

EPA Public Access

Author manuscript

Mar Pollut Bull. Author manuscript; available in PMC 2021 December 30.

About author manuscripts

Submit a manuscript

Published in final edited form as:

Mar Pollut Bull. 2020 October ; 159: 111387. doi:10.1016/j.marpolbul.2020.111387.

Development of a reef fish biological condition gradient model with quantitative decision rules for the protection and restoration of coral reef ecosystems

Patricia Bradley¹, Ben Jessup¹, Simon J Pittman², Christopher F G Jeffrey³, Jerald S Ault⁴, Lisamarie Carrubba⁵, Craig Lilyestrom⁶, Richard S Appeldoorn⁷, Michelle T Schärer⁷, Brian K Walker⁸, Melanie McField⁹, Deborah L Santavy¹⁰, Tyler B Smith¹¹, Graciela García-Moliner¹², Steven G Smith⁴, Evelyn Huertas¹³, Jeroen Gerritsen¹, Leah M Oliver¹⁴, Christina Horstmann¹⁵, Susan K Jackson¹⁶

^{1.}Tetra Tech, Inc., Owing Mills, MD, USA.

².Seascape Analytics Ltd, Plymouth, UK.

^{3.}CSS-Inc., Fairfax, VA, USA; Under Contract to NOAA, National Centers for Coastal Ocean Science, Marine Spatial Ecology Division, Biogeography Branch, Silver Spring, MD, USA.

⁴ University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami, FL, USA.

⁵NOAA, National Marine Fisheries Service, Silver Spring, MD, USA.

⁶Puerto Rico Department of Natural and Environmental Resources, San Juan, PR, USA.

⁷ University of Puerto Rico, Mayagüez, PR, USA.

⁸Nova Southeastern University, Halmos College of Natural Sciences and Oceanography, Fort Lauderdale, FL, USA.

⁹.Smithsonian Marine Station, Fort Pierce, FL, USA.

^{10.}U.S. Environmental Protection Agency (US EPA), Office of Research and Development (ORD), Center for Environmental, Measurement and Modeling (CEMM), Gulf Ecosystem Measurement and Modeling Division (GEMMD), Gulf Breeze, FL, USA.

¹¹.University of the Virgin Islands, St. Thomas, VI, USA.

¹²NOAA, Caribbean Fisheries Management Council, San Juan, PR, USA.

^{13.}U.S. Environmental Protection Agency, Region 2, Guaynabo, PR, USA.

^{14.}U.S. Environmental Protection Agency (US EPA), Office of Research and Development (ORD), Center for Environmental, Measurement and Modeling (CEMM), Gulf Ecosystem Measurement and Modeling Division (GEMMD), Gulf Breeze, FL, USA.

Corresponding Author: Deborah L Santavy, santavy.debbie@epa.gov; 850-934-9358; US Environmental Protection Agency, Gulf Ecology Division, ORD, Gulf Breeze, FL.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

^{15.}U.S. Environmental Protection Agency (US EPA), Office of Research and Development (ORD), Center for Environmental, Measurement and Modeling (CEMM), Gulf Ecosystem Measurement and Modeling Division (GEMMD), Gulf Breeze, FL, USA; Oak Ridge Institute for Science Education Fellow, US EPA, ORD, CEMM, GEMMD, Gulf Breeze, FL, USA.

^{16.}U.S. Environmental Protection Agency, Office of Water, Washington, DC, USA.

Abstract

Coral reef ecosystems are declining due to multiple interacting stressors. A bioassessment framework focused on stressor-response associations was developed to help organize and communicate complex ecological information to support coral reef conservation. This study applied the Biological Condition Gradient (BCG), initially developed for freshwater ecosystems, to fish assemblages of U.S. Caribbean coral reef ecosystems. The reef fish BCG describes how biological conditions changed incrementally along a gradient of increasing anthropogenic stress. Coupled with physical and chemical water quality data, the BGC forms a scientifically defensible basis to prioritize, protect and restore water bodies containing coral reefs. Through an iterative process, scientists from across the U.S. Caribbean used fishery-independent survey data and expert knowledge to develop quantitative decision rules to describe six levels of coral reef ecosystem condition. The resultant reef fish BCG provides an effective tool for identifying healthy and degraded coral reef ecosystems and has potential for global application.

Keywords

Biological attributes; Biocriteria; Thresholds; Sustainability

Introduction

While climate changes are affecting reefs globally (Hughes et al., 2003; Hoegh-Guldberg et al., 2007, Hoegh-Guldberg et al., 2011, Hoegh-Guldberg et al., 2017; Carpenter et al., 2008; Knowlton and Jackson, 2008), local anthropogenic stressors contribute directly to reef declines and can exacerbate climate change impacts (Rogers, 1990; Edinger et al., 1998; Jackson et al., 2001; Fabricius et al., 2005; Mora, 2008; Bejarno and Appeldoorn, 2013; Vega Thurber et al., 2014; Ennis et al., 2016; Robinson et al., 2017; Moustaka et al., 2018). Fishes represent a diverse taxonomic group providing ecological functions that are critical to the ecological integrity of coral reef ecosystems (Pratchett et al., 2014; Lefcheck et al., 2019). As such, fishes are important measures of the biological condition of coral reef ecosystems. For example, herbivores provide top-down control of algae that may otherwise replace living corals (Hughes, 1994; Burkepile and Hay, 2008), large predators provide top-down control on the fishes that prey on herbivores (Mumby et al., 2006; Stallings, 2008, Stallings, 2009), and invertivores aid in controlling the abundance of coral feeders and bioeroders. Reef fish also provide economic and cultural value, such as food provisioning via subsistence and commercial fishing, and support tourism and recreational activities (Pendleton, 1995; Hawkins and Roberts, 2004; Principe et al., 2012; Ault et al., 2008, Ault et al., 2014; Brander and van Beukering, 2013; Spalding et al., 2017). Given their diverse functional roles in the ecosystem, using reef fish as indicators of coral reef ecosystem

condition can help managers set targets for protection and restoration of coral reefs. For coral reefs, biological assessments using underwater survey techniques are commonly employed to directly measure the status of one or more taxonomic assemblage (e.g., corals, fish) and the chemical and physical attributes that support those assemblages (Jameson et al., 2001; Hill and Wilkinson, 2004; Jokiel et al., 2004; Brandt et al., 2009; Smith et al., 2011; Santavy et al., 2012; Jackson et al., 2014). These assessments are routinely used by states and territories to evaluate coral reef status and trends (Turgeon and Asch, 2002; Waddell, 2005; Waddell and Clarke, 2008). In the U.S. Gulf of Mexico and Caribbean, over-fishing and habitat degradation, including loss of nursery areas, have dramatically altered fish community composition across coral reef ecosystems (Claro, 1991; Paddack et al., 2009; Graham et al., 2017; Kadison et al., 2017). Reef fish species at all trophic levels have been subjected to intense fishing pressure (Munro, 1983; Hughes, 1994; Jackson et al., 2001; Pandolfi et al., 2003; Newman et al., 2006; Ault et al., 2005). Large groupers, snappers, hogfishes, and parrotfishes are now rare, with a resultant loss of predation and herbivory (Pittman et al., 2010; Appeldoorn, 2011; Ault et al., 2005, Ault et al., 2013). Sedimentation from development along tropical shorelines and runoff from agricultural land use is widely considered to have adversely impacted fish communities, particularly through suppressed feeding capability, poor water quality, and changes to benthic habitat (Rogers, 1990; Bejarno and Appeldoorn, 2013; Wenger et al., 2015; Neves et al., 2016; Brown et al., 2017).

Coral reef managers have little control over global or continental scale changes in climate and other environmental conditions; however, they may be able to substantially reduce local anthropogenic stresses by developing and enforcing laws, regulations and policies for waterbody activities and watershed land use. The U.S. Clean Water Act (CWA) (33 USC § 1251 et seq., 1972) can be used to protect coral reef ecosystems (Bradley et al., 2008, Bradley et al., 2009, Bradley et al., 2010). The CWA long-term objective is to restore and maintain the chemical, physical and biological integrity of the nation's waters. To help achieve this visionary objective, the CWA directs jurisdictions (states, territories and tribes) to adopt water quality standards (WQS) as provisions of their laws or regulations. A key component of WQS is water quality criteria (physical, chemical and biological criteria). Water quality criteria are scientifically defensible thresholds established to protect the goals, or designated uses, for a waterbody. When the WQS are not attained, the waterbody is determined to be impaired and management response is needed to address the impairment.

As part of the WQS process, the Environmental Protection Agency's (EPA) guidance recommends jurisdictions to develop and adopt into their water quality standards biological criteria (henceforth "biocriteria") (U.S. Environmental Protection Agency (EPA), 1990, U.S. Environmental Protection Agency (EPA), 2002, U.S. Environmental Protection Agency (EPA), 2011b, U.S. Environmental Protection Agency (EPA), 2013b, U.S. Environmental Protection Agency (EPA), 2016) to protect aquatic life. Biological monitoring surveys provide the foundational information for bioassessments and establishing biocriteria (U.S. Environmental Protection Agency (EPA), 1990, U.S. Environmental Protection Agency (EPA), 2002, U.S. Environmental Protection Agency (EPA), 2011a, U.S. Environmental Protection Agency (EPA), 2013b, U.S. Environmental Protection Agency (EPA), 2002, U.S. Environmental Protection Agency (EPA), 2011a, U.S. Environmental Protection Agency (EPA), 2013b, U.S. Environmental Protection Agency (EPA), 2016; Ault et al., 1999; Davis and Simon, 2004; Bradley et al., 2010; Smith et al., 2011; Bryan

et al., 2016). Biological assessment programs and, in some places, biocriteria have been implemented nationwide for streams and rivers (EPA, 2016).

The Biological Condition Gradient (BCG) is an approach to assess the biological condition of a waterbody relative to natural expectations comparable to the concept of biological integrity. Biological integrity has been defined as a balanced, integrated, adaptive community of organisms having a composition and diversity comparable to that of the natural habitats (Frey, 1977). This definition includes the ecosystem functions and processes that generate and maintain the community (Karr and Chu, 2000). As such, biological integrity is integral to concept of ecological integrity which embodies four main components: nativeness, pristineness, diversity, and resilience (Schallenberg et al., 2011). Resilience refers to the ability of an ecosystem to maintain key functions and processes in the face of stresses or pressures by resisting and then adapting to change (Holling, 1973; Nystrom and Folke, 2001). Coral reef resilience has been linked to certain physical and ecological characteristics that provide some reefs with a greater likelihood of resisting and/or recovering from disturbance (Salm et al., 2001; West and Salm, 2003).

Originally developed and applied for freshwater ecosystems, the BCG is part of EPA's biological assessment and criteria "toolbox" that includes biological indices, models, statistical methods, and practical guidance (Davies and Jackson, 2006; U.S. Environmental Protection Agency (EPA), 2011a, U.S. Environmental Protection Agency (EPA), 2013b, U.S. Environmental Protection Agency (EPA), 2016). The BCG (Fig. 1) provides a common language to describe how biological attributes of an aquatic ecosystem (ordinate, y-axis) are expected to change along a gradient of increasing anthropogenic stress (abscissa, x-axis) ranging from observable biological condition found at undisturbed or minimally-disturbed reference sites (i.e., sites with high environmental quality, pristine, or intact conditions) to sites with high anthropogenic stress (i.e., partially to completely degraded). Biological attributes include aspects of size-structured population abundance, community composition, inter-habitat connectivity and ecosystem function. Although the theoretical stressor-response curve is continuous, condition levels are discrete intervals defined along the stress gradient by a consistent, cogent narrative for each level.

A set of resilience indicators has been developed and applied to various coral reef ecosystems (Obura and Grimsditch, 2009; McClanahan et al., 2012; Maynard et al., 2015). The BCG method enables incorporation of indicators of ecological resilience directly into the model. The BCG ordinate can include indicators of biological resilience, while indicators of physical and chemical resilience can be incorporated in the BCG abscissa.

Freshwater BGC developments have typically separated fishes and benthic invertebrates, leading to BCG models for each (e.g. EPA, 2016; Gerritsen et al., 2017). Benthic invertebrates are an obvious choice because they have high site fidelity (limited mobility), primarily integrate stressors at much smaller scales, and are not immediately impacted by stressors not directly rated to water quality (e.g., fishing pressure). Fishes can be highly mobile and wide-ranging, but their absence in a given location may be a reflection of acute or chronic stressors. Coral reef fish site fidelity varies in scale depending on the species, growth stage, and local habitat availability (Walker et al., 2009; Grober-Dunsmore et al.,

2007; Kuffner et al., 2007; Pittman et al., 2007), however, assemblages are specific to certain habitat combinations and ecosystem regions (Ames, 2017). Their stressors vary from those of benthic invertebrates, especially due to the many species targeted for food, sport, and the aquarium trade. Loss of assemblages has been related to decreases in water quality and habitat degradation (Knowlton and Jackson, 2008).

Some jurisdictions have used the BCG to support various aspects of water quality management, including: (1) more precise definitions of designated aquatic life uses; (2) setting goals for protection or restoration of aquatic life; (3) identification and protection of high quality waters; (4) assessing condition and identifying degraded waterbodies; (5) tracking progress in restoration and protection; and, (6) development of biological criteria. The BCG is an effective tool for clear communication with the public and stakeholders of the biological condition of their waters in the context of the CWA biological integrity objectives, and the likely outcomes of water quality management decisions (U.S. Environmental Protection Agency (EPA), 2011a, U.S. Environmental Protection Agency (EPA), 2016).

In 2004 the U.S. Ocean Action Plan recommended EPA develop biological assessment methods and biological criteria methods for states and territories to evaluate the health of coral reefs and associated water quality (The White House, 2004; Bradley et al., 2008, Bradley et al., 2010). EPA developed a rapid bioassessment protocol (RBP) for stony coral demographics (Fisher, 2007) that was successfully tested in the Florida Keys (Fisher et al., 2007). EPA subsequently tested the stony coral indicators derived from the RBP to determine their responsiveness to anthropogenic disturbance (Fisher et al., 2008) and developed a probabilistic survey design with spatially-balanced random site selection for St. Croix in 2007 and St. Thomas and St. John in 2009 (Fisher et al., 2014). EPA expanded their survey methodology to include fish, gorgonians and sponges (Santavy et al., 2012). In 2009 the U.S. Coral Reef Task Force (USCRTF) selected the Guánica Bay watershed as the location for its first multi-agency initiative to reduce watershed impacts on coral reefs in the coastal zone, leading EPA to focus its bioassessment development efforts on southern Puerto Rico.

Materials and methods

A quantitative reef fish BCG model was developed for coral reef ecosystems. Development of the reef fish BCG model included five steps:

- 1. collect statistically robust data that are fully representative of the study domain where the BCG is to be applied, and encompass most, if not all, of the possible BCG levels;
- 2. conduct preliminary data assimilation and analysis, putting data into formats readily used in the development process, and examine stressor-response relationships for individual taxa and community assemblages relative to proposed gradients;

- **3.** convene an expert panel familiar with the local and regional environment and species, including expected species and assemblage responses to stressors in the region of concern;
- 4. develop the quantitative decision rules for the reef fish BCG model; and
- 5. test the model, adjust, iterate and recalibrate.

2.1 Step 1: Collect and organize bioassessment data

Two underwater coral reef fish surveys were conducted by EPA in 2010 and 2011 along the south coast of Puerto Rico that support development of the coral reef fish BCG. The 2010 survey was designed to reflect coral reef impacts due to increased sediment exposure resulting from land-based human disturbances at 76 stations (Oliver et al., 2014; Bradley et al., 2014) (Fig. 2). Stations were selected to represent a range of potential land-based sediment and pollution threats as modeled by WRI and NOAA (2006) "Reefs at Risk" and NOAA's "Summit to Sea" respective approaches. This project analyzed sediment production on land using soil type and relative erodibility, precipitation data and slope, coupled with an inverse distance weighting function to simulate reduced sediment threat to coastal habitats located further from shore. Puerto Rico 2010 stations were selected from the WRI and NOAA (2006) geospatial dataset, which assigned relative sedimentation threat to mapped coastal habitats (Kendall et al., 2001). The 2011 survey used a probability-based design (Fig. 3) to determine status and biological condition of reef fish and coral communities (Fisher et al., 2019). Both surveys were conducted on coral reefs within 4.8 km of shore (including shores of small islands) at depths 12 m as characterized in NOAA's benthic habitat map (Kendall et al., 2001) to reduce depth effects on assemblage structure and to reflect exposure to land-based stressors in nearshore waters. The surveys included visual assessments of all reef fishes (species size-structured abundance), stony corals (taxa, individual 3D colony sizes, amount of live tissue on coral colonies, and the occurrence of adverse health conditions such as bleaching, disease or overgrowth by boring sponges), reef rugosity, selected macroinvertebrates (e.g., queen conch, spiny lobster, reef crabs, sea urchins and long-spined urchins), and morphometric data for gorgonians and sponges (colony height, diameter, and morphology) (Santavy et al., 2012).

