Ecological Indicators 44 (2014) 120–127

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Percent recent mortality (PRM) of stony corals as an ecological indicator of coral reef condition

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ARTICLE INFO

Article history:
Received 26 June 2013
Received in revised form 15 October 2013
Accepted 18 October 2013

Keywords:
Coral indicators
Partial mortality
Florida reefs
Caribbean

ABSTRACT

The reef communities of the Florida coral reef tract play a major role in supporting the regional economy but are threatened by increased exploitation and environmental factors. Coral reef ecosystem services are vital to the economy of SE Florida where revenue and jobs depend on the status of reef resources. Here, we used an extensive, reef monitoring database collected by the Florida Reef Resilience (FRRP, 2003–2011) and the Atlantic and Gulf Rapid Reef Assessment (AGRRA, 1997–2011) programs to evaluate percent recent mortality (PRM) as a robust ecological indicator of coral colony and coral reef status. PRM, the proportion of a coral colony that has experienced recent tissue mortality so that corallite structures in the non-living parts of the coral are still intact and identifiable to species, can be attributed to disturbances taking place within days to a few months preceding the surveys.

Based on data from >50,000 colonies from 11 coral species and nearly 1400 sites, we propose a benchmark level of <1% PRM and <5% prevalence of partial mortality for Florida reefs during periods of background, low-stress environmental conditions. PRM levels >1.0% and prevalence levels >5% can be used as early warning indicators of degrading conditions. Average PRM values >2% are indicative of increasingly stressful conditions as those experienced during temperature anomalies and major hurricanes. Finally, PRM values considerably >2% are reflective of significantly stressful conditions and warning signals of potential major coral mortality as evidenced by mean PRM levels of >10% recorded in Florida as a consequence of the 2010 extreme cold-water event. PRM and prevalence values from Florida reefs compared favorably with those recorded in the Caribbean and the Mesoamerican region where a benchmark of 2% for background levels of PRM under low-level, chronic stress was proposed. The status of this indicator can be easily communicated to stakeholders and will benefit managers by providing: (1) a baseline to assess the status of coral populations; and (2) early-warning indicators of unfavorable conditions that may trigger management actions such as temporary closures or the establishment of more permanent protection such as MPAs.

1. Introduction

The reef communities of the Florida coral reef tract extend about 500 km from the Dry Tortugas northward to Martin County, USA. The location of these unique resources adjacent to large metropolitan centers, and the role they play in supporting the local economy, has resulted in increasing human pressures and impacts on these resources and their consideration as an "ecosystem at risk" (Bryant et al., 1998). In Florida, documented rates of reef decline over the last three decades are similar to those reported by Gardner et al. (2003) for the whole Caribbean region, with key reef-building taxa like *Acropora* spp. and *Montastraea*/*Orbicella* spp., having suffered especially serious declines (Dustan, 1999; Miller et al., 2002; Porter et al., 2002).

The factors responsible for the observed declines in Florida are consistent with those in other reef ecosystems around the world (Brown, 1997). These include: hurricanes (Lirman and Fong, 1997); ship groundings (Lirman et al., 2010); reduction in key herbivore abundance like the sea urchin *Diadema antillarum* (Forcucci, 1994); macroalgal competition (Dustan, 1999; Lirman, 2001); diseases (Porter et al., 2001; Richardson and Voss, 2005); eutrophication (Lapointe et al., 2002); overfishing (Ault et al., 1998, 2005a,b, 2008, 2009); sedimentation (Dustan, 1999); high temperatures and bleaching (Jaap, 1979; Manzello et al., 2007); cold snaps (Hudson, 1981; Walker et al., 1982; Lirman et al., 2011); and blooms of phytoplankton (Hu et al., 2003) and cyanobacteria (Butler et al., 1995; Paul et al., 2005).

