos abundances by reef type for Reef Set 2. Significant differences ($\alpha < 0.01$) between reef types are shown by an asterisk, and circles drawn around clusters.

APPENDICES

Appendix 1. Example of repeated measures analysis of variance between reef types for total fish abundance, and *Lutjanus campechanus* on artificial reefs pooled over all surveys for Reef Set 1. Significance ($\alpha < 0.10$) is shown by an asterisk.

Total

Source	DF	SS	MS	F	Pr > F
Reef type	1	1183.4	1183.4	18.6	< 0.01*
Survey period	4	30102.3	7525.6	94.9	< 0.01*
Interaction	4	2297.1	574.3	7.2	< 0.01*
Error	90	6856.2	142.9		
Total	99	40439.0			

Lutjanus campechanus

Source	DF	SS	MS	F	Pr > F
Reef type	1	114.5	114.5	3.3	0.088*
Survey period	4	2119.3	529.8	22.6	< 0.01*
Interaction	4	41.1	10.3	0.4	0.781
Error	90	2324.5	58.7		
Total	99	4599.3			

Appendix 2. Mean fish abundance (m^{-2}), and percent abundance for species < 1% of the total abundance on Reef Set 1.

Species	Mean	%
Equetus umbrosus (Jordan & Eigenmann)	0.12	0.79
Leiostomus xanthurus (Lacepéde)	0.11	0.71
Gobiidae	0.10	0.66
Monacanthus setifer (Bennett)	0.08	0.53
Apogon pseudomaculatus (Longley)	0.07	0.44
Lagodon rhomboides (L.)	0.05	0.31
Chromis enchrysura (Jordan & Gilbert)	0.03	0.22
Epinephelus niveatus (Valenciennes)	0.03	0.22
Stenotomus caprinus (Jordan & Gilbert)	0.03	0.22
Serranus subligarius (Cope)	0.03	0.18
Holacanthus spp. (Lacepéde)	0.01	0.09
Pomacanthus spp. (Lacepéde)	0.01	0.09
Archosargus rhomboidalis (L.)	0.01	0.04

(continued)

Appendix 2, continued.

Species	Mean	%
Chaetodon ocellatus (Bloch)	0.01	0.04
Equetus lanceolatus (L.)	0.01	0.04
Ginglymostoma cirratum (Bonnaterre)	0.01	0.04
Lutjanus griseus (L.)	0.01	0.04
Paralichthys albigutta (Jordan & Gilbert)	0.01	0.04
Rhomboplites aurorubens (Cuvier)	0.01	0.04
Rypticus maculatus (Holbrook)	0.01	0.04

Appendix 3. Mean epibenthos coverage (cm^2 100 cm^{-2}), and percent coverage for species < 1% of the total coverage on Reef Set 1.

Species	Mean	%
Costoanachis floridana (Rehder)	0.50	0.87
Anomia simplex (D'Orbigny)	0.40	0.71
Serpulidae (Johnston)	0.39	0.68
Anachis lafresnayi (Fischer & Bernardi)	0.36	0.63
Alpheoidea (Rafinesque)	0.35	0.62
Polychaeta	0.29	0.52
Chlorophyta	0.28	0.50
Ascidiacea	0.28	0.49
Anadara spp. (Gray)	0.26	0.47
Stramonita haemastoma (L.)	0.24	0.42
Crepidula fornicata (L.)	0.18	0.32
Terebellidae (Malmgren)	0.13	0.24
Actiniaria	0.12	0.21

(continued)

Appendix 3, continued.

Species	Mean	%
Blenniidae	0.03	0.06
Bivalvia (L.)	0.03	0.06
Nudibranchia (Blainville)	0.02	0.04
Megabalanus sp. (Hoek)	0.01	0.03
Dromidia antillensis (Stimpson)	0.01	0.02
Anadara notabilis (Roding)	0.01	0.01
Stenorhynchus seticornis (Herbst)	0.01	0.01
Cerithiidae (Fleming)	0.005	0.01
Argopecten spp. (Monterosato)	0.005	0.01
Epitoniidae (Berry)	0.004	0.01
Ophiuridae (Lyman)	0.003	0.01
Lithophaga spp. (Roding)	0.002	0.00
Diogenidae (Ortmann)	0.001	0.00
Niso aeglees (Bush)	0.001	0.00
Neverita duplicata (Say)	0.000	0.00

Appendix 4. Mean fish abundance (m^{-2}), and percent abundance for species < 1% of the total abundance on Reef Set 2.

Species	Mean	%
Lagodon rhomboides (L.)	0.17	0.85
Halichoeres spp. (Rüppell)	0.12	0.60
Equetus umbrosus (Jordan & Eigenmann)	0.08	0.43
Apogon pseudomaculatus (Longley)	0.07	0.34
Chaetodipterus faber (Broussonet)	0.02	0.09
Epinephelus niveatus (Valenciennes)	0.02	0.09
Mycteroperca sp. (Gill)	0.02	0.09
Serraniculus pumilio (Ginsburg)	0.02	0.09
Rhomboplites aurorubens (Cuvier)	0.02	0.09

Appendix 5. Mean epibenthos coverage (cm^2 100 cm^{-2}), and percent coverage for species < 1% of the total coverage on Reef Set 2.

Species	Mean	%
Actiniaria	0.34	0.80
Astrangia poculata (Ellis & Solander)	0.26	0.62
Serpulidae (Johnston)	0.25	0.60
Polychaeta	0.24	0.56
Stramonita haemastoma (L.)	0.19	0.46
Terebellidae (Malmgren)	0.11	0.26
Alpheoidea (Rafinesque)	0.10	0.25
Actiniaria, larger variety	0.10	0.23
Anadara spp. (Gray)	0.08	0.18
Anomia simplex (D'Orbigny)	0.05	0.13
Chama spp. (L.)	0.04	0.11
Nudibranchia (Blainville)	0.04	0.09
Blenniidae	0.03	0.08

(continued)

Appendix 5, continued.

Species	Mean	%
Ophiuridae (Lyman)	0.03	0.06
Gastropoda (Cuvier)	0.02	0.06
Stenorhynchus seticornis (Herbst)	0.02	0.05
Microphrys bicornutus (Latreille)	0.02	0.04
Epitoniidae (Berry)	0.01	0.04
Patelloida pustulata (Helbling)	0.01	0.03
Crepidula fornicata (L.)	0.01	0.03
Bivalvia (L.)	0.01	0.03
Calliostoma sp. (Swainson)	0.01	0.02
Neverita duplicata (Say)	0.01	0.02
Diogenidae (Ortmann)	0.01	0.02
Dromidia antillensis (Stimpson)	0.01	0.02
Niso aeglees (Bush)	0.01	0.01
Cladocora arbuscula (Lesueur)	0.003	0.01

(continued)

Appendix 5, continued.

Species	Mean	%
Brachyura (Latreille)	0.003	0.01
Cerithiidae (Fleming)	0.002	0.01