2.2. Step 2: Conduct preliminary data analysis and data preparation

Survey data were subjected to a thorough QA/QC procedure to eliminate uncorrectable unmatched or conflicting data, sites deemed to be in non-target habitat types, and to correct older taxonomic names or synonyms. The data were then put into an Excel workbook for use by the experts. Except for fishing pressure, literature on stressor/response relationships that ties individual stressors to reef fish community metrics was limited (Bradley et al., 2014; Bradley et al., 2016), so limited stressor information was provided in the experts' workbooks.

For each site surveyed, information included depth, distance from shore and shelf edge, reef type, habitat type, and rugosity. Roberts and Ormond (1987) stated that depth alone can be a good indicator of fish species richness; however, depth is also a defining variable for reef type (Walker et al., 2009). Distance from the shore was included because certain

fish species are more likely to migrate from nearby near-shore nursery habitats to adult reef habitats (Appeldoorn et al., 1997, Appeldoorn et al., 2003; Lindeman et al., 2000; Nagelkerken et al., 2015; Dahlgren and Eggleston, 2000; Cocheret de la Morinière et al., 2002; Christensen et al., 2003; Aguilar-Perera, 2004; Mumby et al., 2004, Mumby et al., 2008; Aguilar-Perera and Appeldoorn, 2007; McField and Kramer, 2007; Meynecke et al., 2008; Schärer-Umpierre, 2009; Sale et al., 2010). Shelf breaks are areas of unique habitats and physical properties (Shcherbina et al., 2008) that support equally unique fish assemblages (Kimmel, 1985; Cerveny, 2006; Pittman et al., 2010). Additionally, they are an important spawning habitat for a variety of species (Thompson and Munro, 1974; Johannes, 1978; Colin et al., 1987; Shapiro et al., 1993; Sadovy et al., 1994a, Sadovy et al., 1994b; Sala et al., 2001; Claro and Lindeman, 2003; Nemeth et al., 2008; Sanchez et al., 2017).

To account for confounding effect of habitat complexity on species richness, we used several measures or indicators. These included the rugosity index: the ratio of the length of a chain over the distance covered along a transect by the chain when draped over stony corals and non-coral substrates (Risk, 1972; Hobson, 1972; Talbot and Goldman, 1972; McCormick, 1994; Rogers et al., 1994; Lang, 2003; Santavy et al., 2012). While the rugosity index accounts for important vertical dimensions, it does not fully reflect the three-dimensional availability of fish habitat. Therefore, the data also included additional indicators of habitat complexity, including colony surface area estimates for the three major sessile benthic populations, stony corals, sponges and gorgonians (Courtney et al., 2007; Santavy et al., 2012; Fisher et al., 2007, Fisher et al., 2014).

Commonly used metrics that characterize the fish community metrics were calculated. These included: species richness, density, mean length and standard deviation, total fish biomass, number of fish schools, percent of fish in various families (i.e., Acanthuridae, Scaridae, Chaetodontidae, Haemulidae, Pomacentridae, Labridae, Lutjanidae and Carangidae and Epinephelidae), and relative biomass of herbivores and piscivores (Caldow et al., 2009; Santavy et al., 2012). Additionally, the list of fish species observed at the site was provided, including density and biomass by species.

2.3. Step 3: Convene an expert panel

A panel of coral reef and reef fish experts was assembled in 2012 (Bradley et al., 2014; Santavy et al., 2016). The experts were chosen based on their scientific expertise in Caribbean coral reef taxonomic groups, as well as community structure, organism condition, ecosystem function and ecosystem inter-habitat connectivity. Experts included research scientists from federal and state organizations, academia, and non-governmental organizations (NGOs), as well as water quality managers and natural resource managers from Puerto Rico and the U.S. Virgin Islands (USVI). A list of the BCG experts is available in Bradley et al. (2016).

2.4. Step 4: Develop BCG model decision rules

Four expert workshops (August 2012, April 2014, October 2015 and March 2019) were held in Puerto Rico to develop, test, and calibrate the BCG model for coral reef ecosystems. The

first workshop provided proof-of-concept that the BCG framework developed for freshwater aquatic ecosystems could be adapted for coral reef ecosystems (Bradley et al., 2014; Santavy et al., 2016). The coral reef experts examined video footage from panoramic and linear transect views and supporting photographs of 12 sites from the bioassessments conducted in 2010 and 2011. The sites were selected to represent a range of biological condition. A blind identification system masked all site locations from the coral reef experts. Each expert was asked to draw upon their personal experience and expertise to rate the reef condition for each site. Workshop materials were organized by site and included a photo diary of key representative photos, so coral reef experts would rate the biological condition of each site to document the traits or characteristics used to support their ratings. The experts were asked to consider all aspects of the reef and specifically instructed to consider the characteristics of the condition of corals, sponges, gorgonians, fish, algae, reef rugosity, and topographical heterogeneity (Bradley et al., 2014).

While our working group simultaneously examined multiple assemblages for potential development of the BCG, after the first workshop we decided to separate into fishes and benthic assemblage subgroups for development of the quantitative BGC model, principally because the experts tended to be knowledgeable about either fishes or benthic organisms, and because the two assemblages respond differently to stressors. This paper describes the model development process and results achieved by the fish experts. The benthic process is described in a separate publication (Santavy et al., 2016).

During facilitated discussions in the second, third and fourth workshops and multiple webinars, the fish experts had three subtasks in the development of decision rules: (1) arrive at a common understanding of the target species that make up the database, including community structure, expected occurrences, and sensitivities to stressors; (2) use their understanding of the species to assign a set of individual sites to BCG levels; and, (3) use these results to develop a narrative and ultimately quantitative descriptions of expected species compositions for each BCG level. For subtask 1, all information appropriate to the target species was used: scientific and technical literature; panel members' knowledge and experience; and, empirical species associations with both natural habitats, as well as anthropogenic stressors. Most coral reef assessment data were collected at the site or reef scale. BCG attributes relevant to this scale included aspects of taxonomic composition and community structure (attributes Isingle bondV) and non-native taxa (attribute VI) (EPA, 2016). Taxa differ in their sensitivity or tolerance to stressors, but sensitivity can vary both among species and by stressor (Davies and Jackson, 2006). The fish experts used the BCG attribute definitions (Table 1), their expert knowledge and experience, available literature, and frequency of a species occurring in the data set to assign 357 Caribbean fish species to the taxonomic attributes based on their sensitivities to two anthropogenic stressors (sediments and fishing). For fishing pressure, the fish experts considered whether each species was subject to fishing pressure, the category of fishing pressure (e.g., commercial, recreational or ornamental), and whether that species was regulated under federal or territorial fishing laws (EPA, 2016). For sensitivity to sediment threat, the experts assigned each fish species to a BCG Attribute based on habitat preferences (e.g., ontogenetic shifts from juvenile to adult habitats, as well as observations where the experts regularly observed a species). Fish response to the two stressor categories often differed, and experts took both

stressors into consideration in assigning the fish to BCG attributes. If a fish species was sensitive to one of the two stressor categories, it was considered to be sensitive (i.e., the assignment was based upon the more sensitive response).

Shifts in taxa as a function of differing sensitivities to disturbance are well documented (e.g., shifts from K-selected to r- selected strategists following disturbance). Non-native species were identified as BCG Attribute VI, reflecting the detrimental effects of nonnative taxa on native species (Davies and Jackson, 2006; EPA, 2016). Some taxa were not associated with any attribute (assigned to "x") because the fish experts were unfamiliar or had little supporting information in the literature relative to stressor tolerance or because the survey methodology did not allow an accurate count of the species (e.g., cryptic species).

In subtask 2, assigning sites to BCG levels, the objective was to assign the levels based solely on natural site classification and species composition. Prior to the second workshop, the facilitation team selected a set of 38 sites from the EPA 2010/2011 surveys to span the range and gradient of stress that occurs in southern Puerto Rico. During the 2nd workshop, the facilitator projected the data for each site onto a screen and pointed out the site data and summary indicators. Site-specific information on potential anthropogenic stressors was withheld from the panel to prevent bias in their assessments. We recognized that some natural classification variables might be confounded with anthropogenic stress; e.g., distance from shore is related to distance from land-based discharges and runoff, and rugosity may be reduced because corals have died. The experts then spent several minutes individually considering the data. The facilitator then called on each expert to propose a BCG level for the site, provide the critical or most important information they used to inform the decision, including any confounding or conflicting information, and how they resolved these conflicts (EPA, 2016; Gerritsen et al., 2017). Once all experts had provided their individual ratings, the experts discussed the ratings and rationales, and revised their individual ratings, if desired.

Experts were often unwilling to select a single, discrete BCG level and rated a site as "better than a 4 but not a 3" for reasons such as low total number of taxa or other factors related to site characteristics versus fish community data. To accommodate this, experts rated sites with additional descriptors of "good", "poor" or "middle" for each BCG level and these were scored as (+) or (–). The quantitative decision model yielded numeric memberships between 0 and 1 for each BCG level, and all memberships summed to 1. This allowed for ties between levels, as well as dominant membership in a single level and smaller memberships in adjacent levels.

Subsequent to the facilitated site rating process, the fish experts provided narrative statements to describe what they expected to see for each BCG level starting from the highest quality condition observed in the data set. This narrative became the basis for BCG rule development.

2.5. Step 5: Test model and review model's performance

Following the deliberations in the second workshop, quantitative rules were developed using the fish experts' narrative statements and distribution statistics for attribute metrics and

other measures of the assemblage in each BCG level. Rules are logic statements that the fish experts used to make their decisions. Once the rules are quantified (Step 5, below), a knowledgeable person can follow them to obtain the same BCG level ratings as the group of fish experts, making the actual decision criteria transparent to water quality managers and stakeholders. Rules and reasoning of the experts, whether quantitative or qualitative, were compared to data summaries of the sites evaluated by the experts. For example, if the panel identified a small to moderate number of sensitive taxa for BCG level 3, then the number of sensitive taxa in samples the panel assigned to BCG level 3 were examined (e.g., sensitive taxa ranged from 4 to 8). The statistical distribution of the data in sites assessed by the panel, including modes and quantiles, were used to establish decision thresholds for classifying sites to each BCG level. Quantiles helped to establish the fuzzy boundaries of the decision rules (see below). This process was repeated for all rules and attributes identified by the panel as being important to their decisions.

The decision rules were tested and refined by the expert panel in webinars following the second workshop. The rules were reviewed at the third workshop (with several new panel members present) to confirm that the rules were consistent with expert logic, observations, and empirical data. Mathematical fuzzy logic that mimicked human reasoning was used to develop an inference model to replicate the fish experts' decision process (EPA, 2016). Fuzzy logic is "a precise logic of imprecision and approximate reasoning" (Zadeh, 2008) that has been directly applied worldwide during environmental assessments where imprecise and incomplete information is used to make decisions on the quality and sustainability of systems (Castella and Speight, 1996; Ibelings et al., 2003; Ionnidou et al., 2003; EPA, 2016; Gerritsen et al., 2017). The development of BCG inference models is explained specifically in Gerritsen et al. (2017), and a general tutorial on fuzzy logic can be found in Klir (2004).

Membership of a site in a given BCG level was interpreted according to rules applicable to each attribute or metric that the panel deemed important for the BCG level. For example, for BCG level 3, the rule for the metric total taxa was: total taxa 20 (15–25). This meant that the panel agreed that the rule for the metric total taxa should be a desired mean value of 20 for that metric, but an absolute minimum of 15, and full membership at a value of 25. Hence, membership of the site in BCG level 3 was 0 (zero) when the metric total taxa was less than or equal to 15, 50% when there were exactly 20 of the metric and 1 (100%) when the value equals or exceeded 25. The panel also specified other rules expressed in the same way. Rules for individual metrics were typically combined with logical AND, i.e., the minimum value of all the memberships was taken as the final membership. Some rules were identified as alternates, i.e., either A or B, and these were combined with a logical OR, i.e., the maximum value of the two alternative rules.

The fish experts reviewed the model rules and results and suggested revisions to their ratings or the rules when needed. As rule development and refinement proceeded, it became apparent that differences among classification variables could be encapsulated by two habitat types: patch reef and hard bottom.

During Workshop 3, the experts were asked to review 11 confirmation sites selected to span the range and gradient of stress that occurs in southern Puerto Rico, to apply the fish rules

that had been established in Workshop 2. Experts were requested to assign a BCG level to each site and to state reasons if they disagreed with any given quantitative rule. The experts requested and received the size structure distributions for all stations and for each species. No disagreements with rules were stated and the experts completed the confirmation stations. There were, however, several issues that arose that warrant further investigation (see Discussion).

Performance of the model was described in terms of agreement between model results and the median of expert ratings per site. We assessed the number of sites where the draft BCG decision model's level rating exactly matched the fish experts' median opinion ("exact match") and the number of sites where the model predicted a BCG level that differed from the median expert opinion ("mismatch" sites). For the mismatched sites, the BCG level rating differences between the fish experts and the model were examined to determine whether there was a bias.

3. Results

During the first workshop, experts rated 12 shallow reef sites from Puerto Rico as either good, fair, or poor based on videos and photos. Using only the 12 sites, the experts developed a preliminary narrative BCG with four distinct levels of condition: very good – excellent; good; fair; and poor (Table 2). The experts agreed that there were no longer any reefs in Puerto Rico that met the BCG level 1 definition corresponding to very good-excellent condition (Bradley et al., 2014).

During the second workshop, the fish experts assigned fish species to BCG Attributes I–VI (Table Appendix A1, Table Appendix A2, Table Appendix A3, Table Appendix A4, Table Appendix A5, Table Appendix A6) with the following frequency:

- Attribute I: Historically Documented, Long-lived, or Regionally Endemic Taxa 15 taxa
- Attribute II: Highly Sensitive Taxa 54 taxa
- Attribute III: Intermediate Sensitive Taxa 108 taxa
- Attribute IV: Intermediate Tolerant Taxa 51 taxa
- Attribute V: Tolerant Taxa 4 taxa
- Attribute VI: Non-native or Intentionally Introduced Taxa 3 taxa
- X Taxa not assigned to an attribute 122 taxa

The fish experts assessed 38 calibration sites from the Puerto Rico surveys during the 2nd and 3rd workshops and several webinars. The fish experts agreed that all the stations had some degree of disturbance, including ubiquitous effects from fishing pressure and reef degradation. No sites were assigned to BCG level 2, so only conceptual rules were developed for level 2. BCG level 1 was not expected to occur in Puerto Rico and was not described conceptually or with model rules by the fish experts. All sites were rated as BCG levels 3–6, and intermediate levels were assigned as '+' (exhibiting characteristic of the next

best conditions but not enough to rank site in higher level) and '-' (exhibiting characteristics that suggest somewhat worse conditions but not enough to rank site in lower level). This information was used to help define the condition thresholds at which experts might assign sites to different BCG levels. The fish experts showed a high degree of agreement in their decisions. The "granularity" of the individual decisions was one third (the difference between level 4 and 4+), and this was used to estimate consistency of the experts. For the calibration sites, 85% of individual assessments were within one third of the BCG level of the group median, and 90% were within two thirds of the BCG level. Fig. 4 (top) shows the distribution of individual panelist scores compared to the group median for each site. Confirmation sites (11) were rated during the third workshop, resulting in fewer very close agreements compared to the calibration ratings: 78% of ratings were within one third of the BCG level of the panel median and 95% were within two thirds of the BCG level (Fig. 4 bottom). The lower agreements were likely due to some "drift" of panel members as a result of the intervening time between workshops. Quantifying the drift would require asking each expert how and why their decision differed from the decision rules. Because the drift was relatively small, we did not pursue this.

The narrative decision rules expressed during deliberations exhibited a general pattern of decreasing richness and biomass, especially of sensitive or specialist fish, as biological condition degrades (Table 3). Most of the narrative rules could be translated to numeric decision rules (Table 4). In BCG deliberations, the experts determined how the rules for each level were to be applied: (1) all rules must be met; (2) some rules have alternate rules (e.g., a very low percentage of tolerant individuals may substitute for a high percentage of sensitive individuals); or, (3) some number of rules for that level must be met (EPA, 2016). For example, the fish experts had higher expectations for fish communities in reef habitat than in hard-bottom habitats. Therefore, in BCG level 3, seven rules are expressed; however, six rules must be met to assign the BCG level 3 in reef habitat, while only five must be met in hard-bottom habitats.

Model performance is summarized in Table 5, showing number and percent of model assessments compared to expert panel assessments. Model output was expressed as membership of a site in a BCG level. While model output was potentially continuous from zero to one, input data and rules were often expressed as whole numbers (e.g., number of species in a family), and model output often included exact half memberships (0.5) of adjacent BCG levels. To avoid false precision greater than the model or data could support, we interpreted intermediate memberships (0.4 to 0.6) as half memberships of two adjacent levels. This was used only to compare model results to panel consensus. The panel did not consider a half-level mismatch with their consensus to be a meaningfully different assessment, and a half-level was similar to the spread in ratings among panel members. Accordingly, the panel did not adjust ratings or modify rules for small mismatches. On average, the quantitative model was 92% accurate in replicating the expert panel assessments within one-half BCG level for the calibration datasets, and 82% accurate for the confirmation dataset. There were no mismatches greater than one BCG level.

