

Gulf of Mexico Science

Volume 29
Number 2 *Number 2*

Article 4

2011

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Jeffrey M. Grim
Northeastern University

John Eme
University of North Texas

Jennie S. Rohrer
Texas Parks and Wildlife Department

Erin Ferer
Virginia Institute of Marine Science

Allison A. Wilkes
Texas A&M University

et al.

DOI: 10.18785/goms.2902.04

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Recommended Citation

Grim, J. M., J. Eme, J. S. Rohrer, E. Ferer, A. A. Wilkes, R. E. Wilborn, K. Radzik, R. L. Croker, A. J. O'Farrell, C. M. Pomory and W. A. Bennett. 2011. Loss of Structural Complexity in Staghorn Coral Rubble Habitats Influences the Density of Damselfish in Dry Tortugas National Park, Florida, USA. *Gulf of Mexico Science* 29 (2). Retrieved from <https://aquila.usm.edu/goms/vol29/iss2/4>

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SHORT PAPERS AND NOTES

Gulf of Mexico Science, 2011(2), pp. 113–118
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LOSS OF STRUCTURAL COMPLEXITY IN STAGHORN CORAL RUBBLE HABITATS INFLUENCES THE DENSITY OF DAMSELFISH IN DRY TORTUGAS NATIONAL PARK, FLORIDA, USA.—Damselfishes (Family: Pomacentridae) are a group of keystone species that influence reef ecology and diversity and are considered good indicators of overall reef health (Longley and Hildebrand, 1941; Emery, 1973; Williams, 1980; Hixon and Brostoff, 1983; Aronson and Precht, 1997; Lieske and Meyers, 1999). Many damselfishes are syntopic as well as sympatric, and species can be intensely territorial, directly competing for resources with con-familials or other fishes (Allen, 1991). Several species maintain and defend algal gardens, which can indirectly affect both corals and fishes (Birkeland, 1977; Hixon and Brostoff, 1983). As a result, damselfishes play a key role in shaping the ecology of coral reefs worldwide (Williams, 1980; Hixon and Brostoff, 1983; Lieske and Myers, 1999).

Quantification of live coral reef habitat utilization by reef fishes, including damselfishes, reveals that decreased rugosity may influence coral reef fish diversity and abundance worldwide (e.g., Luckhurst and Luckhurst, 1978; Clark, 1996; Lirman, 1999; Holbrook et al., 2000; Jones et al., 2004; Gratwicke and Speight, 2005). Thus far, reports of damselfish abundance within the Gulf of Mexico have generally been limited to the ecology of damselfishes occupying moderately affected or pristine low-energy patch reefs (e.g., Emery, 1973; Wallman et al., 2004; Precht et al., 2010). Previously, we reported that damselfish densities vary significantly between live strands of very highly rugose staghorn coral (*Acropora cervicornis*) and dead, very-low-rugosity *A. cervicornis* rubble (Wilkes et al., 2008). Although previous work by our group and others has addressed differences in damselfish abundance and diversity between the extreme habitat conditions (live, highly rugose vs low live cover/dead, low-rugosity habitats), the relationship over a continuum of coral rubble rugosity and fish abundance, however, is not clearly established (e.g., Luckhurst and Luckhurst, 1978; McCormick, 1994; Gratwicke and Speight, 2005).

The loss of three-dimensional structure as dead coral collapses is a striking and ongoing

situation in the Dry Tortugas National Park (DTNP), which boasts one of the largest and most pristine reef systems in the continental United States. Coral reefs of DTNP were dominated by large, monotypic strands of *A. cervicornis* that supported a diversity of fish typical of the Caribbean (Longley and Hildebrand, 1941). Over the past 40 yrs, however, cold events, storms, and disease outbreaks have essentially eliminated live staghorn coral, *A. cervicornis*, within DTNP (Davis, 1982; Bohnsack, 1983).

