

Importance of Seascape Complexity for Resilient Fish Habitat and Sustainable Fisheries

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ABSTRACT

Seascape ecology studies indicate that the spatial arrangement of habitat types and the topographic complexity of the seascape are major environmental drivers of fish distributions and diversity across coral reef ecosystems. Impairment of one component of an ecologically functional habitat mosaic and reduction in the architectural complexity of coral reefs is likely to lower the quality of habitat for many fish including important fished species. Documented declines in coral cover and topographic complexity are reported from a decade of long-term coral reef ecosystem monitoring in SW Puerto Rico. To examine broader scale impacts we use “reef flattening scenarios” and spatial predictive modeling to demonstrate how declining seascape complexity will lead to contractions and fragmentation in the local spatial distribution of fish. This change may result in impaired connectivity, cascading impacts to ecological functioning and reduced resilience to environmental stressors. We propose that a shift in perspective is needed towards a more holistic and spatially-explicit seascape approach to ecosystem-based management that can help monitor structural change, predict ecological consequences, guide targeted restoration efforts and inform spatial prioritization in marine spatial planning.

KEY WORDS: Topographic complexity, seascape ecology, predictive modeling

Importancia de la Complejidad del Paisaje Marino para el Habitat Resistente de Peces y las Pesquerías Sostenibles

PALABRAS CLAVE: Complejidad del paisaje marino, ecología marina, modelos de predicción

Importance de Complexité de Paysage Marin pour L'habitat Resilient de Poissons et la Pêche Sustainable

MOTS CLÉS: Complexité de paysage marin, l'écologie marine, modélisation prédictive

INTRODUCTION

Coral reef ecosystems exhibit complex spatial heterogeneity in physical structure across a range of spatial scales (Hatcher 1997). Studies that have applied a multiscale landscape ecology approach have demonstrated that the composition and spatial configuration of two-dimensional seascape mosaics (Grober-Dunsmore et al. 2008, Huntington et al. 2010), as well as, the three-dimensional terrain morphology are important drivers of the distribution, abundance, and behavior of marine organisms (Pittman and Brown 2011). Although more studies are now incorporating two-dimensional models of the seascape in marine ecology (such as thematic benthic habitat maps), these are comprised of discrete patch types and sharp discontinuities representing seascape heterogeneity only in the horizontal dimension, essentially, “a flatscape”. Yet, the three-dimensional topographic complexity of the seascape rarely is modeled at spatial scales that are operationally meaningful for management frameworks. In recent years, however, airborne remote sensing techniques are providing highly accurate and relatively fine resolution spatial representations of three-dimensional seafloor structure (Brock et al. 2004). Techniques such as bathymetric LiDAR (Light Detection and Ranging) provide high resolution digital bathymetry from which vertical seafloor complexity can be quantified

at multiple spatial scales. The seafloor heterogeneity can then be analysed as a terrain using tools more typically applied in terrestrial geomorphology and industrial meteorology, where measures of troughs and peaks and anomalies in surface roughness are important. Using a wide range of surface metrics, Pittman et al. (2009) and Pittman and Brown (2011) demonstrated the utility of LiDAR bathymetry (and lidar derived vertical seafloor complexity) for predicting the distribution and abundance of fish and corals in southwest Puerto Rico.

However, structurally complex coral reefs are proving vulnerable in the face of rapid environmental change. Human activity in the coastal zone - combined with hurricanes, bio-erosion, disease and thermal stress - have resulted in region-wide loss and degradation of biogenic structure created by reef forming scleractinian corals (Hughes et al. 2003, Gardner et al. 2003). Furthermore, the loss of structure and any recovery from loss may be compounded by ocean acidification, with as yet unknown impacts for Caribbean coral reefs. A pan-Caribbean meta-analysis using data on coral reef rugosity estimated that coral reef complexity had declined by more than 50% since its 1960's levels (Alvarez-Filip et al. 2009) (Figure 1). A concurrent decline in the abundance of a wide range of fish species across the region has also occurred that is thought to be partly a result of habitat degradation (Paddack et al.