The 4th workshop focused on potential transferability of the Puerto Rico model to a different jurisdiction (e.g., Florida Keys) and possible management applications of the model. To

test transferability of the model, the experts rated 14 stations collected in the Florida Keys and Dry Tortugas at depths shallower than 16 m, which were co-sampled by both the fish and benthic teams (Bohnsack and Bannerot, 1986). The stations were selected by the Reef Visual Census (RVC) leads across a stressor gradient: water quality (low anthropogenic impact – Dry Tortugas, low-moderate impact – Florida Keys forereef, and high impact – Hawk's Channel); and fishing pressure based upon management zones (low – Dry Tortugas National Park, medium – Florida Keys, Marine Protected Areas, high – Florida Keys outside of Marine Protected Areas). The quantitative BCG model developed for Puerto Rico was 79% accurate in replicating the expert panel assessments within one-half BCG level for the Florida Keys calibration. The biomass metric was the rule that was not met in the mis-matched sites. The experts felt that species attribute levels might need to be revisited based on location, particularly because fishing pressure varies significantly by jurisdiction.

The experts were asked to consider how the benthic and fish models could be used together for evaluating sites. They applied the BCG rules for both assemblages to several sites. One example scenario was when the benthic organisms met the benthic level 3 rules, but the fish only met the fish level 5 rules. The panel assessed the site as *degraded but with high potential for recovery of the fish population because important habitat and food for fish present.*

4. Discussion

Since 2005, several U.S. states and other entities (e.g., river basin associations and counties) have either calibrated, or are in the process of calibrating, the BCG for freshwater aquatic ecosystems (EPA, 2016). These methods have been shown to be applicable to several stream and riverine environments and taxa: perennial freshwater streams for benthic macroinvertebrates (primarily insects) throughout the United States; freshwater fishes in streams and lakes (EPA, 2016; Gerritsen et al., 2017); and benthic diatoms (Hausmann et al., 2016). This paper extends that utility to reef fishes in coral reef ecosystems.

A regional panel of experts assigned fish species inhabiting Puerto Rico's near-shore linear coral reefs to attributes of sensitivity to human disturbance, natural prevalence, historic species importance in the Caribbean, and native or exotic origin. The experts developed fish rules for six levels of coral reef condition, with a well-defined narrative for each level.

A quantitative decision model had a high degree of fidelity to the expert decisions: the model replicated the expert consensus within one BCG level for 100% of sites and replicated the expert consensus within a half BCG level for 82% to 92% of the sites. This degree of predictive accuracy is as good or better than the examples described for freshwater systems (Gerritsen et al., 2017; Hausmann et al., 2016).

BCG model development, calibration, and validation were successful for the available data using the expert process described. However, there were several issues that arose during workshop and webinar discussions that could be further investigated for incorporation into future BCG model revisions or model result interpretations. The issues addressed fish characteristics (size-structure expectations, longevity, and reproductive strategies),

site condition effects (the undisturbed baseline condition and water quality indicators), fish community variations related to habitat (habitat classifications and inter-habitat connectivity), and data collection methods (consistency and sufficiency). These issues are discussed below with possible approaches for resolution.

4.1. Size-structure expectations

Observations of juvenile and adult fish at a reef site might indicate that a full life cycle is supported at the site, inferring inter-habitat connectivity at the site for certain species. With observation of a single life stage, experts were uncertain about the propensity of the reef site to support nursery function for juveniles or maintenance of an adult population. Therefore, in the BCG rating process, experts requested information about the size-structured abundance distribution of the fish observed. The experts were familiar with critical sizes that might indicate single or multiple life stages and could relate the size and life-stage information to the biological condition of the reef fish community. Unfortunately, fish sizes were recorded at 5-cm intervals for all species, but association of juvenile and adult stages had not yet been completed for this dataset. A listing of juvenile and adult size ranges for fish species might be available in the literature or could be created by the experts based on expert judgment. Stevens et al.'s (2019) recent synthesis of life history demographic parameters for Florida and Caribbean reef fishes could greatly facilitate these efforts. Enumeration of juvenile and adults for future rating exercises would allow calculation of life-stage metrics for reef fish. The life stage metrics might allow better discrimination of BCG levels and inter-habitat connectivity.

4.2. Longevity and reproductive strategies

In coral reef ecosystems, large-bodied, slow-growing, late-maturing fishes (K-strategists) are generally more sensitive to exploitation than faster-growing, shorter-lived species (r-strategists) (Beverton and Holt, 1957; Man et al., 1995; Jennings et al., 1998; Coleman et al., 2000; Goodwin et al., 2006; Ault et al., 1998, Ault et al., 2008). Consideration of K/r strategies informs coral reef fish population responses to environmental stress, which is largely determined by life-history traits with K-strategists being more susceptible to fishing pressure than r-strategists (Musick et al., 2000; Ault et al., 2005, Ault et al., 2008, Ault et al., 2014). The BCG Attribute definitions (Davies and Jackson, 2006) include considerations of these life history traits: Attributes I and II include long-lived, late maturing, low fecundity species; while Attributes IV and V include early colonizers with rapid turn-over times and "boom/bust" population characteristics. However, species-specific life history data was not included in this BCG evaluation and was therefore not considered in the assignment of species to coral reef BCG attributes.

4.3. Undisturbed baseline condition

A challenge in developing the coral reef BCG was the difficulty in determining reference conditions for biological integrity because fish populations in Puerto Rico have been exploited since at least the 15th century and were already decimated by the 1950s (Goreau, 1959; Jackson, 1997; Greenstein et al., 1998; Jackson and Sala, 2001; Jackson et al., 2001; Jameson et al., 2003; Pandolfi et al., 2003), and no anthropogenically unimpacted reference sites were available in Puerto Rico. During the 1st workshop, the BCG experts

discussed using the Healthy Reefs Initiative (HRI) data thresholds for the Mesoamerican reef as possible reference conditions for Puerto Rico. HRI based these thresholds on the wider Atlantic and Gulf Rapid Reef Assessment (AGRRA) data for the Wider Caribbean, which the experts considered to be comparable to the U.S. EPA methodology. The fish experts reviewed the HRI thresholds (HRI, 2012), and then, through a methodical, facilitated process, used their expert judgment to define a preliminary set of attributes for reference conditions for Puerto Rico. Calibrating the model with surveys from relatively unimpaired areas elsewhere in the Caribbean may eventually be useful in further testing the reference condition attributes; however, differences in fish observation protocols may present a complication.

4.4. Water quality indicators

The U.S. EPA coral reef research in south Puerto Rico and USVI evaluated potential relationships between reef condition metrics and estimates of coral reef stressors, with each stressor incorporating relative proximity from reef survey locations to a human disturbance. Methods to designate disturbance ranged in complexity from general sources of disturbance such as towns and industrial centers (Fisher et al., 2008; Oliver et al., 2014), and distance to bays with impaired water quality (Oliver et al., 2018), ST (Oliver et al., 2018), to measures that integrate spatially-explicit land use/land cover such as the Landscape Development Intensity Index (LDI) (Oliver et al., 2011, Oliver et al., 2018) and ST (Oliver et al., 2018). Reef survey methods progressed from an initial focus on stony coral communities (Fisher, 2007) to include fish, gorgonians, and sponges (Santavy et al., 2012). The LDI showed the most, and consistently inverse relationships with measures of coral cover, rugosity, colony size and species diversity (Oliver et al., 2011, Oliver et al., 2018), consistent with other studies (Rogers, 1990; Fabricius and De'ath, 2001; Fabricius et al., 2005; Cleary et al., 2006) and a general hypothesis that intensifying land-based human activities in watersheds is associated with a decline of adjacent reefs. The BCG expert panelists were concerned about fishing pressure and sedimentation threat to fish communities. Large scale modeling of sediment plumes and potential delivery to Indonesian reefs offers a potential approach to coupling watershed sediment production with an ocean transport model that accounts for current dynamics and particle settling (Rude et al., 2016). The predictive potential for LDI (Oliver et al., 2011) to indicate deteriorated reef condition was demonstrated despite simple assumptions applied to connect St. Croix watershed LDI values to reef survey locations without accounting for ocean currents, wind or bathymetry that undoubtedly influence transport of specific stressors to coral reef communities. Refinements in stressor modeling needed to inform a comprehensive stressor gradient for the BCG require data with appropriate scale to the reef communities of interest. Coral reef stressor gradients cannot be as clearly defined as those in streams. Streams have a distinct catchment and actual flow distance from a source to particular sampling sites can be measured. Coral reefs and all coastal marine ecosystems are not linear systems, and land-based stressors from multiple watersheds may impact a given reef as they become dispersed by wave action, wind and oceanic currents.

The journal's reviewers recommended that we use multivariate statistical techniques to examine indicators of different environmental gradients by linking fish species composition

to proxies of exposure to various stressors. Ordination and cluster permutation analyses (i.e., PRIMER-e Ver. 7; Clarke and Gorley, 2015; Clarke et al., 2014) were used to identify how the BCG Level groups were related within and among the four BCG Levels 3–6 (Table 6), and how Levels were related to the environmental gradients used in our study (Fig. 5). The environmental variables tested were distance to shore, distance to shelf, distance to disturbance, sediment threat (ST), reef rugosity, coral colony density, coral species richness, and percent two-dimensional coral cover. A cluster analysis identified similarly patterns among the evaluated sites to find major fish species associated with each BCG Level (Table 7). Ordination techniques (non-metric Multiple-dimensional Scaling) showed how environmental variables mapped in relationship to the fish BCG Levels.

Three environmental variables were seen to explain some of the fish species composition (i.e., ST, percent live coral cover (2-D) and rugosity). Increased sediment threat was related to decreasing biological condition (BCG Levels 5 and 6), whereas increased rugosity and live 2D coral cover were correlated to good and fair BCG Levels (3 and 4). As rugosity increased so did live coral cover (2D) and coral density, all variables related to increased ecosystem complexity through higher topography and amount of live coral on reefs essential for the habitats, foraging and refugia needs of many reef fish species. The distance to shore, distance to shelf and distance to disturbance as defined did not provide any explanatory information for the biotic patterns. This might imply the need to consider a different approach for estimating distance from disturbance.

Based on fish density and biomass, BCG Levels 3 and 4 were not significantly different from one another, and BCG Levels 5 and 6 were not significantly different from one another (Table 6). The primary fish species within BCG Levels 3 and 4 were Thalassoma bifasciatum and Sparisoma aurofrenatum, with eight other fish species also present in both BCG Levels 3 and 4. This similarity caused BCG Levels 3 and 4 to be not different. This is an example where expert judgment considering the importance of the biology and ecology of different species and their functional contributions could outweigh the importance of just density or biomass of fish species determined by a statistical analysis. These statistical analyses corroborate the conclusion that expert judgment is essential in this process to provide the knowledge of nuanced ecological functions for which data were not available.

4.5. Habitat classifications

In coral reef ecosystems, there is a strong positive correlation of habitat complexity with fish species richness (Luckhurst and Luckhurst, 1978; Carpenter et al., 1981; Roberts and Ormond, 1987; McClanahan, 1994; McCormick, 1994; Green, 1996; Friedlander and Parrish, 1998; Sale, 1991; Friedlander et al., 2003; Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b; Kuffner et al., 2007; Pittman et al., 2007; Aguilar-Perera and Appeldoorn, 2008; Walker et al., 2009; Smith et al., 2011). Reef fish data can be associated with the NOAA benthic habitat maps to help determine the expected assemblages in different habitats throughout a mapped space (Pittman et al., 2007). For example, the main factors used to determine reef fish assemblages in biogeographic regions on the Southeast Florida reef tract were reef vs. hardbottom substrates, depth, relief, and geographic space (Smith et al., 2011; Fisco, 2016; Ames, 2017). Important species traits might show patterns

only found at inshore or offshore survey sites, exhibiting a distribution restricted by water depth, or geographically widespread across depth, which might influence their potential role as indicators in the BCG model. For example, the absence of a fish species from a nearshore site may not be indicative of the condition of the coral reef ecosystem if that species' range does not occur in nearshore reefs. Similarly, the frequent occurrence of a species in waters known to be impaired due to the influx of land-based pollutants may mean the species is more pollution-tolerant than a species found only in waters that do not contain influxes of land-based pollutants, assuming benthic variables are similar in both locations. The combination of the depth distribution, distance to shore, and the frequency of occurrence provide an indication of relative abundance for each fish species and a simplified geographical habitat width for each species. Improved information on species and functional traits for Caribbean fish could aid in improving and interpreting results when applying the BCG fish model to other Caribbean locations.

4.6. Inter-habitat connectivity

As mentioned, the distance to shore was recognized as a possible site variable because it represented inter-habitat connectivity among larval, juvenile, and adult fish habitats. Beneficial off-reef habitats for reef fish are not all near the shore. These off-reef habitats must be accessible to benefit certain reef fish species. Knowledge of the inter-habitat connectivity between sampling locations and off-reef habitats and the necessity of such habitats for each fish species would improve assessments and interpretation of assessments for reef fish samples and sites. The experts recommended that high-resolution reef bottom topography (e.g., LIDAR) would allow for better estimation of inter-habitat connectivity. With high-resolution topography, features related to inter-habitat connectivity would be recognizable and quantifiable. High-resolution topography would also indicate elements of rugosity as well as inter-habitat connectivity, allowing characterization of broad-scale relief and a possible basis for classification of reefs.

4.7. Data collection methods

Some experts felt that the data collection methods (Santavy et al., 2012; NOAA, 2013a) were not optimal for assessing fish assemblages. Transect methods for reef fish are biased in that some species disperse before they are counted (Ydenberg and Dill, 1986; Januchowski-Hartley et al., 2011; Lindfield et al., 2014; Emslie et al., 2018), significantly impacting estimates of reef fish richness and density (Chapman et al., 1974; Kulbicki, 1998; Kulbicki and Sarramégna, 1999). Some experts recommended using the stationary point count (SPC) fish survey method (Bohnsack and Bannerot, 1986; Ault et al., 1998, Ault et al., 2005, Ault et al., 2014; Brandt et al., 2009; Richards et al., 2011; Smith et al., 2011), which allows the fishes time to adjust to the presence of a diver before counting begins. In this method, pairs of divers record the number, size and species of all fishes observed within cylinders visually estimated at 15 m in diameter. Other fish experts preferred the transect method (Santavy et al., 2012; NOAA, 2013a), suggesting that the fish counter has more opportunity to observe cryptic species than when using the point-count method. They also suggested that the belt transect is also much better for low-visibility environments, which are very common in Puerto Rico and the U.S. Virgin Islands. The fish experts reached consensus that a single commonly used method of counting fish would be much better than using different methods

and would reduce variance in getting density estimates. The fish experts also recommended revising the field method for measuring topographic complexity (e.g., rugosity) for each reef station where fish were counted. They felt that methods which measure vertical relief along the entirety of a transect (e.g., Dustan et al., 2013; NOAA, 2013b) could provide more information about reef rugosity.

4.8. Application

To facilitate use by water quality managers, the BCG rule application will be automated once finalized. Additionally, clear instructions will be provided for each BCG fish rule. For example, the fish rule "at least one large-bodied parrotfish present" requires clarification of what scientists mean by "large-bodied parrotfish" (Appendix A Table A7). A precise definition is being documented for each rule, and guidance material is being developed so the tool can be easily applied and interpreted.

The BCG provides a powerful framework for an operational monitoring and assessment program, for communicating resource condition to the public, and for assisting in management decisions to protect or remediate water resources. The levels of the BCG are biologically recognizable, measurable stages in condition of coral reef ecosystems. As such, the BCG can be used to inform biological assessments of Caribbean coral reefs. The BCG is a defensible means to translate scientific understanding to support both regulatory and non-regulatory water quality and natural resource programs and inform biological criteria development. Biologically based aquatic life uses coupled with numeric biological criteria provide a direct measure of the aquatic resource that is being protected (e.g., coral reefs), complimenting the stressor and exposure criteria which are comprised of chemical, toxicological, and physical parameters. The BCG provides a framework that can help relate chemical, physical and biological assessments and criteria for a more integrated, comprehensive evaluation of the condition of a waterbody. Additionally, the fish and benthic BCG models can be combined for a robust interpretation since these communities can respond differently to stressors.

While the BCG model was developed using data from Puerto Rico, it is important to note that the BCG is a general framework that could potentially be applied to other coral reef ecosystems, as demonstrated by the proof-of-concept work done using sites from Florida Keys and Dry Tortugas. In order to use the BCG, states and territories would need to adapt it to their own coral reef habitat and monitoring data and develop a numeric model scheme specific to their jurisdiction. In summary, (1) the BCG conceptual framework is applicable to other coral reef ecosystems; (2) the methods used to develop the BCG in Puerto Rico are likely applicable to other coral reef ecosystems (e.g., the process to elicit expert judgment); (3) the qualitative rules may be applicable, but will require vetting by regional experts, using regional datasets to test and refine the rules; and, (4) quantitative rules are jurisdiction-specific.