In the current study, we exploited the lack of live *A. cervicornis* within DTNP, low cover of macroalgae, similar physical characteristics of DTNP reefs, and the lack of fishing pressure (all factors that are known to influence the dynamics of reef fishes) to isolate the effects of habitat rugosity on the abundance and diversity of a keystone fish family Pomacentridae (damselfishes). We hypothesized that coral rubble habitats within DTNP may contain varying levels of habitat rugosity and that damselfish densities within DTNP would decrease with declines in coral rubble habitat rugosity. Additionally, we hypothesized that not all damselfishes would respond similarly to decreases in habitat rugosity, with the densities of the largest-bodied fishes being affected to a greater extent than smaller-bodied species as habitat rugosity decreases. To test these hypotheses, we utilized a modified chain-and-tape method to quantify three-dimensional structure of *A. cervicornis* rubble and estimated the species-specific density for five common Caribbean damselfishes on belt transects within DTNP. This study provides novel insight into the utilization of compacted coral rubble habitats by damselfishes within DTNP, and may provide useful information for the management of reef habitats, with the goal of maintaining fish diversity typical of healthy coral reefs.

Materials and methods.—We utilized belt transects to quantify habitat rugosity in three coral rubble habitats located within DTNP from 16–22 May 2005. A modified chain-and-tape method (Risk, 1972, reviewed by McCormick, 1994) was used to assess the structural complexity (rugosity) at each of the three sites. Site rugosity was estimated as:

$$(1 - \text{length of a 1-m chain as it followed the substratum contour} / \text{the straight-line length of the chain}) \times 100 \quad (1)$$

with relatively flat surfaces (low rugosity) having rugosity values near 0 and topographically complex sites (high rugosity) having rugosity values approaching 100. As we previously reported (Wilkes et al. 2008), site 1 ($24^{\circ}22'18.6''\text{N}$ $82^{\circ}52'18.1''\text{W}$) contained the skeletal remains of the last living stand of *A. cervicornis* in DTNP. Coral rubble at this site was attached to the substratum in its original upright position, and represented high structural complexity. Site 2 ($24^{\circ}22'44.1''\text{N}$ $82^{\circ}33'18.5''\text{W}$) contained collapsing *A. cervicornis* rubble, which retained substantial three-dimensional structure representing intermediate structural complexity. Site 3 ($24^{\circ}22'10.6''\text{N}$ $82^{\circ}31'22.1''\text{W}$) was dominated by *A. cervicornis* rubble, which had almost completely collapsed, representing low structural complexity. With the exception of differences in habitat rugosity, sites were otherwise similar, and the study sites were within 3 km of each other (Fig. 1). The range of rugosities being studied is naturally occurring within DTNP, and therefore could not otherwise be manipulated to avoid spatial segregation of sites. Spatial separation of sites for this reason is not an uncommon occurrence in these types of studies (e.g., Öhman and Rajasuriya, 1998).

Within each of the three study sites, the densities (fish $\cdot \text{m}^{-2}$) of five damselfishes were estimated during daylight hours using 10-m \times 1-m belt transects haphazardly placed at approximately 2-m depth. Transect length was based on the ability to fit an individual transect in an area with the same level of rugosity and water depth while maintaining distances between transects greater than fish territory sizes. Transects were spaced > 5 m apart, and territory sizes for the species counted are normally much less than the distance between any two transects (Allen, 1991). Therefore transects were treated as independent replicates relative to the density of fish vs rubble complexity question.

Two snorkelers swimming shoulder to shoulder swam each 10-m \times 1-m belt transect at a rate of 1 $\text{m} \cdot \text{min}^{-1}$, with one team per transect at any one time. Two snorkelers swimming in this manner while maintaining the transect line as the midline between them spanned approximately 1 m. This approach was used to standardize the area sampled (1 m total – 0.5 m on either side of the transect) by each team. Each of the four teams of two snorkelers enumerated the five most common damselfishes inhabiting DTNP (Longley and Hildebrand, 1941): beaugregory (*Stegastes leucostictus*), cocoa (*S. variabilis*), dusky (*S. fuscus*), three-spot (*S. planifrons*), and yellowtail (*Microspathodon chrysurus*) by counting individuals within 0.5 m of either side of the transect

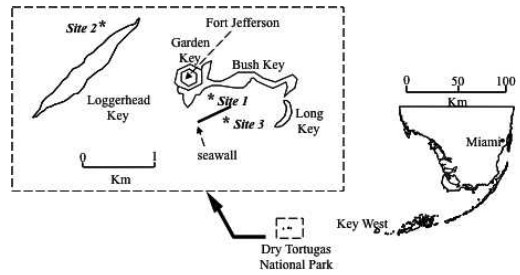


Fig. 1. Dry Tortugas National Park (DTNP), FL. Selected keys from the park are magnified with study-site locations denoted by an asterisk (*). DTNP is approximately 113 km west of Key West, FL.

line. Body shape, fin characteristics, and coloration patterns were used to identify damselfish to species level following Smith (2002). Each snorkeling team represented a single transect replicate. A mean count of damselfishes from all four teams was used as a single datum representing each transect. A total of 16 transects were sampled in this manner at sites 1 and 2, and 12 transects were sampled at site 3.