2009). These declines are likely to have triggered cascading impacts throughout the ecosystem (Cheal et al. 2008), adding fresh impetus to the urgent need to understand broad-scale environmental correlates, such as topographic complexity that influence species distributions across tropical seascapes (Pittman and Brown 2011).

The ecological significance of LiDAR derived seafloor complexity to marine fish provides the key to a new cost-effective tool for forecasting and hindcasting some impacts to fish from changes to the surface complexity of coral reef ecosystems. The ability to predict impacts will support the development of realistic expectations for recovery and restoration for coral reef areas that are either accreting or eroding and will help anticipate the effects of reductions in habitat suitability for commercially important food fish. Here we highlight the importance of topographic complexity in maintaining intact coral reef ecosystems in SW Puerto Rico using data collected by the National Oceanic and Atmospheric Administration's Biogeography Branch. Using in-situ monitoring data we show a decline in both live coral cover and the structural complexity of coral reefs in SW Puerto Rico during the past decade. Then using simulated flattening of surface complexity for the entire study area, we predict and map the impact that declining complexity will have on habitat suitability for

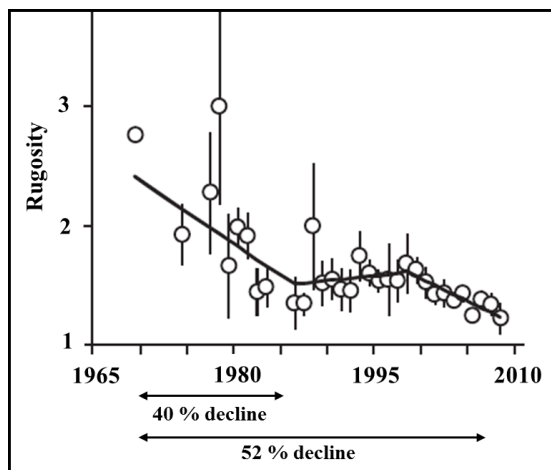


Figure 1. Changes in reef rugosity across the Caribbean between 1969 and 2008. Steepest decline occurred between 1969-1985 and rugosity after the mid-2000s was at the lowest levels recorded in the time series (Adapted from Alvarez-Filip et al. 2009).

two species of fish associated with Caribbean coral reefs.

Seafloor Terrain Complexity as an Important Spatial Predictor for Coral Reef Ecosystems

It is generally accepted as axiomatic in ecology that within a region, environments with greater architectural complexity support higher species richness and higher abundance for certain species than nearby environments with low complexity (MacArthur and MacArthur 1961). Coral reef ecosystems have been shown to exemplify the

positive influence of structural complexity on marine faunal distributions and ecological processes, but the majority of evidence comes from relatively fine-scale studies conducted across meter and sub-meter spatial scales. Recent evidence demonstrates that high resolution (1 - 4 m) measures of topographically complexity collected across tropical seascapes (100s - 1000s meters), also provides powerful predictive capability for modeling broader scale spatial patterns of biodiversity and species distribution. In SW Puerto Rico, Pittman et al. (2009) compared a wide range of measures of topographic complexity derived from LiDAR bathymetry and found that the "slope of the slope" (a first derivative of slope) contributed most to models of fish species richness and distributions of individual species. Models and mapped predictions for individual species were subsequently refined by inclusion of the statistical interactions between slope of the slope and the geographical location across the insular shelf (distance to shore & shelf) in SW Puerto Rico (Pittman & Brown 2011). For example, in SW Puerto Rico, high habitat suitability for *Stegastes planifrons* (threespot damselfish) increased almost linearly with increasing complexity, although spatially the species was restricted by the interaction with depth and by cross-shelf location. Similarly, studies from Jamaica, Belize, Cayman Islands, Florida and Bahamas demonstrated that the availability of shallow water topographically complex microhabitats were the most important proximal controls on *S. planifrons* distribution and abundance (Precht et al. 2010). Threshold effects are also evident where, below a certain level of complexity, the habitat becomes sub-optimal for a species and can no longer support its occurrence at that location. Identifying these critical threshold values and describing the associated precursor conditions that lead to tipping points will be crucial for anticipating the ecological consequences of eroding and collapsing coral reefs.