Many organizations produce periodic report cards that provide information on coral reef status and trends, as well as management strategies being employed to improve these ecosystems (e.g., The Healthy Reefs Initiative, The Atlantic and Gulf Rapid Reef Assessment, The Florida Keys National Marine Sanctuary, Australia Institute of Marine Science (AIMS) Long Term Monitoring Program for The Great Barrier Reef, etc.). The

BCG is complementary to these report cards and can be used to help communicate monitoring results.

Conclusion

Coral reef resources have historically been managed by natural resource agencies employing a variety of approaches, including fisheries regulations, marine protected areas, and endangered species protection (Bradley et al., 2010). Regulations, including those for fisheries and protected species may be enhanced by an integrated and ecologically broad systems science approach (e.g., Ault et al., 2005). Such an integrated approach is the coral reef fish BCG model. For example, water quality managers could use the BCG to distinguish high-quality coral habitats for greater protection, or to gauge the effectiveness of management actions to meet restoration goals for coral reefs adjacent to urban and agricultural areas. Successful BCG development for Puerto Rico reef fish communities provides a common framework that can be used by other jurisdictions. However, quantitative calibrations and validations may likely be region specific. Therefore, broader application in the Caribbean or the Pacific will require additional focused study.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We would like to thank the Caribbean Coral Reef Institute for hosting the 1st and 4th workshops on Magueyes Island; the El Yunque National Forest Headquarter for providing the conference facilities for the 2nd workshop; and the Caribbean Landscape Cooperative (CLCC) and the International Institute of Tropical Forestry (IITF) for providing the conference facilities for the 3rd workshop. Also, we wish to acknowledge the continuing support received from William Fisher and Buddy LoBue (U.S. EPA).

The U.S. Environmental Protection Agency (EPA) through its Office of Research (ORD) and Development and Office of Water (OW) funded and collaborated in the research described here under two contracts to Great Lakes Environmental Center: Contract EP-C-09-001, Work Assignment #3-01, and Contract #EP-C-14-016, Work Assignment 1-1. The views expressed in this paper are those of the authors and do not necessarily reflect the views or policies of the U.S. EPA. This document has been reviewed by the U.S. EPA, Office of Research and Development, Office of Water, and Region 2, and has been approved for publication. Any mention of trade names, products, or services does not imply an endorsement by the U.S. Government or the U.S. EPA. The U.S. EPA does not endorse any commercial products, services, or enterprises.

Appendix A.: Assignment of Fish Species to BCG Attribute Levels I-VI and Large bodied fish species

Fish Species Attribute Assignments made by the expert during multiple workshops and webinars. Assigned BCG attributes for fish species are based upon sensitivity to fishing pressure and sediment stress across the US Caribbean and South Florida. Assignment of fish species to BCG Attribute Levels I-VI: Level I species are historically documented, long lived, or regionally endemic taxa (Table Appendix A1); Level II species are highly sensitive to fishing pressures and sediment threats (Table Appendix A2); Level III species are intermediately sensitive taxa to fishing pressures and sediment threats (Table Appendix A3); Level IV species are intermediately tolerant taxa to fishing pressures and sediment threats (Table Appendix A4); Level V species are tolerant taxa to fishing pressures and

sediment threats; and Level VI species are non-native or intentionally introduced species (Table Appendix A5). Abbreviations for the trophic guilds are: H=herbivore, P=piscivores, I=invertivore, and Z=zooplanktonivore (from Caldow et al. 2009). Piscivore size indicated as either large (P-L) or small (P-S).

Table Appendix A1.

BCG Attribute I species are historically documented, long-lived, or regionally endemic taxa in the US Caribbean and Florida.

Species Name	Common Name	Trophic Guild
Acanthostracion polygonius	Honeycomb cowfish	Ι
Acanthostracion quadricomis	Scrawled cowfish	Ι
Carcharhinus limbatus	Blacktip shark	P-L
Carcharhinus perezii	Caribbean reef shark	P-L
Epinephelus itajara	Atlantic goliath grouper	P-L
Epinephelus morio	Red grouper	Ι
Epinephelus striatus	Nassau grouper	P-L
Mycteroperca bonaci	Black grouper	P-L
Mycteroperca interstitialis	Yellowmouth grouper	P-S
Mycteroperca tigris	Tiger grouper	P-L
Mycteroperca venenosa	Yellowfin grouper	P-L
Scarus coelestinus	Midnight parrotfish	Н
Scarus coeruleus	Blue parrotfish	Н
Scarus guacamaia	Rainbow parrotfish	Н
Sphyrna mokarran	Great hammerhead shark	P-L

Table Appendix A2.

BCG Attribute II species are highly sensitive taxa to fishing pressures and sediment threats in the US Caribbean and Florida.

Species Name	Common Name	Trophic Guild
Aetobatus narinari	Spotted eagle ray	Ι
Aluterus scriptus	Scrawled filefish	Ι
Amblycirrhitus pinos	Red-spotted hawkfish	Z
Anisotremus surinamensis	Black margate	Ι
Astrapogon stellatus	Conchfish	Ι
Aulostomus maculatus	Trumpetfish	P-S
Cantherhines macrocerus	America white-spotted filefish	Ι
Cantherhines pullus	Orange-spotted filefish	Н
Caranx crysos	Blue runner	P-S
Caranx hippos	Crevalle jack	P-L
Cephalophilus furcifer	Atlantic creolefish	Z

Species Name	Common Name	Trophic Guild
Chaenopsis limbaughi	Yellowface pikeblenny	Ι
Chaetodipterus faber	Atlantic spadefish	Ι
Chromis cyanea	Blue chromis	Z
Chromis multilineata	Brown chromis	Z
Clepticus parrae	Creole wrasse	Z
Dactylopterus volitans	Flying gurnard	Ι
Dasyatis americana	Southern stingray	Ι
Elacatinus genie	Cleaner goby	Н
Elacatinus multifasciatus	Green-banded goby	Ι
Elacatinus oceanops	Neon goby	Ι
Elacatinus prochilos	Broad stripe goby	Ι
Elacatinus saucrum	Leopard goby	Ι
Enchelycore nigricans	Viper moray	P-S
Fistularia tabacaria	Blue-spotted cornet fish	P-S
Galeocerdo cuvier	Tiger shark	P-L
Ginglymostoma cirratum	Nurse shark	P-L
Gramma loreto	Fairy basslet	Ι
Haemulon chrysargyreum	Smallmouth grunt	Ι
Halichoeres radiatus	Puddingwife	Ι
Heteropriacanthus cruentatus	Glasseye snapper	Z
Holacanthus ciliaris	Queen angelfish	Ι
Holacanthus tricolor	Rock beauty	Ι
Hypoplectrus gemma	Blue hamlet	
Hypoplectrus hybrid	Hybrid hamlet	
Lachnolaimus maximus	Hogfish	Ι
Lactophrys triqueter	Smooth trunkfish	Ι
Lactophrys bicaudalis	Spotted trunkfish	Ι
Lactophrys trigonus	Trunkfish	Ι
Lutjanus analis	Mutton snapper	Ι
Lutjanus cyanopterus	Cubera snapper	P-L
Lutjanus jocu	Dog snapper	P-L
Melichthys niger	Black durgon	Н
Negaprion brevirostris	Lemon Shark	P-L
Pareques acuminatus	Highhat	Ι
Priacanthus arenatus	Bigeye	Ι
Priolepis hipoliti	Rusty goby	Ι
Prognathodes aculeatus	Longsnout butterflyfish	Ι
Scomberomorus regalis	Cero	P-S
Seriola dumerili	Greater amberjack	P-L

Species Name	Common Name	Trophic Guild
Seriola rivoliana	Almaco jack	P-L
Serranus tigrinus	Harlequin bass	Ι
Thalassoma bifasciatum	Bluehead	Ι
Trachinotus falcatus	Permit	Ι
Trachinotus goodei	Palometa	P-S
Xanthichthys ringens	Sargassum triggerfish	Z

Table Appendix A3.

BCG Attribute III fish species are intermediately sensitive taxa to fishing pressure and sediment threats in the US Caribbean and Florida.

Species Name	Common Name	Trophic Guild
Abudefduf taurus	Night sergeant	Н
Acanthemblemaria aspera *	Roughhead blenny	Ι
Acanthemblemaria maria	Secretary blenny	Ι
Acanthemblemaria spinosa	Spinyhead blenny	Ι
Acanthurus chirurgus	Doctorfish	Н
Acanthurus coeruleus	Blue tang	Н
Acanthurus tractus	Ocean surgeonfish	Н
Apogon aurolineatus	Bridle cardinalfish	Z
Apogon binotatus	Barred cardinalfish	Z
Apogon lachneri	Whitestar cardinalfish	Z
Apogon quadrisquamatus	Sawcheek cardinalfish	Z
Astrapogon puncticulatus	Blackfin cardinalfish	Ι
Balistes vetula	Queen triggerfish	Ι
Bodianus pulchellus	Spotfin hogfish	Ι
Bodianus rufus	Spanish hogfish	Ι
Canthidermis sufflamen	Ocean triggerfish	Ι
Caranx latus	Horse-eye jack	P-S
Caranx lugubris	Black jack	P-L
Centropomus undecimalis	Common snook	P-S
Centropyge aurantonotus	Flameback angelfish	Н
Cephalopholis cruentata	Graysby	P-S
Cephalopholis fulva	Coney	P-S
Chaetodon capistratus	Foureye butterflyfish	Ι
Chaetodon ocellatus	Spotfin butterflyfish	Ι
Chaetodon striatus	Banded butterflyfish	Ι
Chilomycterus antennatus	Bridled burrfish	Ι
Chromis insolata	Sunshine fish	Z

Species Name	Common Name	Trophic Guild
Coryphopterus dicrus *	Colon goby	Ι
Coryphopterus eidolon *	Pallid goby	Ι
Coryphopterus lipernes	Peppermint goby	Ι
Cosmocampus elucens	Shortfin pipefish	Ι
Diodon holocanthus	Balloonfish	Ι
Echidna catenata	Chain moray	Ι
Elacatinus chancei	Shortstripe goby	Ι
Elacatinus louisae	Spotlight goby	Ι
Emmelichthyops atlanticus	Bonnetmouth	P-S
Epinephelus adscensionis	Rock hind	Ι
Epinephelus guttatus	Red hind	P-S
Equetus lanceolatus	Jackknife fish	Ι
Equetus punctatus	Spotted drum	Ι
Gymnothorax miliaris	Goldentail moray	P-S
Gymnothorax vicinus	Purplemouth moray	P-S
Haemulon album	Margate (white)	Ι
Haemulon carbonarium	Caesar grunt	Ι
Haemulon flavolineatum	French grunt	Ι
Haemulon macrostomum	Spanish grunt	Ι
Haemulon parra	Sailors choice	Ι
Halichoeres garnoti	Yellowhead wrasse	Ι
Halichoeres maculipinna	Clown wrasse	Ι
Halichoeres pictus	Rainbow wrasse	Ι
Hippocampus reidi	Longsnout seahorse	Ι
Holocentrus adscensionis	Squirrelfish	Ι
Holocentrus rufus	Longspine squirrelfish	Ι
Hypoplectrus aberrans	Yellowbelly hamlet	Ι
Hypoplectrus chlorurus	Yellowtail hamlet	Ι
Hypoplectrus guttavarius	Shy hamlet	Ι
Hypoplectrus indigo	Indigo hamlet	Ι
Hypoplectrus nigricans	Black hamlet	P-S
Hypoplectrus puella	Barred hamlet	Ι
Hypoplectrus randallorum	Tan hamlet	Ι
Hypoplectrus unicolor	Butter hamlet	P-S
Kyphosus sectator	Chub (Bermuda/yellow)	Н
Labrisomus nuchipinnis	Hairy blenny	I
Liopropoma rubre	Peppermint basslet	I
Lutjanus buccanella	Blackfin snapper	P-S
Lutjanus mahogoni	Mahogany snapper	P-S

Species Name	Common Name	Trophic Guild
Lutjanus synagris	Lane snapper	P-S
Malacanthus plumieri	Sand tilefish	Ι
Malacoctenus aurolineatus *	Goldline blenny	Ι
Malacoctenus macropus *	Rosy blenny	Ι
Malacoctenus versicolor	Barfin blenny	Ι
Megalops atlanticus	Tarpon	P-L
Microspathodon chrysurus	Yellowtail damselfish	Н
Monacanthus ciliatus	Fringed filefish	Н
Monacanthus tuckeri	Slender filefish	Z
Mulloidichthys martinicus	Yellow goatfish	Ι
Myrichthys breviceps	Sharptail eel	Ι
Myrichthys ocellatus	Gold-spotted eel	Ι
Myripristis jacobus	Blackbar soldierfish	Ι
Neonifon marianus	Longjaw squirrelfish	Ι
Odontoscion dentex	Reef croaker	Z
Ophichthus ophis	Spotted snake eel	P-S
Opistognathus aurifrons	Yellowhead jawfish	Z
Opistognathus macrognathus	Banded jawfish	I
Opistognathus whitehursti	Dusky jawfish	I
Parablennius marmoreus *	Seaweed blenny	Z
Pempheris schomburgkii	Glassy sweeper	Ι
Pomacanthus arcuatus	Gray angelfish	Ι
Pomacanthus paru	French angelfish	Ι
Pseudupeneus maculatus	Spotted goatfish	Ι
Rypticus saponaceus	Greater soapfish	
Sargocentron bullisi	Deepwater squirrelfish	Ι
Sargocentron coruscum	Reef squirrelfish	Ι
Scarus iseri	Striped parrotfish	Н
Scarus taeniopterus	Princess parrotfish	Н
Scarus vetula	Queen parrotfish	Н
Scomberomorus cavalla	King mackeral	
Scomberomorus maculatus	Spanish mackeral	
Scorpaena plumieri	Spotted scorpionfish	Ι
Selar crumenophthalmus	Bigeye scad	P-S
Serranus tabacarius	Tobaccofish	P-S
Sparisoma atomarium	Greenblotch parrotfish	Н
Sparisoma chrysopterum	Redtail parrotfish	Н
Sparisoma rubripinne	Yellowtail parrotfish	Н
Sparisoma viride	Stoplight parrotfish	Н

Species Name	Common Name	Trophic Guild
Sphoeroides spengleri	Bandtail puffer	Ι
Sphyraena barracuda	Great barracuda	P-L
Sphyraena picudilla	Southern sennet	P-S
Stegastes partitus	Bicolor damselfish	Н

* Species not assigned to BCG attribute level in Florida.

Table Appendix A4.

BCG Attribute IV species are intermediately tolerant taxa to fishing pressures and sediment threats in the US Caribbean and Florida.

Species Name	Common Name	Trophic Guild
Abudefduf saxatilis	Sergeant major	Ι
Alphestes afer	Mutton hamlet	Ι
Anisotremus virginicus	Porkfish	Ι
Apogon maculatus	Flame fish	Z
Apogon pseudomaculatus	Two-spot cardinalfish	Z
Apogon townsendi	Belted cardinalfish	Z
Archosargus rhomboidalis	Sea bream	Н
Bothus lunatus	Peacock flounder	P-S
Bothus ocellatus	Eyed flounder	P-S
Calamus bajonado	Jolthead porgy	Ι
Calamus calamus	Saucereye porgy	Ι
Calamus nodosus	Knobbed porgy	Ι
Calamus penna	Sheepshead porgy	Ι
Calamus pennatula	Pluma	Ι
Calamus proridens	Littlehead porgy	
Calamus UNK	Porgy	Ι
Canthigaster rostrata	Sharpnose puffer	Ι
Carangoides bartholomaei	Yellow Jack	P-L
Carangoides ruber	Bar jack	P-S
Chloroscombrus chrysurus	Atlantic bumper	Z
Conger triporiceps	Many tooth conger	P-S
Coryphopterus glaucofraenum *	Bridled goby	Ι
Coryphopterus personatus/hyalinus *	Masked/Glass goby	Ι
Cryptotomus roseus	Blue-lip parrotfish	Н
Ctenogobius saepepallens *	Dash goby	Ι
Diodon hystrix	Porcupine fish	Ι
Eucinostomus argenteus	Spotfin mojarra/Silver mojarra	
Eucinostomus jonesii	Slender mojarra	Ι
Eucinostomus melanopterus	Flagfin mojarra	Ι

Species Name	Common Name	Trophic Guild
Gnatholepis thompsoni *	Gold-spot goby	Н
Gymnothorax funebris	Green moray	P-S
Gymnothorax moringa	Spotted moray	P-S
Haemulon aurolineatum	Tomtate	Ι
Haemulon plumierii	White grunt	Ι
Haemulon sciurus	Blue-striped grunt	Ι
Halichoeres bivittatus	Slippery dick	Ι
Inermia vittata	Boga	Z
Lutjanus apodus	Schoolmaster	P-S
Lutjanus griseus	Gray snapper	P-S
Ocyurus chrysurus	Yellowtail snapper	Z
Ophioblennius macclurei *	Redlip blenny	Н
Paradiplogrammus bairdi	Lancer dragonet	Ι
Sargocentron vexillarium	Dusky squirrelfish	Ι
Serranus baldwini	Lantern bass	Ι
Serranus flaviventris	Twinspot bass	P-S
Serranus tortugarum	Chalk bass	Z
Sparisoma aurofrenatum	Redband parrotfish	Н
Sparisoma radians	Bucktooth parrotfish	Н
Stegastes adustus	Dusky damselfish	Н
Stegastes diencaeus	Longfin damselfish	Н
Stegastes leucostictus	Beaugregory	Н
Stegastes planifrons	Threespot damselfish	Ι
Stegastes variabilis	Cocoa damselfish	Н
Xyrichtys splendens	Green razorfish	Ζ

* Species not assigned to BCG attribute level in Florida.