One-way analysis of variance (ANOVA) or Kruskal–Wallis tests were used to compare rugosity measures, density of total damselfish, and density of damselfish by species among the three sites. Significant ANOVA or Kruskal–Wallis analyses were followed by Tukey's or Dunn's post hoc tests, respectively. Statistical determinations of site rugosity and density of total damselfish were evaluated using $\alpha = 0.05$, and the density of individual damselfish species were compared at $\alpha = 0.01$ to control for type I error.

Results.—The relative rugosity of *A. cervicornis* rubble differs by location within the boundaries of DTNP. The study sites examined in the current work contained three distinct levels of structural rugosity (ANOVA; $F_{2,12} = 700$, $P < 0.0001$), including high-, medium-, and low-rugosity *A. cervicornis* rubble (Fig. 2).

The total densities of damselfishes varied among the three study sites (Fig. 3). Total density of damselfishes was approximately 2- and 3.3-times greater on high-rugosity transects than either medium- or low-rugosity transects, respectively (Kruskal–Wallis; $H_3 = 34.94$, $P < 0.001$).

Four of the five damselfish species sampled were observed within all levels of rugosity, with greatest densities for most species on high-rugosity transects (Fig. 3). Mean density of *S. leucostictus* was comparable between high- and low-rugosity transects, which were on average two times greater than on medium-rugosity transects (ANOVA; $F_{2,41} = 26.95$, $P < 0.0001$; Fig. 3).

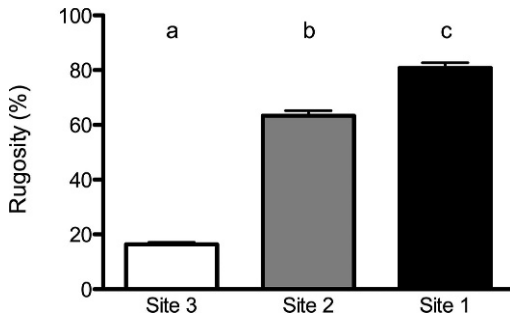


Fig. 2. Rugosity values for *Acropora cervicornis* coral rubble in three study sites within Dry Tortugas National Park, Florida. Values are reported as mean \pm SEM. Differences in rugosity among sites are indicated by superscript letters.

Mean density of *S. variabilis* was over five times greater on high-rugosity transects relative to medium- and low-rugosity rubbles (Kruskal–Wallis; $H_3 = 21.05$, $P < 0.0001$; Fig. 3). Mean density of *S. fuscus* was 7.5–times greater on medium-rugosity transects relative to low-rugosity transects, with high-rugosity transects in between (Kruskal–Wallis; $H_3 = 19.21$, $P < 0.0001$; Fig. 3). *S. planifrons* showed the largest change in mean density, with an over 20–times increase in high-rugosity transects relative to medium- and low-rugosity rubbles (Kruskal–Wallis; $H_3 = 20.06$, $P < 0.0001$; Fig. 3). Finally, the mean density of *M. chrysurus* was 4.3–times greater on high-rugosity transects relative to medium-rugosity transects (Kruskal–Wallis; $H_3 = 30.08$, $P < 0.0001$; Fig. 3). Notably, *M. chrysurus* was absent in the low-rugosity site.

Discussion.—Over the past 40 yrs, live *A. cervicornis* within DTNP has become nonexistent, and consequently coral rubble has become increasingly common. A declining abundance of healthy *A. cervicornis* over its entire range led the National Oceanic and Atmospheric Administration (U.S.A.) to classify the species as threatened under the Endangered Species Act (Hogarth, 2006). Following a previous trip to DTNP in 2004, we reported that only a single patch (65 m²) of live *A. cervicornis* remained in shallow water from the once-extensive (44 ha) staghorn coral formations that surrounded the Dry Tortugas platform (Agassiz, 1883; Wilkes et al., 2008). We now report that this remaining patch of live *A. cervicornis* is dead, and is beginning to lose structural complexity.