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http://dx.doi.org/10.1016/j.ecolind.2013.10.021

Globally, total net benefit of the world's coral reef ecosystems is nearly $30 billion/year (Cesar et al., 2003); moreover, the average global value of coral reef recreation has been estimated at $184 per visitor (Brander et al., 2007). The services provided by coral reefs are directly related to their structure, which, in turn, is a direct result of the growth of the stony coral components of reef communities. Coral reef ecosystem services are vital to the economy of SE Florida where a substantial portion of revenue and jobs depend directly and indirectly on the status of reef resources (Ault et al., 2005a; Collier et al., 2008; Donahue et al., 2008). The importance of coral reef habitats to the economic welfare of Florida was highlighted in a study by Johns et al. (2001), which reported that coral reefs in southeastern Florida and the Florida Keys provide the ecological foundation for vital fisheries and a tourism-based economy that generated an estimated 71,000 jobs and US$6 billion of economic activity in 2001. In addition to the intrinsic value of coral reefs as centers of biodiversity and critical habitats for fish and macroinvertebrates, these also provide shoreline protection, sand production, building materials, nutrient cycling, carbon sequestration, pharmaceutical and biomedical products, as well as societal services such tourism revenues, education and recreation opportunities, and cultural resources (Cesar et al., 2003).

The value of coral reefs to humans as well as their recent patterns of decline have prompted the implementation of large-scale, long-term monitoring programs to assess the status and trends of these ecosystems and to support management decisions such as the establishment of no-take marine reserves (NTMRs; Bohnsack et al., 2004; Meester et al., 2004; Ault et al., 2006, 2013; Jeffrey et al., 2012) or the development of restoration activities (Johnson et al., 2011; Young et al., 2012). Central to these efforts is the selection of ecological indicators (metrics) and benchmarks that provide sufficient information to managers that enhance decision-making in a time- and cost-efficient manner.

In this study, we evaluated percent recent mortality (PRM) as an indicator of coral colony and coral reef community status in the Florida coral reef ecosystem. To accomplish this, we used monitoring data from the Florida Reef Resilience Program (FRRP) from 2003 to 2011 (Lirman et al., 2011). Data from Florida were compared to data collected from reefs throughout the Caribbean collected by the Atlantic and Gulf Rapid Reef Assessment (AGRRA; Kramer and Lang, 2003) program between 1997 and 2011. Data from these programs were used to evaluate species and habitat-specific responses to sea temperature anomalies, establish ecological benchmarks, and test background benchmark levels against indicator values recorded during extreme climatic events.

2. Methods

2.1. Tissue mortality and reef status

Recent, fresh-tissue damage or mortality to individual coral colonies was purported to be a key metric for quantifying reef vitality (Dustan, 1977, 1994). Sources of recent mortality identified in that study included sedimentation, algal and invertebrate (e.g., sponges, zoanthids) overgrowth, disease, bleaching, and fish (bites) predation. Recent tissue mortality was evaluated as an indicator in the Florida reef tract by Ginsburg et al. (1996, 2001). Recent tissue mortality was formally incorporated into the suite of indicators developed by the AGRRA program to rapidly assess coral reef condition in 1997. Recent mortality on a coral colony has been defined as any "non-living parts of the coral in which the corallite structures are still intact and identifiable to species" (Kramer and Lang, 2003) (Fig. 1). Since over time "recent" mortality transitions into "old" mortality, recent mortality is that taking place within the previous few days to a few months (Kramer, 2003). This short time-frame was determined to be the period it would take for factors like sedimentation, bioerosion, and algal or sponge overgrowth to prompt the transition from recent to old mortality (i.e., the time where skeletal properties are lost and prevent identification of a given coral skeleton to species) (Kramer, 2003). Old mortality represents portions of colonies with eroded or encrusted skeletons for which the time and potential cause of tissue death cannot be determined and little skeletal structure remains. The short "shelf-life" of this metric allows recent mortality measurements to be related to recent changes in the environment as a potential means of exploring causation.

Percent recent mortality (PRM) patterns in response to stressors such as diseases and extreme ocean temperatures have been measured in the Caribbean and Florida (Bruckner and Bruckner, 2006; Miller and Williams, 2007; Muller et al., 2008; Lirman et al., 2011). Increases in stress were correlated with tissue loss and increased recent mortality. While complete mortality provides a binary indicator of condition (live or dead), it does not provide an early metric of stressful conditions or a continuous spectrum of responses that relate to the intensity of disturbance (Jameson et al., 1998). Thus, partial mortality provides an early indicator of stressful conditions and a flexible metric that can be related to stress levels across a wide range of factors (Cooper et al., 2009).