Table Appendix A5.

BCG Attribute Level V species are tolerant taxa to fishing pressures and sediment threats and Level VI species are non-native or intentionally introduced species in the US Caribbean and Florida.

BCG Attribute No.	Species Name	Common Name	Trophic Guild
V	Diplodus argenteus	Silver porgy	Н
V	Gerres cinereus	Yellowfin mojarra	Ι
V	Mugil cephalus	Striped mullet	Z
V	Sphoeroides testudineus	Checkered puffer	Ι
V	Synodus foetens	Inshore lizardfish	P-S
VI	Callogobius clitellus	Saddled goby	Ι
VI	Pterois volitans	Red lionfish	Р

Table Appendix A6.

Fish species not assigned to an attribute as the survey methods used were insufficient to detect these species (often cryptic) in the US Caribbean and Florida.

Species Name	Common Name	Trophic Guild
Ablennes hians	Flat needlefish	P-S
Acanthemblemaria UNK	Tube Blenny	Ι
Acanthocybium solandri	Wahoo	
Acanthurus UNK	Surgeonfish	Н
Acentronura dendritica	Pipehorse	Ι
Albula vulpes	Bonefish	Ι
Alectis ciliaris	African pompano	P-S
Apogon UNK	Cardinalfish	Z
Archosargus probatocephalus	Sheepshead	Ι
Atherinomorus stipes	Hardhead silverside	Z
Balistes capriscus	Gray triggerfish	Ι
Bathygobious soporator	Frillfin goby	Ι
Belonidae UNK	Needlefish	P-S
Bollmannia boqueronensis	White-eye goby	Ι
Bothus UNK	Flounder	P-S
Canthigaster jamestyleri	Goldface toby	Ι
Canthigaster UNK	Puffer	Ι
Carcharhinus leucas	Bull shark	
Caranx UNK	Jack	P-S
Centropristis striata	Black sea bass	P-S
Centropyge argi	Cherubfish	Н
Chaenopsis ocellata	Bluethroat pikeblenny	Ι
Chaenopsis UNK	Pike blenny	Ι
Chaetodon sedentarius	Reef butterflyfish	Ι
Chromis enchrysura	Yellowtail reeffish	Ι
Chromis scotti	Purple reeffish	Z
Clupeidae UNK	Herrings	Z
Coryphopterus UNK	Goby	Ι
Coryphopterus punctipectophorus	Spotted goby	
Ctenogobius stigmaticus	Marked goby	Ι
Decapterus macarellus	Mackerel scad	Z
Decapterus punctatus	Round scad	
Decapterus UNK	Scad	Z
Dermatolepis inermis	Marbled grouper	P-S
Diplectrum bivittatum	Dwarf sand perch	Ι
Diplectrum formosum	Sand perch	P-S

Species Name	Common Name	Trophic Guild		
Diplodus holbrooki	Spottail pinfish	Н		
Doratonotus megalepis	Dwarf wrasse	Ι		
Echeneis naucrates	Sharksucker	Z		
Echeneis neucratoides	Whitefin sharksucker	Z		
Elacatinus dilepis	Orangesided goby	I		
Elacatinus evelynae	Sharknose goby	I		
Elacatinus horsti	Yellowline goby			
Elacatinus macrodon	Tiger goby			
Elacatinus UNK	Goby	I		
Elacatinus xanthiprora	Yellowprow goby			
Elagatis bipinnulata	Rainbow runner	P-S		
Emblemaria pandionis	Sailfin blenny	Z		
Emblemaria sp	Tube blenny	Z		
Emblemariopsis UNK	Blenny	I		
Engraulidae UNK	Anchovies	Z		
Enneanectes UNK	Triplefin	Н		
Eucinostomus gula	Silver jenny	I		
Eucinostomus UNK	Mojarra	I		
Euthynnus alletteratus	Little tuny	P-S		
Gobiidae UNK	Goby	I		
Gobiosoma grosvenori	Rockcut goby	I		
Gymnothorax UNK	Moray eel	P-S		
Haemulon melanurum	Cottonwick	I		
Haemulon UNK	Grunt	I		
Haemulon striatum	Striped grunt	Z		
Halichoeres burekae	Mardi gras wrasse	I		
Halichoeres caudalis	Painted wrasse	I		
Halichoeres cyanocephalus	Yellowcheek wrasse	I		
Halichoeres poeyi	Blackear wrasse	I		
Halichoeres UNK	Wrasse	I		
Harengula jaguana	Scaled sardine			
Hemiemblemaria simulas	Wrasse blenny			
Hemiramphus brasiliensis	Ballyhoo			
Heteroconger halis	Brown garden eel	Z		
Heteroconger longissimus	Brown garden eel	Z		
Hippocampus UNK	Pipefish	I		
Holacanthus bermudensis	Blue angelfish	I		
Holocanthus Townsendi	Townsend angelfish			
Holacanthus UNK	Angelfish	I		

Species Name	Common Name	Trophic Guild
Hypleurochilus bermudensis	Barred blenny	Ι
Hypoplectrus UNK	Hamlet	Ι
Jenkinsia UNK	Herring	Z
Labrisomus filamentosus	Quillfin blenny	Ι
Lagodon rhomboides	Pinfish	Ι
Lonchopisthus micrognathus	Swordtail jawfish	Z
Lophogobius cyprinoides	Crested goby	Ι
Lutjanus campechanus	Red snapper	P-S
Lutjanus UNK	Snapper	P-S
Malacoctenus boehlkei	Diamond blenny	Ι
Malacoctenus gilli	Dusky blenny	Ι
Malacoctenus triangulatus	Saddled blenny	I
Malacoctenus UNK	Scaly blenny	Ι
Manta birostris	Giant manta	Z
Microgobius carri	Seminole goby	Z
Microgobius signatus	Microgobius signatus	Z
Microgobius UNK	Goby UNK	Н
Mullidae UNK	Goatfishes	I
Muraenidae UNK	Moray eel	P-S
Mycteroperca microlepis	Gag	P-S
Mycteroperca phenax	Scamp	P-S
Mycteroperca UNK	Grouper UNK	P-S
Myrichthys UNK	Snake eel	Ι
Nes longus	Orange-spotted goby	Ι
Nicholsina usta	Emerald parrotfish	Н
Ogcocephalus nasutus	Shortnose batfish	Ι
Ophichthidae UNK	Snake eel UNK	P-S
Opistognathus UNK	Jawfish	Z
Oxyurichthys stigmalophius	Spotfin goby	I
Pareques umbrosus	Cubbyu	I
Platybelone argalus	Keeltail needlefish	P-S
Pomacanthus UNK	Angelfish	I
Ptereleotris calliura	Blue dartfish	
Ptereleotris helenae	Hovering dartfish	Z
Remora remora	Common remora	Z
Rypticus bistrispinus	Freckled soapfish	P-S
Rypticus maculatus	White-spotted soapfish	P-S
Scartella cristata	Molly miller	Н
Scarus UNK	Parrotfish	Н

Species Name	Common Name	Trophic Guild
Scorpaena UNK	Scorpionfish UNK	Ι
Scorpaenodes caribbaeus	Reef scorpionfish	
Serraniculus pumilio	Pygmy sea bass	Ι
Serranus subligarius	Belted sandfish	Ι
Serranus UNK	Seabass UNK	P-S
Sparisoma UNK	Parrotfish	Н
Sphyraena borealis	Northern sennet	P-S
Stephanolepis hispidus	Planehead filefish	Н
Stephanolepsis setifer	Pygmy filefish	Н
Stromateidae UNK	Butterfish	P-S
Syacium UNK	Sand flounder	Ι
Sygnathus dawsoni	Pipefish	Ι
Synodus intermedius	Sand diver	P-S
Synodus saurus	Blue-striped lizardfish	P-S
Tigrigobius dilepis	Orange-sided goby	Ι
Trachinocephalus myops	Snakefish	Ζ
Triglidae UNK	Searobin Family	Ι
Tylosurus crocodilus	Houndfish	P-S
Urobatis jamaicensis	Yellow stingray	
Xyrichtys martinicensis	Rosy razorfish	Ι
Xyrichtys novacula	Pearly razorfish	Ι
Xyrichtys UNK	Razorfish	Ι

Table Appendix A7.

Large-bodied species for reef fish using 90 cm length threshold to distinguish between large and small body sizes.

Fish Species	Common Name	Piscivore
Aetobatus narinari	Spotted eagle ray	
Carangoides bartholomaei	Yellow jack	Х
Caranx hippos	Crevalle jack	Х
Caranx lugubris	Black jack	Х
Carcharhinus limbatus	Blacktip shark	Х
Carcharhinus perezii	Caribbean Reef shark	Х
Dasyatis americana	Southern stingray	
Epinephelus striatus	Nassau grouper	Х
Epinephelus itajara	Atlantic goliath grouper	Х
Epinephelus morio	Red grouper	Х
Galeocerdo cuvier	Tiger shark	Х

Fish Species	Common Name	Piscivore
Ginglymostoma cirratum	Nurse shark	Х
Lachnolaimus maximus	Hogfish	
Lutjanus analis	Mutton snapper	
Lutjanus cyanopterus	Cubera snapper	Х
Lutjanus jocu	Dog snapper	Х
Megalops atlanticus	Tarpon	Х
Mycteroperca bonaci	Black grouper	Х
Mycteroperca tigris	Tiger grouper	Х
Mycteroperca veenosa	Yellowfin grouper	Х
Negaprion brevirostris	Lemon shark	Х
Scarus coelestinus	Midnight parrotfish	
Scarus coeruleus	Blue parrotfish	
Scarus guacamaia	Rainbow parrotfish	
Seriola dumerili	Greater amberjack	Х
Seriola rivoliana	Almaco jack	Х
Sphyraena barracuda	Great barracuda	Х
Sphyrna mokarran	Great hammerhead shark	Х

Appendix B.: Large-bodied reef fish species. Note: 90 cm maximum size cut-off used as threshold between large and small; small predators are still an indicator of good condition and are reflected as a rule in BCG Level 3

Fish species	Common name	Piscivore
Aetobatus narinari	Spotted eagle ray	
Carangoides bartholomaei	Yellow jack	Х
Caranx hippos	Crevalle jack	Х
Caranx lugubris	Black jack	Х
Carcharhinus limbatus	Blacktip shark	Х
Carcharhinus perezii	Caribbean reef shark	Х
Dasyatis americana	Southern stingray	
Epinephelus striatus	Nassau grouper	Х
Epinephelus itajara	Atlantic goliath grouper	Х
Epinephelus morio	Red grouper	Х
Galeocerdo cuvier	Tiger shark	Х
Ginglymostoma cirratum	Nurse shark	X
Lachnolaimus maximus	Hogfish	
Lutjanus analis	Mutton snapper	
Lutjanus cyanopterus	Cubera snapper	X

Page	32
------	----

Fish species	Common name	Piscivore
Lutjanus jocu	Dog snapper	Х
Megalops atlanticus	Tarpon	Х
Mycteroperca bonaci	Black grouper	Х
Mycteroperca tigris	Tiger grouper	Х
Mycteroperca venenosa	Yellowfin grouper	Х
Negaprion brevirostris	Lemon shark	Х
Scarus coelestinus	Midnight parrotfish	
Scarus coeruleus	Blue parrotfish	
Scarus guacamaia	Rainbow parrotfish	
Seriola dumerili	Greater amberjack	Х
Seriola rivoliana	Almaco jack	Х
Sphyraena barracuda	Great barracuda	Х
Sphyrna mokarran	Great hammerhead shark	Х

Appendix C.: Cluster and Ordination Analyses relating Fish Densities to Environmental Gradients

Cluster and Ordination Analyses relating Fish Densities to Environmental Gradients (In SI)

References

- 33 USC §1251 et seq, 1972. Federal Water Pollution Control Amendments of 1972 (aka The Clean Water Act).
- Aguilar-Perera JA, 2004. Coastal Habitat Connectivity of Reef Fishes From Southwestern Puerto Rico (PhD Thesis). University of Puerto Rico, Mayagüez, Puerto Rico.
- Aguilar-Perera A, Appeldoorn RS, 2007. Variation in juvenile fish density along the mangroveseagrass-coral reef continuum in SW Puerto Rico. Mar. Ecol. Prog. Ser 348, 139–148.
- Aguilar-Perera A, Appeldoorn RS, 2008. Spatial distribution of marine fishes along a cross-shelf gradient containing a continuum of mangrove-seagrass-coral reefs off southwestern Puerto Rico. Estuar. Coast. Shelf Sci 76, 378–394.
- Ames C, 2017. Reef Fish Assemblage Biogeography Along the Florida Reef Tract (Master's thesis). Nova Southeastern University Retrieved from NSUWorks. https://nsuworks.nova.edu/cgi/viewcontent.cgi?article=1459&context=occ_stuetd.
- Appeldoorn RS, 2011. Can we stop the madness? Managing for resilience in coral reef fisheries. Proc. Gulf Caribb. Fish. Inst 63, 6–9.
- Appeldoorn RS, Recksiek CW, Hill RL, Pagan FE, Dennis GD, 1997. Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. In: Proceedings of the Eighth International Coral Reef Symposium. 2. pp. 1917–1922.
- Appeldoorn RS, Friedlander A, Sladek Nowlis J, Ussegilo P, Mitchell-Chui A, 2003. Habitat connectivity on the insular platform of Old Providence-Santa Catalina, Colombia: mechanisms, limits and ecological consequences relevant to marine reserve design. Gulf Caribb. Res 14, 61–77.
- Ault JS, Bohnsack JA, Meester GA, 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fish. Bull 96 (3), 395–414.
- Ault JS, Luo J, Smith SG, Serafy JE, Wang JD, Diaz GA, Humston R, 1999. A spatial dynamic multistock production model. Can. J. Fish. Aquat. Sci 56 (S1), 4–25.