METHODS

Study area

The coral reef ecosystems of the insular shelf of southwestern Puerto Rico (Figure 2) exist as a spatial mosaic of habitat types dominated by coral reefs, seagrasses, mangroves and patches of sand. The seafloor is highly heterogeneous in assemblage composition and topographic structure resulting in a diverse and productive fish community, with important ecological, economic and cultural value. Like many Caribbean coral reef ecosystems the study area has experienced environmental changes on land and sea that have resulted in loss of structural and functional integrity. The environmental history and ecology of the region was documented in Pittman et al. (2010).

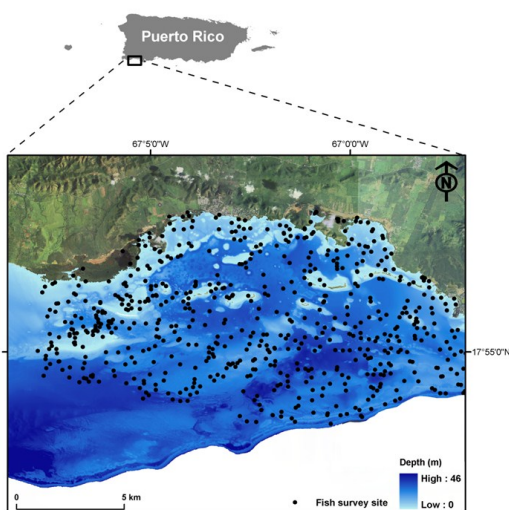


Figure 2. Study area of SW Puerto Rico showing LiDAR derived bathymetry across the insular shelf and the locations of stratified-random biological survey sites conducted between 2001 and 2008 by NOAA's Biogeography Branch.

Underwater Survey Methods for Fish and Benthic Structure

Underwater visual surveys of fish and benthic habitat were conducted semi-annually (Jan/Feb and Sept/Oct) across the insular shelf at La Parguera (322 km²) between 2001 and 2008 as part of a broader long-term monitoring program. Survey sites (n = 1,018) were selected using a stratified-random sampling design whereby sites were randomly located within two mapped strata (i.e., hardbottom and softbottom) derived from National Oceanic and Atmospheric Administration's nearshore benthic habitat map.

Fish surveys were conducted within a 25 m long and 4 m wide (100 m²) belt transect deployed along a randomly selected bearing (0 - 360°). Constant swimming speed was maintained for a fixed duration of fifteen minutes to standardize the search time. Abundance data for five common species were converted to presence-only data. Fish data are available online at http://www8.nos.noaa.gov/biogeography_public/query_main.aspx.

To conduct benthic habitat surveys and collect percentage cover data on scleractinian corals, an observer placed a 1 m² quadrat at five random locations along the fish transect. The quadrat was divided into 100 smaller squares (10 x 10 cm). Corals were identified to genus (and species where possible) and percent cover was estimated to the nearest 0.1 %. Rugosity was measured with a six meter chain (1.3 cm chain link) draped over the contoured surface at two positions along the fish transect. The straightline horizontal distance was measured with a tape. An index of rugosity was calculated as the ratio of contoured surface distance to linear distance, using $R = 1-d/l$, where d is the contoured distance and l is the horizontal distance (6 m).

Chain-and-tape rugosity was only measured over hardbottom sites in the study area.