2.2. Reef monitoring data

Coral monitoring data from Florida were collected yearly from 2003 to 2011 during summer months (August–October), at the peak of high-temperature stress for corals. These surveys were focused on documenting spatial bleaching patterns and temperature-related mortality. In addition, a winter survey was conducted in January–February 2010 within weeks of a record-breaking cold temperature event that caused significant mortality to both marine and terrestrial organisms (Lirman et al., 2011). AGRRA data used here were collected throughout the Caribbean from 1997 to 2011 (www.agrra.org). To provide a direct comparison with the Florida data, only AGRRA data collected from shallow (<20 m) fore-reef and patch-reef habitats for the same 11 species evaluated in Florida were selected as these were those habitats (and species) considered for the Florida analysis.

Detailed descriptions of sampling methods and site-selection criteria for the FRRP (www.frrp.org; Ault et al., 2006; Smith et al., 2011a,b) and AGRRA (www.agrra.org; Kramer and Lang, 2003) programs are beyond the scope of this study. However, it is important to note that the probabilistic survey design employed in Florida allows for unbiased and precise estimation of a suite of population-level coral metrics, increased change-detection power, and robust extrapolation to regional scales (Smith et al., 2011a,b).

Survey methods varied slightly between the AGRRA and FRRP programs (mainly in the use of 10-m^2 belt transects (FRRP) or 10-m line transects for benthic surveys (AGRRA)), but the methods used to quantify colony-based percent recent mortality (PRM) are similar. It is important to note that the newest version of AGRRA (v. 5) now incorporates the use of 10-m^2 belt transects. After a stony coral colony is identified, maximum diameter and height measurements are recorded. Then, the percentage (0–100%) of the skeletal unit (colony) covered by recent mortality is recorded as described by Kramer and Lang (2003). While FRRP calculates PRM for the whole colony, AGRRA estimates of PRM are confined to the outward-facing surfaces. Considering that PRM is estimated as a proportion of the colony being assessed and that for species with simple morphologies (e.g., massive, encrusting) the whole colony is easily visible from the vintage point of a diver positioned right over the colony, we believe the PRM estimates to be comparable between survey methods. Nevertheless, since there still remains a possibility that

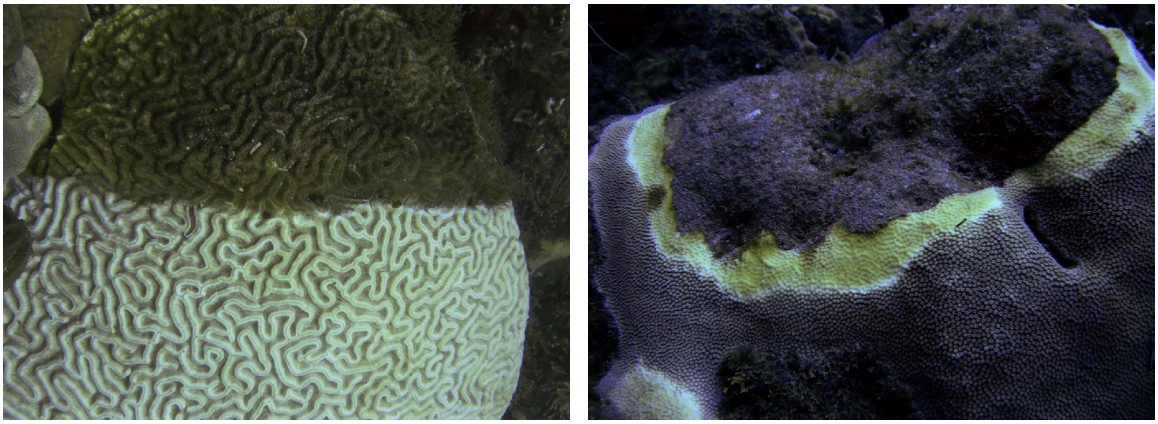

Fig. 1. Colonies of *Colpophyllia* (left) and *Orbicella* (right) showing signs of recent mortality (white portions of the colonies). While the skeleton is devoid of live tissue, skeletal features remain intact and allow colony identification to species (Kramer, 2003). Images provided by James Byrne (TNC).

the different survey programs introduce a systematic bias in the way PRM is calculated, we refrain from comparing PRM between survey methods statistically here. Another difference between the programs (up to recently), which prevents a full statistical comparison, is the minimum size of colonies included in the surveys. FRRP includes coral colonies ≥4 cm. Early AGRRA surveys only included colonies ≥25 cm in diameter. Subsequent surveys included colonies ≥10 cm, while the most recent version of AGRRA (v. 5), like FRRP, includes colonies ≥4 cm.