- Ault JS, Smith SG, Bohnsack JA, 2005. Evaluation of average length as an estimator of exploitation status for the Florida coral reef fish community. J. Mar. Sci 62, 417–423.
- Ault JS, Smith SG, Luo J, Monaco ME, Appeldoorn RS, 2008. Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. Environ. Conserv 35, 221–231.
- Ault JS, Smith SG, Bohnsack JA, Luo J, Zurcher N, McClellan DB, Zeigler TA, Hallac DE, Patterson M, Feeley MW, Ruttenberg BI, Hunt J, Kimball D, Causey B, 2013. Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. Fish. Res 144, 28–37.
- Ault JS, Smith SG, Browder JA, Nuttle W, Franklin EC, Luo J, DiNardo GT, Bohnsack JA, 2014. Indicators for assessing the ecological and sustainability dynamics of southern Florida's coral reef and coastal fisheries. Ecol. Indic 44, 164–172.
- Bejarno I, Appeldoorn RS, 2013. Seawater turbidity and fish communities on coral reefs of Puerto Rico. Mar. Ecol. Prog. Ser 474, 217–226.
- Beverton RJH, Holt SJ, 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations Series II XIX Ministry of Agriculture, Fisheries and Food, Lowestoft (533 p).
- Bohnsack JA, Bannerot SP, 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. In: NOAA Technical Report NMFS. 41.
- Bradley P, Davis W, Fisher W, Bell H, Chan V, LoBue C, Wiltse W, 2008. Biological criteria for protection of U.S. coral reefs. In: Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7–11 July 2008.
- Bradley P, Fisher WS, Bell H, Davis WS, Chan V, LoBue C, Wiltse W, 2009. Development and implementation of coral reef biocriteria in U. S. jurisdictions. Environ. Monit. Assess 150, 43–51. [PubMed: 19052888]
- Bradley P, Fore L, Fisher W, Davis W, 2010. Coral Reef Biological Criteria: Using the Clean Water Act to Protect a National Treasure. U.S. EPA, ORD, AED, Narragansett, RI (EPA/600/R-10/054).
- Bradley P, Santavy DL, Gerritsen J, 2014. Workshop on Biological Integrity of Coral Reefs, August 21–22, 2012, Caribbean Coral Reef Institute, Isla Magueyes, La Parguera, Puerto Rico. U.S. EPA, ORD, AED, Narragansett, RI (EPA/600/R-13/350).
- Bradley P, Jessup B, Gerritsen J, Gallindo A, 2016. The Coral Reef Biological Condition Gradient: Moving Toward Quantitative Criteria From Species-Based Attributes. TetraTech, Inc (Prepared for the U.S. Environmental Protection Agency, Office of Water, Office of Science and Technology, Washington, D.C).
- Brander L, van Beukering P, 2013. The Total Economic Value of U.S. Coral Reefs: A Review of the Literature. National Oceanic and Atmospheric Administration's Coral Reef Conservation Program. NOAA, Silver Spring, Maryland.
- Brandt ME, Zurcher N, Acosta A, Ault JS, Bohnsack JA, Feeley MW, Harper DE, Hunt JH, Kellison GT, McClellan DB, Patterson ME, Smith SG, 2009. A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem. In: Natural Resource Report NPS/SFCN/NRR 2009/150. National Park Service, Fort Collins, Colorado.
- Brown CJ, Jupiter SD, Lin HY, Albert S, Klein C, Maina JM, Tulloch VJ, Wenger AS, Mumby PJ, 2017. Habitat change mediates the response of coral reef fish populations to terrestrial run-off. Mar. Ecol. Prog. Ser 576, 55–68.
- Bryan DR, Smith SG, Ault JS, Feeley MW, Menza CW, 2016. Feasibility of a regionwide probability survey for coral reef fish in Puerto Rico and the U.S. Virgin Islands. Mar. Coast. Fish 8 (1), 135–146.
- Burkepile DE, Hay ME, 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci 105, 16201–16206. [PubMed: 18845686]
- Cairns J, 1977. Quantification of Biological Integrity. In: Ballentine RK, Guarrain LJ (Eds.), The Integrity of Water. U.S. Environmental Protection Agency, Office of Water, Washington, DC, USA, pp. 171–187.
- Caldow C, Clark R, Edwards K, Hile S, Menza C, Hickerson E, Schmahl GP, 2009. Biogeographic Characterization of Fish Communities and Associated Benthic Habitats Within the Flower Garden Banks National Marine Sanctuary: Sampling Design and Implementation of Scuba Surveys on

the Coral Caps. NOAA/National Centers for Coastal Ocean Science, Silver Spring, MD (NOAA Technical Memorandum NOS NCCOS 81).

- Carpenter KE, Miclat RI, Albaladejo VD, Corpuz VT, 1981. The influence of substrate structure on the abundance and diversity of Philippine reef fishes. In: Proceedings of the Fourth International Coral Reef Symposium. 2. pp. 497–502.
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E, 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321, 560–563. [PubMed: 18653892]
- Castella E, Speight MCD, 1996. Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. Ecol. Model 85, 13–25.
- Cerveny K, 2006. Distribution Patterns of Reef Fishes in Southwest Puerto Rico, Relative to Structural Habitat, Cross—Shelf Location, and Ontogenetic Stage (Master's Thesis). University of Puerto Rico— Mayagüez.
- Chapman CJ, Johnstone ADF, Dunn JR, Creasey DJ, 1974. Reactions of fish to sound generated by divers' open-circuit underwater breathing apparatus. Mar. Biol 27, 357–366.
- Christensen JD, Jeffrey CFG, Caldow C, Monaco ME, Kendall MS, Appeldoorn RS, 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf Caribb. Res 14, 9–27.
- Clarke KR, Gorley RN, 2015. PRIMER Version 7: User Manual/Tutorial. PRIMER-E, Plymouth, UK.
- Clarke KR, Gorley RN, Somerfield PJ, Warwick RM, 2014. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 3rd edition. PRIMER-E, Plymouth, UK.
- Claro R, 1991. Changes in fish assemblage structure by the effect of intense fisheries activity. Trop. Ecol 32, 36–46.
- Claro R, Lindeman KC, 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. Gulf Caribb. Res 14, 91–106.
- Cleary DFR, Suharsono, Hoeksema BW, 2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. Biodivers. Conserv 15, 3653–3674.
- Cocheret de la Morinière E, Pollus BJA, Nagelkerken I, van der Velde G, 2002. Postsettlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuar. Coast. Shelf Sci 55, 309–321.
- Coleman FC, Koenig CC, Huntsman GR, Musick JA, Eklund AM, McGovern JC, Chapman RW, Sedberry GR, Grimes CB, 2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25, 14–21.
- Colin PL, Shapiro DY, Weiler D, 1987. Preliminary investigations of reproduction of two species of groupers. Epinephelus guttatus and E. striatus in the West Indies. Bull. Mar. Sci 40, 220–230.
- Courtney LA, Fisher WS, Raimondo S, Oliver LM, Davis WS, 2007. Estimating three-dimensional colony surface area of field corals. J. Exp. Mar. Biol. Ecol 351, 234–242.
- Dahlgren CP, Eggleston DB, 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81 (8), 2227–2240 2000.
- Davies SP, Jackson SK, 2006. The biological condition gradient: a descriptive model for interpreting change in aquatic ecosystems. Ecol. Appl 16, 1251–1266. [PubMed: 16937795]
- Davis WS, Simon T. (Eds.), 2004. Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. CRC Press LLC, Boca Raton, Florida, USA (432 pp).
- Dustan P, Doherty O, Pardede S, 2013. Digital reef rugosity estimates coral reef habitat complexity. PLoS One 8 (2), e57386. [PubMed: 23437380]
- Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Risk MJ, 1998. Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. Mar. Pollut. Bull 36, 617–630.

- Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HPA, 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. PeerJ 6, e4886. 10.7717/peerj.4886. [PubMed: 29844998]
- Ennis RS, Brandt ME, Wilson KR, Smith TB, 2016. Coral reef health response to chronic and acute changes in water quality in St. Thomas, United States Virgin Islands. Mar. Pollut. Bull 111, 418– 427. [PubMed: 27499526]
- Fabricius K, De'ath G, 2001. Environmental factors associated with the spatial distribution of crustose coralline algae in the Great Barrier Reef. Coral Reefs 19, 303–309.
- Fabricius K, De'ath G, McCook L, Turak E, Williams DM, 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar. Pollut. Bull 51, 384–398. [PubMed: 15757737]
- Fisco D, 2016. Reef Fish Spatial Distribution and Benthic Habitat Associations on the Southeast Florida Reef Tract (Master's thesis). Nova Southeastern University.
- Fisher WS, 2007. Stony Coral Rapid Bioassessment Protocol. US Environmental Protection Agency. EPA/600/R-06/167, July 2007. Office of Research and Development, Washington, DC.
- Fisher WS, Davis WP, Quarles RL, Patrick J, Campbell JG, Harris PS, Hemmer BL, Parsons M, 2007. Characterizing coral condition using estimates of three-dimensional colony surface area. Environ. Monit. Assess 125, 347–360. [PubMed: 17225074]
- Fisher WS, Fore LS, Hutchins A, Quarles RL, Campbell JG, LoBue C, Davis W, 2008. Evaluation of stony coral indicators for coral reef management. Mar. Pollut. Bull 56, 1737–1745. [PubMed: 18715598]
- Fisher WS, Fore LS, Oliver LM, LoBue C, Quarles RL, Campbell JG, Harris PS, Hemmer BL, Vickery S, Parsons M, Hutchins A, Bernier K, Rodriguez D, Bradley P, 2014. Regional status assessment of stony corals in the U.S. Virgin Islands. Environ. Monit. Assess 186, 7165–7181. [PubMed: 25052328]
- Fisher WS, Vivian DN, Campbell J, LoBue C, Hemmer RL, Wilkinson S, Harris P, Santavy DL, Parsons M, Bradley P, Humphrey A, Oliver LM, Harwell L, 2019. Biological assessment of coral reefs in southern Puerto Rico: supporting coral reef protection under the U.S. Clean Water Act. Coast. Manag 47, 429–452.
- Frey DG, 1977. Biological integrity of water: an historical approach. In: The Integrity of Water. Proceedings of a Symposium. US Environmental Protection Agency, Washington, DC, pp. 127– 140.
- Friedlander AM, Parrish JD, 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol 224, 1–30.
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS, 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22, 291–305.
- Gerritsen J, Bouchard RW Jr., Zheng L, Leppo EW, Yoder CO, 2017. Calibration of the Biological Condition Gradient in Minnesota streams: a quantitative expert-based decision system. Freshw. Sci 36, 427–451.
- Goodwin NB, Grant A, Perry AL, Dulvy NK, Reynolds JD, 2006. Life history correlates of densitydependent recruitment in marine fishes. Can. J. Fish. Aquat. Sci 63, 494–509.
- Goreau TF, 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40, 67–90.
- Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Cinner JE, Huchery C, Holmes TH, 2017. Human disruption of coral reef trophic structure. Curr. Biol 27, 231–236. [PubMed: 28089513]
- Gratwicke B, Speight MR, 2005a. Effects of habitat complexity on Caribbean marine fish assemblages. Mar. Ecol. Prog. Ser 292, 301–310.
- Gratwicke B, Speight MR, 2005b. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol 66, 650–667.
- Green AL, 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (family Labridae). Mar. Ecol. Prog. Ser 133, 1–11.

- Greenstein BJ, Curran A, Pandolfi JM, 1998. Shifting ecological baselines and the demise of Acropora cervicornis in the western North Atlantic and Caribbean province: a Pleistocene perspective. Coral Reefs 17, 249–261.
- Grober-Dunsmore R, Frazer T, Lindberg W, Beets J, 2007. Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. Coral Reefs 26, 201–216.
- Hausmann S, Charles DF, Gerritsen J, Belton TJ, 2016. A diatom-based Biological Condition Gradient (BCG) approach for assessing impairment and developing nutrient criteria for streams. Sci. Total Environ 562, 914–927. [PubMed: 27128024]
- Hawkins JP, Roberts CM, 2004. Effects of artisanal fishing on Caribbean coral reefs. Conserv. Biol 18, 215–226.
- Healthy Reefs for Healthy People Initiative (HRI), 2012. Report Card for the Mesoamerican Reef 2012. 25 p. URL. http://www.healthyreefs.org/cms/reportcards.
- Heyman WD, Kjerfve B, 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. Bull. Mar. Sci 83, 531–551.
- Hill J, Wilkinson C, 2004. Methods for Ecological Monitoring of Coral Reefs. Australian Institute of Marine Science, Townsville.
- Hobson RD, 1972. Surface roughness in topography: quantitative approach. In: Chorley RJ (Ed.), Spatial Analysis in Geomorphology. Methuen and Co., Ltd, London, pp. 221–245.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME ME, 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742. [PubMed: 18079392]
- Hoegh-Guldberg O, Ortiz JC, Dove S, 2011. The future of coral reefs. Science 334, 1494-1495.
- Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S, 2017. Coral reef ecosystems under climate change and ocean acidification. Front. Mar. Sci 4. 10.3389/fmars.2017.00158.
- Holling CS, 1973. Resilience and stability in ecological systems. Annu. Rev. Ecol. Syst 4, 1–23.
- Hughes TP, 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551. [PubMed: 17801530]
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgraden J, 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301 (5635), 929–933. [PubMed: 12920289]
- Ibelings BW, Vonk M, Los HFJ, Van Der Molen DT, Mooij WM, 2003. Fuzzy modeling of cyanobacterial surface waterblooms: validation with NOAA-AVHRR satellite images. Ecol. Appl 13, 1456–1472.
- Ionnidou IA, Paraskevopoulos S, Tzionas P, 2003. An interactive computer graphics interface for the introduction of fuzzy inference in environmental education. Interact. Comput 18 (4), 683–708.
- Jackson JBC, 1997. Reefs since Columbus. Coral Reefs 16, S23–S32.
- Jackson JBC, Sala E, 2001. Unnatural oceans. Sci. Mar 65, 273–281.
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR, 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637. [PubMed: 11474098]
- Jackson JBC, Donovan MK, Cramer KL, Lam VV (Eds.), 2014. Status and Trends of Caribbean Coral Reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Jameson SC, Erdmann MV, Karr JR, Gibson GR Jr., Potts KW, 2001. Charting a course toward diagnostic monitoring: a continuing review of coral reef attributes and a research strategy for creating coral reef indexes of biotic integrity. Bull. Mar. Sci 69, 701–744.
- Jameson SC, Karr JR, Potts KW, 2003. Establishing Reference Conditions for the Diagnostic Monitoring and Assessment of Coral Reefs. U.S.EPA, Office of Water, Washington, DC (44 p).
- Januchowski-Hartley FA, Graham NAJ, Feary DA, Morove T, Cinner JE, 2011. Fear of fishers: human predation explains behavioural changes in coral reef fishes. PLoS One 6 (8), e22761. [PubMed: 21853046]

- Jennings S, Reynolds JD, Mills SC, 1998. Life history correlates of responses to fisheries exploitation. Proc. R. Soc. Biol. Sci 265, 333–339.
- Johannes RE, 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish 3, 65–84.
- Jokiel PL, Brown EK, Friedlander A, Rodgers SK, Smith WR, 2004. Hawai'i coral reef assessment and monitoring program: spatial patterns and temporal dynamics in reef coral communities. Pac. Sci 58, 159–174.
- Kadison E, Brandt M, Nemeth R, Martens J, Blondeau J, Smith T, 2017. Abundance of commercially important reef fish indicates different levels of overexploitation across shelves of the U.S. Virgin Islands. PLoS One 12, e0180063. [PubMed: 28704387]
- Karr JR, Chu EW, 2000. Sustaining living rivers. Hydrobiologia 422, 1-14.
- Kendall MS, Kruer CR, Buja KR, Christensen JD, Finkbeiner M, Warner RA, Monaco ME, 2001. Methods Used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands. NOAA Technical Memorandum 152. NOS NCCOS CCMA Silver Spring, MD.
- Kimmel JJ, 1985. A Characterization of Puerto Rican Fish Assemblages (Doctoral Dissertation). University of Puerto Rico—Mayagüez.
- Klir GJ., 2004. Fuzzy Logic: A Specialized Tutorial. In: Demicco Robert V., Klir George J. (Eds.), Fuzzy Logic in Geology. Elsevier Academic Press, pp. 352.
- Knowlton N, Jackson JB, 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. 6, e54. 10.1371/journal.pbio.0060054. [PubMed: 18303956]
- Kuffner IB, Brock JC, Grober-Dunsmore R, Bonito VE, Hickey TD, Wright CW, 2007. Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. Environ. Biol. Fish 78, 71–82.
- Kulbicki M, 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J. Exp. Mar. Biol. Ecol 222, 11–30.
- Kulbicki M, Sarramégna S, 1999. Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae. Aquat. Living Resour 12, 315–325.
- Lang JC, 2003. Status of coral reefs in the western Atlantic: results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Res. Bull 496, 1–630.
- Lefcheck JS, Innes-Gold AA, Brandl SJ, Steneck RS, Torres RE, Rasher DB, 2019. Tropical fish diversity enhances coral reef functioning across multiple scales. Sci. Adv 5 (3), 6420.
- Lindeman KA, Pugliese R, Waugh GT, Ault JS, 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bull. Mar. Sci 66 (3), 929–956.
- Lindfield SJ, Harvey ES, McIlwain JL, Halford AR, 2014. Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. Methods Ecol. Evol 5, 1061–1069.
- Luckhurst BE, Luckhurst K, 1978. Analysis of substrate variables on coral reef fish communities. Mar. Biol 49, 317–323.
- Man A, Law R, Polunin NVC, 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biol. Conserv 71, 197–204.
- Maynard JA, McKagan S, Raymundo L, Johnson S, Ahmadia GN, Johnston L, Houk P, Williams GJ, Kendall M, Heron SF, van Hooidonk R, McLeod E, Tracey D, Planes S, 2015. Assessing relative resilience potential of coral reefs to inform management. Biol. Conserv 192, 109–119.
- McClanahan TR, 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity and sea urchins. Coral Reefs 13, 231–241.
- McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Alemu JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby PJ, Paddack MJ, Selig ER, van Woesik R, 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7 (8), e42884. 10.1371/ journal.pone.0042884. [PubMed: 22952618]
- 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.