Results from the current work support our hypothesis that *A. cervicornis* rubble within DTNP contains varying degrees of rugosity. The col-

lapse of live coral into varying degrees of less structurally complex rubble is a gradual process, with the amount of degradation related to biotic factors (e.g., abundance of corallivores and herbivores), exposure to chronic wave action, destructive storms, human impact, and time from initial death (Huston, 1985; Rasser and Riegl, 2002; Lesser, 2004). Unless balanced by coral growth and recruitment, areas with dead coral generally become less rugose over time, resulting in decreasing structural complexity of available microhabitats. The study sites are generally similar with regard to the abiotic factors discussed above, and as a result, the wide range of habitat rugosities we report for spatially proximate *A. cervicornis* rubbles within DTNP (Fig. 2) is probably explained by differences in time since coral death. Unfortunately, it seems likely that both the loss of structural complexity and damselfish abundance and diversity within DTNP is inevitable as the distance from neighboring reefs leaves little potential for recruitment of either coral or damselfishes (Hughes, 1985; Ayre and Hughes, 2004; Allen, 1991; Cowen et al., 2006).

As hypothesized, decreased rugosity of *A. cervicornis* habitats within DTNP was accompanied by dramatic declines in the total density of damselfishes (Fig. 3). The most likely explanation for this observation is that the three-dimensional structure of *A. cervicornis* provides a refuge from predation, and the differential use of space by fishes, partly on the basis of size of the species and life history stage, can affect species composition (Chabanet et al., 1997; Nemeth, 1998; Holbrook et al. 2002; Almany, 2004; Mateo and Tobias, 2004; Gratwicke and Speight, 2005). Additionally, we have shown that intermediate levels of coral rubble rugosity are accompanied by intermediate declines in damselfish abundance. These data provide some of the first evidence that damselfish communities change gradually as reef habitats are degrading. When densities of individual damselfishes are examined (Fig. 3), it appears that the intermediate changes in total damselfish density discussed above are likely driven by an increased density of *S. fuscus* in medium-rugosity habitats, relative to low-rugosity sites. Furthermore, the magnitude of loss in damselfish density in low-rugosity habitats is likely obscured because densities of *S. leucostictus* in low-rugosity habitats were similar to values from high-rugosity sites (Fig. 3).

Although the densities of damselfishes in total declined with a loss of habitat rugosity within DTNP, as hypothesized, not all species were equally affected. Densities of all damselfishes