Spatial Predictive Modeling

Fish species occurrence (or species presence) data from underwater visual surveys was linked statistically to a suite of spatial predictors derived from LiDAR bathymetry following the multiscale analytical approach of Pittman and Brown (2011). Topographic complexity was modeled as the slope of the slope averaged in a 25 m radius moving window across the entire study area from the landward fringe to the shelfedge. MaxEnt (Maximum Entropy Distribution Modeling) software (Phillips et al 2006; Phillips and Dudik 2008) was used to model and map spatial predictions as probabilities of species presence. Using MaxEnt we exploit the strength of the fish-terrain relationship to develop preliminary and exploratory models of species distributions under varying scenarios of reef flattening. Using GIS tools, our slope of the slope layer was uniformly reduced across the entire terrain by 25 % to represent the estimated decadal decline for SW Puerto Rican coral reefs, and 50 % approximating Caribbean-wide declines since the 1960s. This was used as a proof-of-concept for our initial forecasting experiments. Predictions of high habitat suitability (using consistent probability threshold for each scenario) were then re-mapped for two common fish species: i) a herbivorous scraper, *Scarus taeniopterus* (Princess parrotfish); and ii) an indicator of live coral cover, *Stegastes planifrons* (threespot damselfish). Mapped predictions were overlain and examined for differences in spatial patterning and area of suitability habitat under different reef flattening scenarios was quantified and compared to measure the change.

RESULTS

Changes to Coral Reef Structure in SW Puerto Rico and the Wider-Caribbean

Underwater visual census from 572 sites where benthic cover had been estimated semi-annually over a seven year period (2001 - 2007) revealed significant declines in live coral cover (Figure 3). Monitoring beyond 2007 showed continued decline to < 4% mean live coral cover across the region by 2010. At these same sites, measures of surface complexity using the chain-tape method indicated that coral reefs had "flattened" significantly in the past 10 years by an estimated 25 % (Figure 4).

Simulated Flattening of Coral Reef Complexity to Model and Map Impacts to Fish

When the predictions from models using variable levels of flattening were overlain in a GIS, visual examination of differences in the spatial patterning of high suitability habitats for both species indicated a clear contraction in range as terrain complexity declined. In addition, the suitable habitat became more fragmented

leaving patches that were small islands of suitable habitat surrounded by large expanses of sub-optimal areas (Figure 5). Suitable habitat for Princess parrotfish (*Scarus taeniopterus*) contracted by 30 % with a 25 % flattening of terrain complexity, and as much as 66 % was lost when terrain was flattened by 50 %. With 25 % flattening, habitat was lost from the edges of large contiguous patches of suitable coral reef, probably where structure had already existed near the lower thresholds of suitability. With a 50 % flattening patches of suitable habitat fragment even more and few large contiguous patches remain, whereas the number of small patches with relatively small interiors of habitat increased across the seascape.

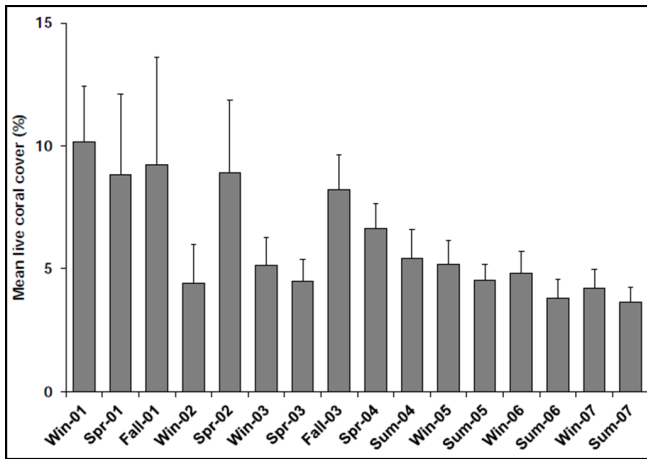


Figure 3. Trend in mean live coral cover (%) for the SW Puerto Rico study area estimated from semi-annual surveys conducted between 2001 and 2008 by NOAA’s Biogeography Branch (source: Pittman et al. 2010).