- McField M, Kramer PR, 2007. Healthy Reefs for Healthy People: A Guide to Indicators of Reef Health and Social Well-being in the Mesoamerican Reef Region. With Contributions by M Gorrez and M McPherson. (208 pp).
- Meynecke JO, Lee SY, Duke NC, 2008. Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biol. Conserv 141, 981–996.
- Mora C, 2008. A clear human footprint in the coral reefs of the Caribbean. Proc. R. Soc. Lond. B 275, 767–773.
- Moustaka M, Langlois TJ, McLean D, Bond T, Fisher R, Fearns P, Dorji P, Evan RD, 2018. The effects of suspended sediment on coral reef fish assemblages and feeding guilds of north-west Australia. Coral Reefs 37 (3), 659–673.
- Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CC, Llewellyn G, 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536. [PubMed: 14765193]
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gil AB, 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311, 98–101. [PubMed: 16400152]
- Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, Sanchirico JN, 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conserv. Biol 22, 941–951. [PubMed: 18477024]
- Munro JL, 1983. Caribbean Coral Reef Fishery Resources. WorldFish (286 pp).
- Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman GR, McGovern JC, Parker SJ, Poss SG, Sala E, Schmidt TW, Sedberry GR, Weeks H, Wright SG, 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25, 6–30.
- Nagelkerken I, Sheaves M, Baker R, Connolly RM, 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish. 16, 362–371.
- National Oceanic and Atmospheric Administration (NOAA), 2013a. DRAFT Belt Transect Fish Survey Protocol for Atlantic/Caribbean. National Coral Reef Monitoring Program (NCRMP), Silver Spring, MD.
- National Oceanic and Atmospheric Administration (NOAA), 2013b. Draft Line Point-Intercept (LPI) Survey Protocol for the Atlantic/Caribbean. National Coral Reef Monitoring Program (NCRMP). National Coral Reef Monitoring Program (NCRMP), Silver Spring, MD.
- Nemeth RS, Kadison E, Herzlieb S, Blondeau J, Whiteman E, 2006. Status of a yellowfin grouper (Mycteroperca venenosa) spawning aggregation in the U.S. Virgin Islands with notes on other species. Proc. Gulf Caribb. Fish. Inst 57, 543–558.
- Neves LM, Teixeira-Neves TP, Pereira-Filho GH, Araújo FG, 2016. The farther the better: effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. PLoS One 11, e0166679. [PubMed: 27907017]
- Newman MJH, Paredes GA, Sala S, Jackson JBC, 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecol. Lett 9, 1216–1227. [PubMed: 17040324]
- Nystrom M, Folke C, 2001. Spatial resilience of coral reefs. Ecosystems 4, 406–417.
- Obura DO, Grimsditch G, 2009. Resilience Assessment of Coral Reefs Assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN Working Group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland (70 pages).
- Ojeda-Serrano E, Appeldoorn RS, Ruíz-Valentín I, 2007a. Reef fish spawning aggregations of the Puerto Rican shelf. Proc. Gulf Caribb. Fish. Inst 59, 467–474.
- Ojeda-Serrano E, Appeldoorn RS, Ruíz-Valentín H, 2007b. Reef fish spawning aggregations of the Puerto Rican shelf. Final report to the Caribbean Coral Reef Institute http://ccri.uprm.edu/researcher/Ojeda/Ojeda_Final_Report_CCRI_SPAG%27s.pdf.
- Oliver LM, Lehrter JC, Fisher WS, 2011. Relating landscape development intensity to coral reef condition in the watersheds of St. Croix, US Virgin Islands. Mar. Ecol. Prog. Ser 427, 293–302.

- Oliver LM, Fisher WS, Dittmar J, Hallock P, Campbell J, Quarles RL, Harris P, LoBue C, 2014. Contrasting responses of coral reef fauna and foraminiferal assemblages to human influence in La Parguera, Puerto Rico. Mar. Environ. Res 99, 95–105. 10.1016/j.marenvres.2014.04.005. [PubMed: 24840256]
- Oliver LM, Fisher WS, Fore L, Smith A, Bradley P, 2018. Assessing land use, sedimentation, and water quality stressors as predictors of coral reef condition in St. Thomas, U.S. Virgin Islands. Environ. Monit. Assess 190, 213–228. [PubMed: 29536196]
- Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, Forrester GE, 2009. Recent region-wide declines in Caribbean reef fish abundance. Curr. Biol 19, 590–595. [PubMed: 19303296]
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC, 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301, 955–958. [PubMed: 12920296]
- Pendleton LH, 1995. Valuing coral reef protection. Ocean Coast. Manag 26, 119–131.
- Pittman SJ, Christensen JD, Caldow C, Menza C, Monaco ME, 2007. Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecol. Model 204, 9–21.
- Pittman SJ, Hile SD, Jeffrey CFG, Clark R, Woody K, Herlach BD, Caldow C, Monaco ME, Appeldoorn R, 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 NOS NCCOS 107. NOS NCCOS CCMA Silver Spring, MD.
- Pratchett MS, Hoey AS, Wilson SK, 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr. Opin. Environ. Sustain 7, 37–43.
- Principe P, Bradley P, Yee S, Fisher W, Johnson E, Allen P, Campbell D, 2012. Quantifying Coral Reef Ecosystem Services. U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC (EPA/600/R-11/206, January 2012).
- Richards BL, Williams ID, Nadon MO, Zgliczynski BJ, 2011. A towed-diver survey method for mesoscale fishery-independent assessment of large-bodied reef fishes. Bull. Mar. Sci 87, 55–74.
- Risk MJ, 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull 152, 1–6.
- Roberts CM, Ormond RFG, 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser 41, 1–8.
- Robinson JPW, Williams ID, Edwards AM, McPherson J, Yeager L, Vigliola L, Baum JK, 2017. Fishing degrades size structure of coral reef fish communities. Glob. Chang. Biol 23 (3), 1009– 1022. [PubMed: 27564866]
- Rogers CS, 1990. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser 62, 185–202.
- Rogers CS, Garrison G, Grober R, Hillis ZM, Franke MA, 1994. Coral Reef Monitoring Manual for the Caribbean and Western Atlantic. U. S. National Park Service, St. John, U. S. Virgin Islands.
- Rude J, Minks A, Doheny B, Tyner M, Maher K, Huffard C, Hidayat NI, Grantham H, 2016. Ridge to reef modelling for use within land–sea planning under data-limited conditions. Aquat. Conserv. Mar. Freshwat. Ecosyst 26 (2), 251–264.
- Sadovy Y, Colin PL, Domeier ML, 1994a. Aggregation and spawning in the tiger grouper, Mycteroperca tigris (Pisces: Serranidae). Copeia 1994, 511–516.
- Sadovy Y, Rosario A, Román A, 1994b. Reproduction in an aggregating grouper, the red hind, Epinephelus guttatus. Environ. Biol. Fish 41, 269–286.
- Sala E, Ballesteros E, Starr RM, 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries 26, 23–30.
- Sale PF, 1991. Habitat structure and recruitment in coral reef fishes. In: Bell SS, McCoy ED, Mushinsky HR (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, pp. 197–210.
- Sale PF, Van Lavieren H, Ablan Lagman MC, Atema J, Butler M, Fauvelot C, Hogan JD, Jones GP, Lindeman KC, Paris CB, Steneck R, Stewart HL, 2010. Preserving Reef Connectivity: A Handbook for Marine Protected Area Managers. Connectivity Working Group, Coral Reef Targeted Research & Capacity Building for Management Program, UNU-INWEH.

- Salm RV, Smith SE, Llewellyn G, 2001. Mitigating the impact of coral bleaching through marine protected area design. In: Coral Bleaching: Causes, Consequences and Response. University of Rhode Island, USA, pp. 81–88.
- Sanchez PJ, Appeldoorn RS, Schärer-Umpierre MT, Locascio JV, 2017. Patterns of courtship acoustics and geophysical features at spawning sites of black grouper (Mycteroperca bonaci). Fish. Bull 115, 186–195. 10.7755/FB.115.2.5.
- Santavy DL, Fisher WS, Campbell JG, Quarles RL, 2012. Field Manual for Coral Reef Assessments. U.S. Environmental Protection Agency, Office of Research and Development, Gulf Ecology Division, Gulf Breeze, FL (EPA/600/R-12/029).
- Santavy DL, Bradley P, Gerritsen J, Oliver L, 2016. The biological condition gradient, a tool used for describing the condition of US coral reef ecosystems. In: Proceedings of the 13th International Coral Reef Symposium, pp. 557–568.
- Schallenberg M, Kelly D, Clapcott J, Death RC, Young R, Sorrell B, Scarsbrook M, 2011. Approaches to Assessing Ecological Integrity of New Zealand Freshwaters. Department of Conservation, Wellington 6143, New Zealand (40 pp).
- Schärer-Umpierre MT, 2009. Using Landscape Ecology to Describe Habitat Connectivity for Coral Reef Fishes (PhD Thesis). University of Puerto Rico, Mayagüez, Puerto Rico (216 pp).
- Shapiro DY, Sadovy Y, McGehee MA, 1993. Size, composition, and spatial structure of the annual spawning aggregation of the Red hind, Epinephelus guttatus (Pisces: Serranidae). Copeia 1993, 399–406.
- Shcherbina AY, Gawarkiewicz GG, Linder CA, Thorrold SR, 2008. Mapping bathymetric and hydrographic features of Glover's Reef, Belize, with a REmuS autonomous underwater vehicle. Limnol. Oceanogr 53, 2264–2272.
- Smith SG, Ault JS, Bohnsack JA, Harper DE, Luo J, McClellan DB, 2011. Multispecies survey design for assessing reef-fish stocks, spatially-explicit management performance, and ecosystem condition. Fish. Res 109, 25–41.
- Spalding M, Burke L, Wood SA, Ashpole J, Hutchison J, Ermgassen P, 2017. Mapping the global value and distribution of coral reef tourism. Mar. Policy 82, 104–113.
- Stallings CD, 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes. Ecology 89, 2090–2095. [PubMed: 18724719]
- Stallings CD, 2009. Predator identity and recruitment of coral-reef fishes: indirect effects of fishing. Mar. Ecol. Prog. Ser 383, 251–259.
- Stevens MH, Smith SG, Ault JS, 2019. Life history demographic parameter synthesis for Florida and Caribbean reef fishes. Fish Fish. 20, 1196–1217. 10.1111/faf.12405.
- Talbot FH, Goldman B, 1972. A preliminary report on the diversity and feeding relationships of reef fishes of One Tree Island, Great Barrier Reef system. In: Proceedings of the First International Symposium on Corals and Coral Reefs. 1. pp. 425–443.
- The White House, 2004. U.S. Ocean Action Plan: The Bush Administration's Response to the U.S. Commission on Ocean Policy. The White House, Washington, DC.
- Thompson R, Munro JL, 1974. The Biology, Ecology and Exploitation and Management of the Caribbean Reef Fishes. Part V. Carangidae (Jacks). (Research report from the Zoology Department, University of the West Indies).
- Turgeon DD, Asch RG (Eds.), 2002. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2002. National Oceanic and Atmospheric Administration/ National Ocean Service/National Centers for Coastal Ocean Science, Silver Spring, MD.
- U.S. Environmental Protection Agency (EPA), 1990. Biological Criteria: National Program for Surface Waters. U.S. Environmental Protection Agency, Office of Water, Washington, DC (EPA-440/5-90-004).
- U.S. Environmental Protection Agency (EPA), 2002. Biological Assessments and Criteria: Crucial Components of Water Quality Programs. EPA-822-F-02-006.
- U.S. Environmental Protection Agency (EPA), 2011a. A Primer on Using Biological Assessments to Support Water Quality Management. EPA 810-R-11–01. U.S. Environmental Protection Agency, Washington, DC.

- U.S. Environmental Protection Agency (EPA), 2011b. A Field-based Aquatic Life Benchmark for Conductivity in Central Appalachian Streams. EPA/600/R-10/023F.
- U.S. Environmental Protection Agency, Office of Research and Development, National Center for Environmental Assessment, Washington, DC. http://cfpub.epa.gov/ncea/cfm/recordisplay.cfm? deid=233809 (Accessed February 2016).
- U.S. Environmental Protection Agency (EPA), 2013a. Biological Assessment Program Review: Assessing Level of Technical Rigor to Support Water Quality Management. EPA 820-R-13-001. U.S. Environmental Protection Agency, Washington, DC.
- U.S. Environmental Protection Agency (EPA), 2013b. Biological Assessment Program Review: Assessing Level of Technical Rigor to Support Water Quality Management. EPA 820-R-13-001. U.S. Environmental Protection Agency, Washington, DC.
- U.S. Environmental Protection Agency (EPA), 2016. A Practitioner's Guide to the Biological Condition Gradient: A Framework to Describe Incremental Change in Aquatic Ecosystems. EPA 842-R-16-001, Wash. DC.
- Vega Thurber RL, Burkepile DE, Fuchs C, Schantz AA, McMinds R, Zanzeveld JR, 2014. Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Glob. Chang. Biol 20, 544–554. [PubMed: 24277207]
- Waddell JE (Ed.), 2005. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. National Oceanic and Atmospheric Administration, Silver Spring, MD.
- Waddell JE, Clarke AM (Eds.), 2008. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008. NOAA Technical Memorandum NOS CCOS 73. NOAA/ NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, Silver Spring, MD.
- Walker BK, Jordan LKB, Spieler RE, 2009. Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. J. Coast. Res 53, 39–48.
- Wenger AS, Fabricius KE, Jones GP, Brodie JE, 2015. Effects of sedimentation, eutrophication, and chemical pollution on coral reef fishes, chap 15. In: Mora C. (Ed.), Ecology of Fishes on Coral Reefs. Cambridge University Press, Cambridge, pp. p145–p153.
- West JM, Salm RV, 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv. Biol 17 (4), 956–967.
- World Resources Institute (WRI), U.S. National Oceanographic and Atmospheric Administration (NOAA), 2006. Land-based Sources of Threat to Coral Reefs in the U.S. Virgin Islands. (Washington, DC. 14 pp).
- Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. Adv. Study Behav 16, 229–249.
- Zadeh LA, 2008. Is there a need for fuzzy logic? Inf. Sci 178, 2751–2799.





Fig. 1.

Conceptual model of the biological condition gradient (Davies and Jackson, 2006).

Bradley et al.



Fig. 2.

Location and distribution of 2010 EPA sampling stations. Seventy-six targeted coral survey locations (red circles) at regular intervals across human disturbance gradients (low, medium and high sediment threat levels) were distributed across linear reefs within 1.5 km of shore (including cays) and between 2 and 12 m depth.

Bradley et al.



Fig. 3.

Location and distribution of 2011 EPA sampling stations (Fisher et al., 2019). Sixty randomly selected coral survey locations (red circles) were distributed across linear reefs within 1.5 km of shore (including cays in the target substrate) and between 2 and 12 m depth. Coral reef and colonized hardbottom substrate shown in gray shading.



Fig. 4.

Distribution of fish panelists' BCG level assignments expressed as difference from the group median in 1/3 BCG level steps. Calibration (top) and confirmation (bottom) stations from the Puerto Rico reef fish dataset.



Fig. 5.

Non-metric multidimensional scaling (nMDS) plot of the fish density composition at the 38 sites that were used in development of the BCG model clustered by Bray-Curtis similarity (Stress = 0.19)I. a) Vector plot overlay shows the direction of linear increase of environmental variable concentrations, and the multiple correlation of each (transformed) variable on the 2D ordination points. The significant gradient vectors are bolded. b-d) Bubble plots overlay the same nMDS plot but with circles of increasing size representing the environmental variable at those sites.

Table 1.

BCG attributes and their descriptions (modified from EPA, 2016).