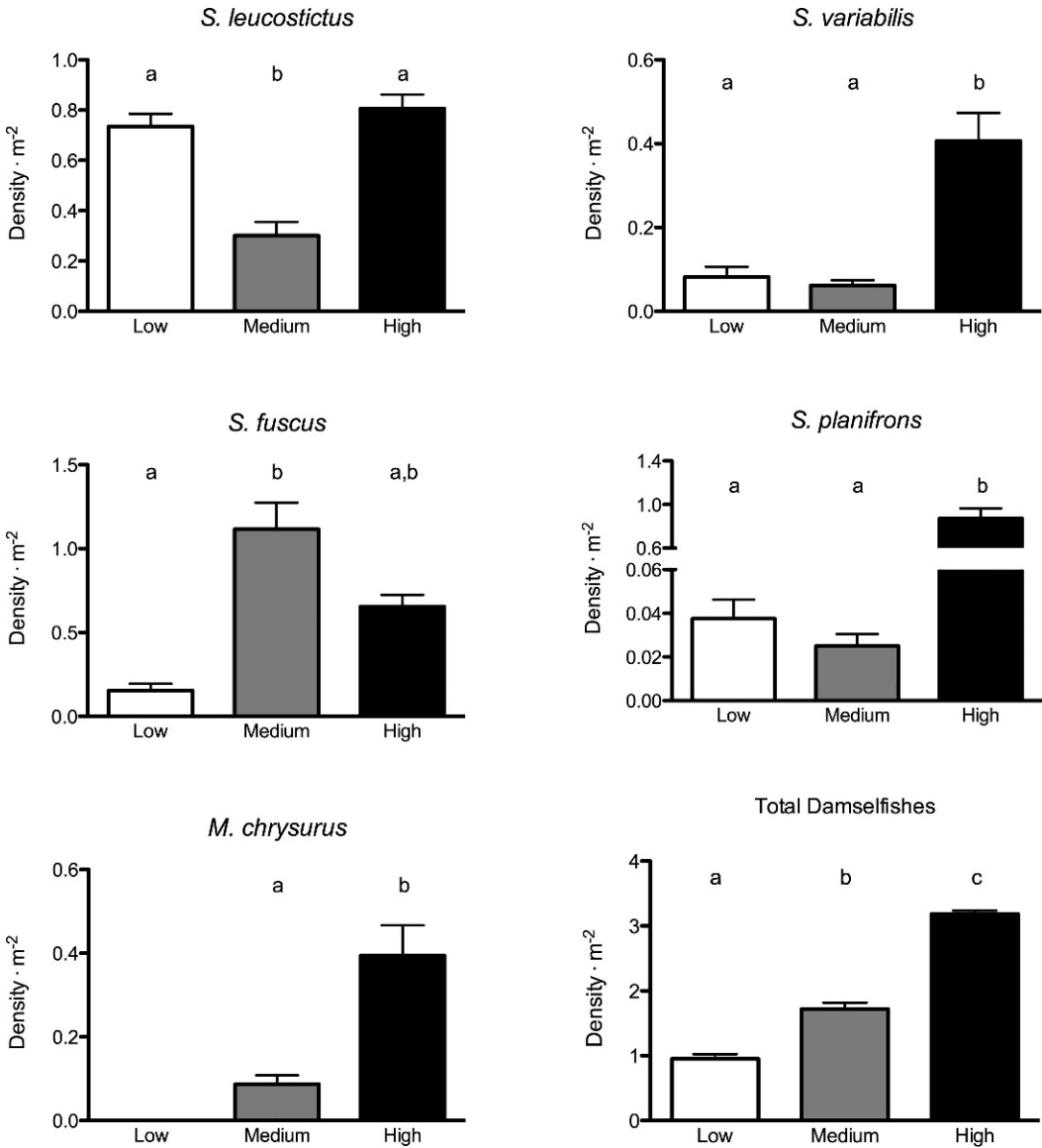


Fig. 3. Density of damselfishes on three levels of structurally complex (rugosity) staghorn coral, *Acropora cervicornis*, rubble in Dry Tortugas National Park, FL. Values are reported as mean \pm SEM. Differences in density among sites are indicated by superscript letters.

except *S. leucostictus* were markedly reduced in low-rugosity habitats, and the loss of structural complexity had the largest impact on *M. chrysurus*. This species was completely excluded from low-rugosity habitats, which is likely a function of the species' relatively large body compared with the other damselfishes. Consequently the low-rugosity rubble probably lacked the appropriate amount of space or "holes" to accommodate the larger-bodied adult fish. All other damselfish species investigated are similar in size to one another and therefore the

decreasing amount of suitably sized habitat cannot alone explain the differences in density among individual damselfishes.

Biological interactions, possibly including interspecific competition between damselfishes, may play a role in shaping population structure and dynamics as reefs continue to degrade (Jones, 1987, Medeiros et al., 2010). Resident fishes that can effectively utilize low-rugosity coral rubble habitats will likely sustain damselfish populations within DTNP. On the basis of data from previous (Wilkes et al., 2008) and current

work, we would predict that low-rugosity rubble habitats will be dominated by *S. leucostictus* and to a lesser extent *S. fuscus*. Although other species (i.e., *S. variabilis* and *S. planifrons*) may be recruited from nearby live patch reefs within DTNP (Wallman et al., 2004), the data suggest that these species may not thrive in newly formed low-rugosity habitats.

The results from the current study provide a direct link between structural complexity of rubble habitats and density of reef fishes (damselfishes). Although several factors in addition to structural complexity have been previously linked to reef fish density, including the nearby presence of live coral, benthic macroalgae, depth, fish community, and relative fishing pressure (Bell and Grazin, 1984; Chabanet et al., 1997; Öhman and Rajasuriya, 1998; Jones et al., 2004; Nagelkerken et al., 2005; Medeiros et al. 2010; Precht et al. 2010), these factors are similar between our study sites (J. Grim et al., unpubl.). As a consequence, our study sites allowed us to test directly the effects of structural complexity on damselfish abundance and diversity. It seems likely that the diversity and abundance of the coral reef ecosystems contained within DTNP will progressively decline as the compaction of rubble habitats continues, and that the loss of both coral and damselfishes may ultimately result in changes to fish recruitment patterns in DTNP and other Caribbean reefs that are progressively degrading (Forrester, 1990; Jones, 1990; Jennings, 2001).