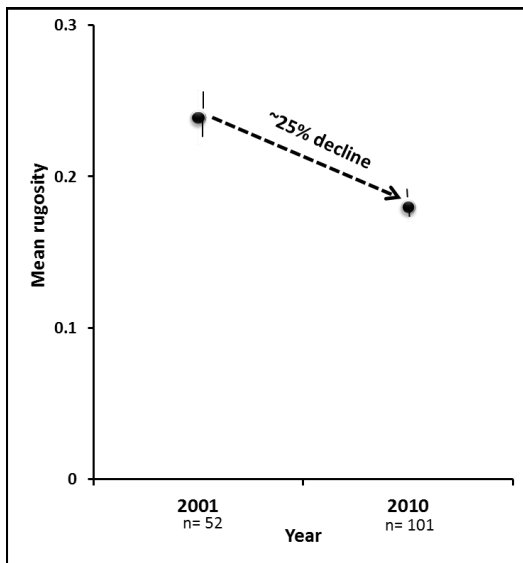


Figure 4. Decline in rugosity of coral reefs in the SW Puerto Rico study area over a ten year period (2001 and 2010) based on chain-tape measurements conducted by NOAA’s Biogeography Branch.

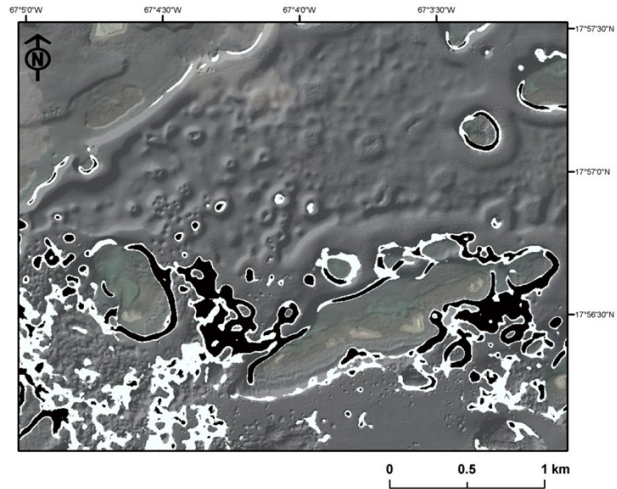


Figure 5. Predicted habitat suitability for threespot damselfish (*Stegastes planifrons*) across a subset of the SW Puerto Rico study area using i.) Unaltered LiDAR-derived topographic complexity; and ii) Numerically flattened topographic complexity to simulate 10 year declines for coral reefs in SW Puerto Rico. MaxEnt was used for modeling predictions.

When impacts to threespot damselfish (*Stegastes planifrons*) habitat suitability were assessed with a 25 % flattening of terrain complexity, model comparison revealed a 56 % loss of suitable habitat. Considerable heterogeneity was observed in the patterns of loss, with some clustering of high loss areas along many of the shallow fringing reef slopes around mid-shelf islands and the coral reefs between the Laurel, San Cristobal, and El Palo reefs. Species-specific differences in the magnitude of lost habitat (i.e. higher for threespot damselfish under a 25 % flattening scenario) are likely to relate to the specificity for habitat requirements determined by a species’, relative position along the specialist-generalist gradient of habitat use, and how close the existing structural complexity is to the threshold of a particular species. A small decline in complexity would be expected to have a greater impact on habitat suitability for areas with complexity already near the tipping point for unsuitable habitat for a particular species. See also color figures of predictions for entire study area in non-print electronic version of the manuscript (Figures 1 & 2 Appendix 1).