Attribute	Description
I. Historically documented, long-lived, or regionally endemic taxa	Taxa known to have been supported according to historical, museum or archeological records, or taxa with restricted distribution (occurring only in a locale as opposed to a region), often due to unique life history requirements. They may be long-lived and late maturing and have low fecundity, limited mobility, multiple habitat requirements as with diadromous species, or require a mutualistic relationship with other species. They may be among listed Endangered or Threatened (E/T) or special concern species. Predictability of occurrence is often low, and therefore requires documented observation. The taxa that are assigned to this category require expert knowledge of life history and regional occurrence of the taxa to appropriately interpret the significance of their presence or absence. Long-lived species are especially important as they provide evidence of multi-annual persistence of habitat condition.
II. Highly sensitive taxa	Taxa that are highly sensitive to pollution or anthropogenic disturbance. Tend to occur in low numbers relative to total population density, but they might make up a large relative proportion of richness. In high quality sites, they might be ubiquitous in occurrence or might be restricted to certain micro-habitats. They often have slow growth – long-lived (K-strategists) vs. short-lived—fast growth (r-strategists). In coral reef ecosystems, large-bodied, slow-growing, late-maturing fishes (K-strategists) are generally more sensitive to fishing pressure and environmental stress than faster-growing, shorter-lived species (Beverton and Holt, 1957; Man et al., 1995; Jennings et al., 1998; Coleman et al., 2000; Goodwin et al., 2006; Ault et al., 2008). The distinguishing characteristic for this attribute category was found to be sensitivity and not relative rarity, although some of these taxa might be uncommon in the data set (e.g., very small percent of sample occurrence or sample density), therefore, these are the first to disappear with disturbance or pollution.
III. Intermediate sensitive taxa	Taxa that are abundant in relatively undisturbed conditions but are sensitive to anthropogenic disturbance/pollution. They have a broader range of tolerance than Attribute II taxa and can be found in reduced density and richness in moderately disturbed or polluted stations. These taxa often comprise a substantial portion of natural communities.
IV. Intermediate tolerant taxa	Taxa that commonly comprise a substantial portion of the fish assemblage in undisturbed habitats, as well as in moderately disturbed or polluted habitats. They exhibit physiological or life-history characteristics that enable them to thrive under a broad range of thermal, flow, or oxygen conditions. Many have generalist or facultative feeding strategies enabling utilization of diverse food types. These species have little or no detectable response to moderate stress, and they are often equally abundant in both reference and moderately stressed sites. Some intermediate tolerant taxa may show an "intermediate disturbance" response, where densities and frequency of occurrence are relatively high at intermediate levels of stress, but they are intolerant of excessive pollution loads or habitat alteration.
V. Tolerant taxa	Tolerant taxa are those that typically comprise a low proportion of natural communities. These taxa are more tolerant of a greater degree of disturbance and stress than other organisms and are, thus, resistant to a variety of pollution or habitat induced stress. They may increase in number (sometimes greatly) under severely altered or stressed conditions. They may possess adaptations in response to organic pollution, hypoxia, or toxic substances. These are the last survivors in severely disturbed systems and can prevail in great numbers due to lack of competition or predation by less tolerant organisms, and they are key community components of level 5 and 6 conditions.
VI. Non-native or intentionally introduced species	Any species not native to the ecosystem. Species introduced or spread from one region of the U.S. to another outside their normal ranges are non-native, or non-indigenous. This category also includes species introduced from other continents and referred to as "alien" species. This attribute represents both an effect of human activities and a stressor in the form of biological pollution. The BCG identifies the presence of native taxa expected under undisturbed or minimally disturbed conditions as an essential characteristic of BCG level 1 and 2 conditions. The BCG only allows for the occurrence of non-native taxa in these levels if those taxa do not displace native taxa and do not have a detrimental effect on native structure and function. Condition levels 3 and 4 depict increasing occurrence of non-native taxa. Extensive replacement of native taxa by tolerant or invasive, non-native taxa can occur in levels 5 and 6.
VII. Organism condition	Anomalies of the organisms; indicators of individual health (e.g., deformities, lesions, tumors).
VIII. Ecosystem function	Ecosystem function refers to processes required for the performance of a biological system expected under naturally occurring conditions (e.g., primary and secondary production, respiration, nutrient cycling, and decomposition). Assessing ecosystem function includes consideration of the aggregate performance of dynamic interactions within an ecosystem, such as the interactions among taxa (e.g., food web dynamics) and energy and nutrient processing rates (e.g., energy and nutrient dynamics) (Cairns, 1977). Additionally, ecosystem function includes aspects of all levels of biological organization (e.g., individual, population, and community condition). Altered interactions between individual organisms and their abiotic and biotic environments might generate changes in growth rates, reproductive success, movement, or mortality. These altered interactions are ultimx`tely expressed at ecosystem levels of organization (e.g., shifts from heterotrophy to autotrophy, onset of eutrophic conditions) and as changes in ecosystem process rates (e.g., photosynthesis, respiration, production, decomposition).
IX. Spatial and temporal extent of detrimental effects	The spatial and temporal extent of stressor effects includes the near-field to far-field range of observable effects of the stressors on a water body. Such information can be conveyed by biological assessments provided the spatial density of sampling sites is sufficient to convey changes along a pollution continuum (USEPA, 2013a). Use of a continuum provides a method for determining the severity (i.e., departure from the desired state) and extent (i.e., distance over which adverse effects are observed) of an impairment from one or more sources. As with attribute VIII above, attribute IX has not yet been developed and applied in BCG models. It is included for future development and application. State scientists involved in the development of the BCG conceptual model stated that this attribute was important to include for future testing and development.

Attribute	Description
X. Ecosystem connectivity	Access or linkage (in space/time) to materials, locations and conditions required for maintenance of interacting populations of aquatic life. It is the opposite of fragmentation and is necessary for persistence of metapopulations and natural flows of energy and nutrients across ecosystem boundaries. Ecosystem connectivity can be indirectly expressed by certain species that depend on their populations. There are two commonly recognized categories of connectivity based upon the typical life history (i.e., two-phase life cycle) of most reef associated fishes: (1) pre-settlement connectivity through larval dispersal and (2) post-settlement connectivity (Aguilar-Perera, 2004).

Table 2.

Preliminary narrative BCG with four distinct levels of condition for all reef assemblages: very good/excellent; good; fair; and poor.

Level	Physical structure	Corals	Gorgonians	Sponges	Fish	Other Vertebrates	Other Invertebrates	Algae/ Plants	Condition
Very- Good – Excellent (BCG 1– 2)	High rugosity or 3D structure; substantial reef built above bedrock; many irregular surfaces provide habitat for fish; very clear water; no sediment, floes or films	High species diversity including rare; large old colonies (<i>Orbicella</i>) with high tissue coverage; balanced population structure (old & middle-sized colonies, recruits); <i>Acropora</i> thickets present	Gorgonians present but sub- dominant to corals	Large autotrophic and highly sensitive sponge species abundant	Populations have balanced species abundance, sizes, biomass, and trophic interactions; Large piscivores present (groupers, barracuda, sharks)	Large, long- lived species present and diverse (turtles, dolphins)	<i>Diadema</i> , lobster, small crustaceans and polychaetes abundant; some large sensitive anemone species	Crustose coralline algae abundant; turf algae present but cropped and grazed by <i>Diadema</i> , low abundance fleshy algae	Low prevalence of disease or tumors; mostly live tissue on colonies
Good (BCG 3)	Moderate to high rugosity; moderate reef built above bedrock; some irregular cover for fish habitat; water slightly turbid; low sediment, floes or film on substrate	Moderate coral diversity; large old colonies (<i>Orbicella</i>) with some tissue loss; varied population structure (usually old colonies, few middle aged and some recruitment); <i>Acropora</i> thickets maybe present; rare species absent	Gorgonians more abundant than in BCG Levels 1–2	Autotrophic species present but highly sensitive species missing	Decline of large apex predators (e.g., groupers, snappers, etc.) noticeable; small reef fish more abundant than Levels 1–2	Large, long- lived species locally extirpated (turtles, eels)	Diadema, lobster, small crustaceans and polychaetes less abundant than Level 1– 2; large sensitive anemones species missing	Crustose coralline algae present but less than Levels 1–2; turf algae present and longer; more fleshy algae present	Disease and tumor prevalence slightly above background level; more colonies have irregular tissue loss
Fair (BCG 4)	Low rugosity, limited reef built above bedrock; erosion of reef structure obvious; water turbid; more sediment accumulation, floes and films; <i>Acropora</i> usually gone or present as rubble for recruitment substrate	Reduced coral diversity; emergence of tolerant species, few or no large old colonies (<i>Orbicella</i>) mostly dead; <i>Acropora</i> thickets gone; large remnants mostly dead	Gorgonians more abundant than in Levels 1–3; replace sensitive corals and sponges species	Mostly heterotrophic sponges with tolerate species and clionids	Near absence of large piscivores; small reef fish abundant (mostly Damsel fish)	Large, long- lived species locally extirpated (turtles, eels)	Diadema absent, Polythoo overgrowing corals, crustaceans, polychaetes, and sensitive anemones conspicuously absent	Some coralline algae; turf is uncropped covered in sediment; lots fleshy algae with high diversity (e.g., <i>Dictyoto</i>); possibly smothering sessile invertebrates; absence of crustose coralline algae	High incidence of diseased coral, sponges, gorgonians; evidence high mortality; usually less tissue than dead portions on colonies

L	evel	Physical structure	Corals	Gorgonians	Sponges	Fish	Other Vertebrates	Other Invertebrates	Algae/ Plants	Condition
P (BC	oor CG 5– 6)	Very low rugosity, no or low reef built above bedrock; poor fish habitat; very turbid water; thick sediment film & high floes covering bottom; no substrate for recruits	Absence of most species, colonies small, only highly tolerant species with little or no tissue	Small & sparse colonies, mostly small sea fans, often diseased	Heterotrophic sponges buried deep in sediment, highly tolerant sponge species	No large fish, few intolerant species, lack of multiple trophic levels	Usually devoid of other vertebrates	Low or no reef invertebrates; high abundance of sediment dwelling organisms such as polychaetes, holothurians	High cover of fleshy algae (Dictyota); possibly smothering sessile invertebrates; no turf or coralline algae; complete absence of crustose coralline algae	High incidence disease on small colonies of corals, sponges gorgonians; if present, low or no tissue

(Source: Bradley et al., 2014)

EPA Author Manuscript

Table 3.

Narrative rules for fish BCG model in Puerto Rico coral reefs.

BCG Level 1	Definition: Biological conditions as they existed (or still exist) in the absence of measurable effects of stressors and provides the basis for comparison to the next five levels.
	Fish Narrative Rules: Populations have balanced species abundance, sizes, biomass, and trophic interactions; Large piscivores present (groupers, barracuda, sharks)
BCG Level 2	Definition: Minimal changes in structure of the biotic community and minimal changes in ecosystem function— virtually all native taxa are maintained with some changes in biomass and/or abundance; ecosystem functions are fully maintained within the range of natural variability
-	Fish Narrative Rules: Populations have balanced species abundance, sizes, biomass, and trophic interactions; Large piscivores present (groupers and snappers, but not sharks); schools of piscivores present [1]
BCG Level 3	Definition: Evident changes in structure of the biotic community and minimal changes in ecosystem function—Some changes in structure due to loss of some rare native taxa; shifts in relative abundance of taxa, but intermediate sensitive taxa are common and abundant; ecosystem functions are fully maintained through redundant attributes of the system
	Fish Narrative Rules: Decline of large apex predators (e.g., groupers, snappers, etc.) noticeable, however still present; small reef fish more abundant than Levels 1–2; large body parrotfish present; high within-family diversity [1]
BCG Level 4	Definition: Moderate changes in structure of the biotic community with minimal changes in ecosystem function. Moderate changes in structure because of replacement of some sensitive- ubiquitous taxa by more tolerant taxa, but reproducing populations of some sensitive taxa are maintained; overall balanced distribution of all expected major groups; ecosystem functions largely maintained through redundant attributes.
	Fish Narrative Rules: Near absence of large piscivores, however t least one piscivore present; small reef fish abundant (mostly Damsel fish and wrasses); parrotfish present
BCG Level 5	Definition: Major changes in structure of the biotic community and moderate changes in ecosystem function. Sensitive taxa are markedly diminished; conspicuously unbalanced distribution of major groups from distributions expected; organism condition shows signs of physiological stress; ecosystem function shows reduced complexity and redundancy.Fish Narrative Rules: No large fish, few intolerant species, lack of multiple trophic levels; more than 4-5 fish species
BCG Level 6	Definition: Severe changes in structure of the biotic community and major loss of ecosystem function. Extreme changes in structure; wholesale changes in taxonomic composition; extreme alterations from normal densities and distributions; organism condition is often poor; ecosystem functions are severely altered.
	Fish Narrative Rules: Does not meet Level 5 rules

Table 4.

BCG reef fish assemblage decision rules. Numbers in parentheses are lower and upper bounds for group membership. Puerto Rico rules are based on 4×25 m belt transect data collected during 2010–2011 (Santavy et al., 2012). Florida rules are based on 15 m dia cylinder RVC point count data (Smith et al., 2011) collected during 2014–2016.

BCG metric	Narrative rules	Quantitative rules				
BCG Level 2 (No survey samples were identified, rules are conceptual)						
Total taxa	Richness is high – valid taxa only	20(15–25)				
Rare, endemic & special species (Attribute I species)	Present	Ι				
Highly sensitive taxa Attribute II species)	Present	1 (0–2)				
Proportion of all sensitive taxa (Attribute I, II, and III species)	Sensitive taxa constitute large proportion of species richness	50% (45 - 55)				
Total biomass	High fish biomass – valid taxa only	Puerto Rico: 65 (50–80 g/m ²) Florida: 11.5 (kg/177 m ²)				
Large groupers	Present (Epinephelus and Mycteroperca)	1(0–1)				
Large predators	Present	1 (0–2)				
Piscivore individuals	Abundant	20 individuals				
BCG Level 3						
Total taxa	Richness moderate to high – valid taxa only	15(10-20)				
Number of all sensitive taxa (Attribute I, I, and III species) Sensitive taxa are a small to moderate proportion species richness		6(4-8)				
Total biomass (g/m ²)	Total fish biomass is moderate to high – valid taxa only	Puerto Rico: 35 (30 – 40 g/m ²) Florida: 6.5 (5.6 – 7.4 kg/177m ²)				
Piscivores	Presence of snappers or other piscivorcs	1				
Parrotilsh Presence of large parrot fish		1 (0-2)				
Damselfish	Don't dominate observed species	<25% (20-30)				
Groupers	Groupers present (Dermatolepis, Epinephelus, Mycteroperca, and Cephalopholis)	1				
Rule application:	Reef Habitats: More stringent requirements Hard- bottom Habitats: Less stringent requirements	Require 6 of 7 rules Require 5 of 7 rules				
BCG Level 4						
Total taxa	Richness low to moderate - valid taxa only	9(4–14)				
Number of all sensitive taxa (Attribute I, II, and III species)	Iumber of all sensitive taxa (Attribute I, Some sensitive taxa I, and III species)					
Total biomass (g/m ²)	Low or higher – valid taxa only	Puerto Rico: 11(7—15 g/m ²) Florida: 1.1 (0.7 – 1.5 kg/177 m ²)				
BCG Level 5						
Total taxa	Sparse – valid taxa only	5(2-8)				
Total biomass (g/m²) Very low – valid taxa only		Islands: 2(1 – 3) (g/m ²) Florida: 0.35 (0.18 – 0.52 kg/177 m ²)				
BCG Level 6	Does not meet Level 5 rules					

^aSee Supplemental Material Appendix A Table A7.

Table 5.

Performance of BCG quantitative fish model for calibration and confirmation datasets, by Puerto Rican reef fish panel. "Better" and "worse" indicate model assessment of coral reef condition compared to panel (e.g., "better" if model assessed BCG Level 2, but panel assessed BCG Level 3, and so forth). Percent differences are reported with the number of differences followied in parentheces.

Dataset	Model Performance Difference					
	Model 1 level better	Model 1/2 level better	Exact match	Model 1/2 level worse	Model 1 level worse	Total
Calibrate	5% (2)	0 (0)	79% (30)	13% (5)	3% (1)	100% (38)
Confirm	9% (1)	9% (1)	73% (8)	0 (0)	9% (1)	100% (11)

(Source: Bradley et al., 2016)

Table 6.

BCG Level relationship to each other Level (BCG Levels 3–6). Dissimilarity calculated using Euclidian Distance Coefficient. Test results from ANOSIM and SIMPER calculated among group dissimilarities.

BCG Levels	R statistic	Significance Level	Among Group Dissimilarity
3 vs 4	0.013	33.9	58.7
3 vs 5	0.681	0.1 ***	74.2
3 vs 6	0.991	0.7 ***	91
4 vs 5	0.439	1.3 **	70.7
4 vs 6	0.934	0.6 ***	80
5 vs 6	0.607	6.7	90

Table 7.

Preliminary narrative BCG with four distinct levels of condition for all reef assemblages: very good/excellent; good; fair; and poor.

BCG Level	Species	Avg. Similarity	Similarity SD	% Individual Contribution	% Cumulative Contribution
BCG Level 3					
42.34% average within group	Thalassoma hifasciatum	6.43	2.06	15.19	15.19
similarity	Spar isoma aurofrenatum	4.44	3.3	10.49	25.68
	Scarus iseri	2,87	1,24	6,78	32,46
	Stegastes partii us	2,83	1,19	6,68	39,14
	Ocyurus chrysurus	2,48	1	5.86	45
	Acanthurns bahianus	2,26	0,97	5,35	50,35
	Acanthurus coeruleus	2,17	1,01	5,11	55,46
	Microspathodon chrysurus	2,05	1,02	4,85	60,31
	Stegastes adustus	1.96	0.68	4.64	64.95
	Acanthurus chirurgus	1.3	0.57	3.08	68.03
	Spar isoma viride	1.29	0.69	3.05	71.09
BCG Level 4					
40.69% average within group	Thalassoma hifasciatum	9,81	4,21	24.11	24,11
similarity	Sparisoma aurofrenatum	4.1	1.27	10.07	34.19
	Stegastes partitus	3,19	0,88	7,84	42,03
	Acanthurus bahianus	2,45	0,77	6,02	48.05
	Ocyurus chrysurus	2,32	0,77	5,71	53.75
	Acanthurus coeruleus	2.14	0.79	5.25	59.01
	Microspathodon chrysurus	2,08	0,78	5,12	64,13
	Halichoeres hivittatus	2.04	0.66	5.01	69.14
	Scarus iseri	1.91	0.65	4.68	73.82
BCG Level 5					
26.35% average within group	Halichoeres hivittatus	7,26	0,91	27.54	27,54
similarity	Stegastes adustus	7,06	0,88	26.8	54,34
	Thalassoma bifasciatum	6,48	0,84	24.61	78,95
BCG Level 6					
65.45% average within group	Stegastes diencaeus	39,93	SD=0!	61.01	61,01
similarity	Stegas tes leucostictus	25.51	SD-0!	38.99	100