Acknowledgments.—Funding provided by Florida Institute of Oceanography and University of West Florida Department of Biology to WAB. Work was conducted under NPS permit #DRTO-2005-SCI-0004 and UWF ACUC protocol #2005-001. We extend our sincerest gratitude to the National Park Service, DTNP Rangers, and the crew and masters of the RV *Bellows* (Florida Institute of Oceanography).

LITERATURE CITED

- AGASSIZ, A. 1883. Explorations of the surface fauna of the Gulf Stream, under the auspices of the United States Coast Survey. II. The Tortugas and Florida Reefs. Mem. Am. Acad. Arts Sci. Cent. 2:107–132.
- ALLEN, G. R. (ED.). 1991. Damselfishes of the world. Mergus Publishers Hans A. Baensch, Melle, Germany.
- ALMANY, G. R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284.
- ARONSON, R. B., AND W. F. PRECHT. 1997. Stasis, biological disturbance, and community structure of a holocene reef. *Paleobiology*. 23:326–346.
- AYRE, D. J., AND T. P. HUGHES. 2004. Climate change, genotypic diversity and gene flow in reef-building corals. *Ecol. Lett.* 7:273–278.
- BELL, J. D., AND R. GRAZIN. 1984. Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* 15:265–274.
- BIRKELAND, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *In: Proceedings of the Third International Coral Reef Symposium*. Miami, FL:1:331–336.
- BOHNSACK, J. A. 1983. Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. *Environ. Biol. Fishes* 9:41–53.
- CHABANET, P., H. RALAMBONDRAINNY, M. AMANIEU, G. FAURE, AND R. GALZIN. 1997. Relationship between coral reef substrata and fish. *Coral Reefs* 16:93–102.
- CLARK, R. D. 1996. Population shifts in two competing fish species on a degrading coral reef. *Mar. Ecol. Prog. Ser.* 137:51–58.
- COWEN, R. K., C. B. PARIS, AND A. SRINIVASAN. 2006. Scaling of connectivity in marine populations. *Science* 311:522–527.
- DAVIS, G. E. 1982. A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bull. Mar. Sci.* 32:608–623.
- EMERY, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull. Mar. Sci.* 23:649–770.
- FORRESTER, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71:1666–1681.
- GRATWICKE, B., AND M. R. SPEIGHT. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish. Biol.* 66:650–667.
- HIXON, M. A., AND W. N. BROSTOFF. 1983. Damselfish as keystone species in reverse: intermediate disturbance and diversity on reef algae. *Science* 220:511–513.
- HOGARTH, W. T. 2006. Endangered and threatened species: final listing determinations for elkhorn coral and staghorn coral. *Fed. Reg.* 71:26852–26861.
- HOLBROOK, S. J., A. J. BROOKS, AND R. J. SCHMITT. 2002. Variation in structural attributes of patch-forming corals and in patterns of associated fishes. *Mar. Fresh. Res.* 53:1045–1053.
- , G. E. FORRESTER, AND R. J. SCHMITT. 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122: 109–120.
- HUGHES, T. P. 1985. Life histories and population dynamics of early successional corals. *Proceedings 5th Int. Coral Reef Congr.* 4:101–106.
- HUSTON, M. A. 1985. Patterns of species diversity on coral reefs. *Ann. Rev. Ecol. Sys.* 16:149–177.
- JENNINGS, S. 2001. Patterns and prediction of population recovery in marine reserves. *Rev. Fish. Biol. Fisheries* 10:209–231.
- JONES, G. P. 1987. Some interactions between residents and recruits in two coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 114:169–182.