DISCUSSION AND FUTURE DIRECTIONS

Understanding the ecological consequences of losing structural complexity of coral reefs is a crucial knowledge gap in our understanding of impacts to coral reef ecosystems (Wilson et al. 2010). Long-term monitoring data collected over multiple years across a wide range of coral reef habitat types has provided an early warning of broad scale declines in the structural complexity of coral reefs in SW Puerto Rico. This structural decline was likely exacerbated by the longer-term trends of declining

branching acroporid species and a shift to a macroalgal dominated benthic community (Pittman et al. 2010, Jeffrey et al. 2010). Together these changes are analogous to changes detected in a Caribbean-wide analyses of rugosity, whereby reductions in coral cover were followed by loss of architectural complexity with little evidence of a time-lag (Alvarez-Filip et al. 2009 and 2011b). Elsewhere in the region, shifts in coral dominance from *Acropora* and *Montastraea* spp. to more stress-resistant and lower complexity species such as *Agaricia* and *Porites* spp. has been documented (Alvarez-Filip et al. 2011b). Where *Montastraea annularis* is still an important reef-building species, growth rates have declined over the past 15 years (Edmunds and Elahi 2007) and *Porites astreoides* has increased (Green et al. 2008). This trend is expected to have major consequences for fish communities, but the spatially explicit implications of reducing terrain surface complexity has not before been examined for Caribbean species.

Although, the ecological ramifications through the ecosystem are still largely unknown, we now know that many fish species and assemblage variables correlate with LiDAR derived measures of terrain surface complexity, which provides opportunities to manipulate the three-dimensional surface structure and investigate corresponding impacts to habitat suitability for fishes. This modeled relationship provides a cost-effective technique to forecast (and hindcast) effects of varying surface complexity. Our proof-of-concept modeling here was a first step in this new direction, yet developing realistic spatial simulations of flattening at relevant spatial scales is challenging. The information required to map the spatial patterns and processes that influence bioerosion, bleaching and physical collapse across highly heterogeneous and connected land-sea ecosystems is still lacking. Neither is information readily available on the likely rates of change at operationally relevant scales. Nevertheless, evidence that structural complexity is declining in many regions is mounting. Ecological impacts will need to be anticipated to ensure that management actions are well targeted and that expectations for recovery after protection are ecologically realistic.

We recognize that more spatially complex scenarios are required to refine our predictions since a uniform flattening is likely to be over-simplistic. Depth will likely be an important consideration, since impacts to deeper coral reefs may be very different to shallow reefs and shallow sheltered reefs may be very different than shallow exposed reefs. Clearly, stressors operate across a hierarchy of scales. Impacts to coral reef structure from hurricanes, bioeroders and direct human activities are spatially heterogeneous processes operating at relatively local scales, whereas thermal stress and ocean acidification operate at considerable broader spatio-temporal scales. Regardless of the type of stressors involved, differential

impacts to topographic complexity will vary by depth, distance to shore, type and intensity of human activities, coral community composition and possibly even patch characteristics. Studies by Alvarez-Filip et al. (2011b) showed that annual rates of change in reef complexity varied significantly between coral reefs across the Caribbean. Yet patterns of change can also be counterintuitive. For example, Alvarez-Filip et al. (2011a) found that coral reef topographic complexity (measured as rugosity) had declined more in marine protected areas than in comparable unprotected areas in the Caribbean. The authors speculate that bioerosion from increasing herbivorous fish populations may have been the cause.

Simulating the spatial impact of these stressors even across the local seascape is a complicated challenge with insufficient information currently available to inform such as model. Development of proxies, however, would allow us to compare a range of scenarios to examine resultant impacts. Integration of data available from detailed ecological studies and long-term monitoring programs should enable us to begin to piece together sufficient information to develop reliable scenarios of structural change which can then be utilized to predict impacts on a wide range of marine biota. Such spatial predictions can then be analyzed using spatial pattern metrics from landscape ecology to quantify and investigate the losses and gains and the magnitude of fragmentation in local patterns of species distributions and biodiversity. Fragmentation of suitable habitat may disrupt movement patterns of individuals, impair metapopulation connectivity leading to isolated dysfunction patches with reduced population viability, shifts in community composition and cascading effects through foodwebs and resiliency of ecosystems. However, existing exploratory studies indicate that species with different habitat requirements and preferences will respond differently to changes in structural complexity; it will be important to identify any species-specific sensitivities and critical threshold beyond which an area no longer provides suitable habitat.

High resolution LiDAR data show strong potential as a data type that, when combined with comprehensive underwater visual survey data and analyzed with sophisticated spatial predictive modeling algorithms, can help determine thresholds in topographic complexity below which habitat no longer supports viable populations of specific fish species.

CONCLUSIONS & RECOMMENDATIONS FOR MANAGEMENT

The SW Puerto Rico study area has experienced marked deterioration in coral reef health concurrent with an increase in stressors and a significant decline of commercially targeted fish, with some local extirpations of several large-bodied and late maturing species (Jeffrey et al. 2010, Pittman et al. 2010). It is conceivable, however, that even if fishing were restricted or excluded in the study

region at some point in the future, the role of degraded benthic habitat must be considered when setting and communicating expectations for rates of recovery and in assessing the suitability of habitat for the most vulnerable and large-bodied fish species. Based on the present trajectory in ecosystem health and stressors, future habitat structure in this region may no longer be capable of offering the necessary ecological functions of food and refuge that it once did; instead it may be impaired to a point where only sub-optimal habitat remains. Therefore, such coral reefs are likely to recover more slowly compared with coral reefs with greater structural integrity. Changes in topographic complexity should not be considered the only seascape measures of habitat suitability for fish associated with coral reefs, since fish are highly mobile and many key species require mosaics of connected habitat to maintain viable populations. Therefore, resource management agencies and associated monitoring programs interested in maintaining or restoring sustainable fisheries must also consider other components of seascape change, such as loss of seagrasses and mangroves, which may reduce the availability of critical resources for fish species or reduce connectivity across ontogenetic life stages (Pittman et al 2007, Grober-Dunsmore et al. 2009). Through interconnectedness, loss and degradation of these surrounding habitat mosaics can also influence the suitability of coral reefs as fish habitat independent of declining coral reef complexity.

Managing Habitat Mosaics and Terrains for Resilient Ecosystems and Sustainable Fisheries

We propose that a shift towards a more holistic and spatially-explicit approach to ecosystem-based management is needed and that a seascape approach can help guide targeted restoration efforts and ecologically relevant spatial prioritization in marine spatial planning. Specifically, we recommend:

- i) A shift in emphasis from monitoring, managing and restoring individual habitat types to a focus on protecting and restoring optimal seascape types based on ecological requirements of species and communities,
- ii) Identifying and prioritizing seascape types that support high biodiversity, productivity and key species of concern,
- iii) Understanding vulnerability of mosaic integrity to environmental stressors in order to predict the consequences of impaired structure for mosaic function including connectivity,
- iv) Utilizing terrain morphology and benthic habitat maps to predict diversity patterns, map essential fish habitat including critical life history spaces such as nursery areas and spawning areas,
- v) Identifying tipping points in habitat structure beyond which abrupt change is expected to help anticipate impacts and set targets for restoration,

and

- vi) Developing management strategies and actions that reduce threats to structural integrity and actively help to re-build lost structure.