- . 1990. The importance of recruitment to the dynamics of a coral reef fish population. *Ecology* 71:1691–1698.
- , M. I. McCORMICK, M. SRINIVASAN, AND J. V. EAGLE. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA* 101: 8251–8253.
- LESSER, M. P. 2004. Experimental biology of coral reef ecosystems. *J. Exp. Mar. Bio. Ecol.* 300:217–252.
- LIESKE, E., AND R. MYERS (EDS.). 1999. *Coral reef fishes: Caribbean, Indian Ocean, and Pacific including the Red Sea*. Princeton Univ. Press, Princeton, NJ.
- LIRMAN, D. 1999. Reef fish communities associated with *Acropora palmata*: relationships to benthic attributes. *Bull. Mar. Sci.* 65:235–252.
- LONGLEY, W. H., AND S. F. HILDEBRAND (EDS.). 1941. *Systematic catalogue of the fishes of Tortugas, Florida: with observations on color, habits, and local distribution*. Carnegie Institution of Washington Publication, Washington, DC.
- LUCKHURST, B. E., AND K. LUCKHURST. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* 49:317–323.
- MATEO, I., AND W. J. TOBIAS. 2004. Survey of nearshore fish communities on tropical backreef lagoons on the southeastern coast of St. Croix. *Car. J. Sci.* 40:327–342.
- MEDEIROS, P. R., A. T. SOUZA, AND M. I. ILARRI. 2010. Habitat use and behavioural ecology of the juveniles of two sympatric damselfishes (Actinopterygii: Pomacentridae) in the south-western Atlantic Ocean. *J. Fish Biol.* 77:1599–1615.
- MCCORMICK, M. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar. Ecol. Prog. Ser.* 112:87–96.
- NAGELKERKEN, I., K. VERMONDEN, O. C. C. MORAES, A. O. DEBROT, AND W. P. NAGELKERKEN. 2005. Changes in coral reef communities and an associated reef fish species, *Cephalopholis cruentata* (Lacépède), after 30 years on Curaçao (Netherlands Antilles). *Hydrobiologia* 549:145–154.
- NEMETH, R. S. 1998. The effect of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. *Environ. Biol. Fishes* 53:129–141.
- ÖHMAN, M. C., AND A. RAJASURIYA. 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. *Environ. Biol. Fish.* 53:19–31.
- PRECHT, W. F., R. B. ARONSON, R. M. MOODY, AND L. KAUFMAN. 2010. Changing patterns of microhabitat utilization by the threespot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PLoS ONE* 5(5):e10835.
- RASSER, M. W., AND B. RIEGL. 2002. Holocene coral reef rubble and its binding agents. *Coral Reefs* 21:57–72.
- RISK, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153:1–6.
- SMITH, C. L. (ED.). 2002. *National Audubon Society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas and Bermuda*. Alfred A. Knopf, New York.
- WALLMAN, H. L., K. J. FITCHETT, C. M. REBER, C. M. POMORY, AND W. A. BENNETT. 2004. Distributions of three common species of damselfish on patch reefs within the Dry Tortugas National Park, Florida. *Science* 67(3):169–176.
- WILKES, A. A., M. A. COOK, A. L. DIGIROLAMO, J. EME, J. M. GRIM, B. C. HOHMANN, S. L. CONNER, C. J. MCGILL, C. M. POMORY, AND W. A. BENNETT. 2008. A comparison of damselfish densities on live staghorn coral (*Acropora cervicornis*) and coral rubble in Dry Tortugas National Park. *Southeast. Nat.* 7(3):483–492.
- WILLIAMS, A. H. 1980. The threespot damselfish: a noncarnivorous keystone species. *Am. Nat.* 116:138–142.
- JEFFREY M. GRIM, JOHN EME, JENNIE S. ROHRER, ERIN FERER, ALLISON A. WILKES, RACHEL E. WILBORN, KARON RADZIK, RENA L. CROKER, ASHLEY J. O'FARRELL, CHRISTOPHER M. POMORY, AND WAYNE A. BENNETT, *University of West Florida, 11000 University Parkway, Pensacola, Florida 32514. Present address (JMG): Northeastern University, Department of Biology, Boston, Massachusetts 02115; Present address (JE): University of North Texas, Department of Biological Sciences, Denton, Texas 76203; Present address (JSR): Texas Parks and Wildlife, Coastal Fisheries Division, 1502 FM 517 East, Dickinson, Texas, 77539. Present address (EF): VIMS, Physical Sciences Department, Gloucester Point, Virginia 23062; Present address (AAW): Texas A&M University, College Station, Texas 77843. Present address (RW): CIMAS-University of Miami, Rosenstiel School, 4600 Rickenbacker Causeway, Miami, Florida 33149; Present address (KR): Alabama Department of Conservation and Natural Resources, Marine Resource Division, P.O. Drawer 458, Gulf Shores, Alabama 36547; Present address (RLC): Longleaf Elementary School, Pensacola, Florida 32526.*