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LITERATURE CITED

- Alvarez-Filip, L. Dulvy, N.K., Gill, J.A., Cote, I.M., and A.R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society Series B* **276**: 3019-3025.
- Alvarez-Filip, L., J.A. Gill, N.K. Dulvy, A.L. Perry, A.R. Watkinson, and I.M. Côté. 2011a. Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*. Online First. DOI: 10.1007/s00338-011-0795-6.
- Alvarez-Filip, L., I.M. Côté, J.A. Gill, A.R. Watkinson, and N.K. Dulvy. 2011b. Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? *Global Change Biology* **17**: 2470-2477.
- Brock, J.C., Wright, C.W., Clayton, T.D., and A. Nayegandhi. 2004. Lidar optical rugosity of coral reefs in Biscayne National Park, Florida. *Coral Reefs* **23**:48-59.
- Cheal, A.J., Wilson, S.K., Emslie, M.J., Dolman, A.M., and H. Sweatman. 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series* **372**: 211-223.
- Edmunds, P.J. and R. Elahi. 2007. Demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* **77**(1): 3-18.
- Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A., and A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**: 958-960.
- Green, D.H., Edmunds, P.J., and R.C. Carpenter. 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* **359**:1-10
- Grober-Dunsmore, R., Frazer, T.K., Beets, J., Lindberg, W.J., Zwick, P., and N.A. Funicelli. 2008. Influence of landscape structure on reef fish assemblages. *Landscape Ecology* **23**:37-53.
- Grober-Dunsmore, R., S.J. Pittman, C. Caldow, M.A. Kendall, T. and Fraser. 2009. Chapter 14: A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. Pages 493-530 in: I. Nagelkerken (ed.) *Ecological Connectivity of Coral Reef Ecosystems*. Springer Publishing, New York, New York USA.
- Hatcher, B.G. 1997. Coral reef ecosystems: how much greater is the whole than the sum of the parts? *Coral Reefs* **16**: S77-S91.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly S.R., et al. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* **301**: 929-933.
- Huntington, B.E., M. Karnauskas, E.A. Babcock, and D. Lirman. 2010. Untangling natural seascape variation from marine reserve effects using a landscape approach. *PLoS ONE* **5**(8): e12327. doi:10.1371/journal.pone.0012327
- Jeffrey, C.F.G., R. Clark, and S.D. Hile. 2010. Spatial patterns in benthic composition of nearshore seascapes and implications for scarid populations and fisheries in La Parguera, SW Puerto Rico. *Proceedings of the 62nd Gulf and Caribbean Fisheries Institute* November 2 - 6, 2009 Cumana, Venezuela.

- MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594–598.
- Paddock, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., Beets, J., et al. 2009. Recent region-wide declines in Caribbean reef fish abundance. *Current Biology* **19**: 590–595.
- Phillips, S.J., Anderson, R.P., and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.
- Phillips, S.J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.
- Pittman, S.J., Hile, S.D., Jeffrey, C.F.G., Caldwell, C., Clark, R., Woody, K., Monaco, M.E., and R. Appeldoorn. 2010. Coral reef ecosystems of Reserva Natural de La Parguera (Puerto Rico): Spatial and temporal patterns in fish and benthic communities (2001-2007). NOAA Technical Memorandum 78.
- Pittman, S.J., and K.A. Brown. 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS ONE* **6**(5): e20583.
- Precht, W.F., Aronson, R.B., Moody, R.M., and L. Kaufman. 2010. Changing patterns of microhabitat utilization by the threespot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PLoS ONE* **5** (5): e10835.
- Wilson, S.K., Adjeroud, M., Bellwood, D.R., Berumen, M.L., Booth, D., Bozec, Y.-Marie, Chabanet, P., Cheal, A., Cinner, J., Depczynski, M., Feary, D.A., Gagliano, M., Graham, Nicholas, Halford, A.H., Halpern, B.S., Harborne, A.R., Hoey, A.S., Holbrook, S.J., Jones, G.P., Kulbiki, M., Letourneur, Y., De Loma, T.L., McClanahan, T., McCormick, M.I., Meekan, M.G., Mumby, P. J., Munday, P.L., Öhman, M.C., Pratchett, M.S., Riegl, B., Sano, M., Schmitt, R.J., and Syms, C. (2010) *Crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes*. *Journal of Experimental Biology* **213**: 894-900.