The FRRP and AGRRA surveyors are asked to go through a calibration training exercise prior to conducting any data collection to ensure consistency of measurements in the field. Additional internal calibration is conducted by each regional survey team as new team members are added. The goals of this exercise in which all surveyors assess the same coral colonies are to ensure that: species identifications are identical, maximum diameter estimates are within 10 cm, and that percent mortality estimates are within 10% among observers. PRM data for all Florida sites, from 2003 to 2011, were averaged for each species within sites and analyzed based on year, reef zone (habitat), and sub-region. In this analysis, only data from the 11 most abundant corals in Florida were used. These include: *Agaricia* spp., *Colpophyllia natans*, *Dichocoenia stokesii*, *Montastraea cavernosa*, *Orbicella faveolata*, *Porites astreoides*, *Porites porites*, *Diploria strigosa*, *Stephanocoenia intersepta*, *Siderastrea radians*, and *Siderastrea siderea*. These species are considered as representative of the whole coral community because they comprise >85% of all stony corals surveyed, are found throughout the study domain, and include branching, fast growing taxa (*P. porites*), slow-growing boulder taxa (*Colpophyllia*), massive reef-builders (*Montastraea*, *Orbicella*), as well as species commonly considered "weedy" or opportunistic (*Porites* and *Siderastrea*). PRM for the AGRRA data were calculated for each site using all colonies of the same 11 coral species selected for Florida, and averaged for each of the 41 surveys included here (each AGRRA survey contains multiple sites, ranging from 2 to 153).

The estimation of PRM at the species level requires taxonomic expertise and adequate training to estimate accurately the percentage of the colony surface area occupied by recent mortality. In cases where such resolution is not required or extensive training not available, surveyors can assess instead the prevalence of recent mortality (i.e., the percentage of colonies within a species, reef, or region with any level of recent mortality) simply as a binary metric (i.e., presence–absence). We explore the usefulness of recent-mortality prevalence as a coarse-level indicator of reef status by examining the same data used to establish PRM benchmarks (i.e., AGRRA, FRRP).

3. Results

3.1. Background levels of PRM (excluding the impacts of the 2010 cold snap)

A total of 53,511 colonies from the 11 coral species selected were measured within 1398 reef sites during summer surveys from 2003 to 2011 along the Florida reef tract (Fig. 1S). When data were grouped for all species and sites, mean PRM ranged from 0.41% to 0.64% from 2003 to 2011 (Fig. 2A). For all sites and years combined, PRM ranged from 0.29% to 0.90% for the 11 most abundant and widely distributed species. The two species with highest PRM levels were *S. radians* (0.78%) and *P. porites* (0.90%) (Fig. 2B). When data for each species were analyzed by year, no significant differences in PRM were documented for any species (Mann–Whitney test, $p > 0.1$).

PRM showed clear latitudinal trends for data pooled by all sites, species, and years. The highest PRM levels documented were in the northernmost counties (i.e., Martin and Palm Beach) with PRM levels >1.14%, while the lowest levels were in the Lower Keys region (0.28%) (Fig. 2C). Finally, only minor differences in PRM were found between reef habitats within regions, with fore-reef habitats of the Florida Keys having higher PRM than patch reefs (0.50% vs. 0.36%), and inner reefs in Broward County having higher PRM than outer reefs (1.11% vs. 0.90%).

PRM did not show any clear relationship to the magnitude of the warm-water anomalies recorded in Florida at the highest level of aggregation (i.e., all colonies and all sites grouped by year). Two years, 2005 and 2007, were classified as "high bleaching" by NOAA's Coral Bleaching Program (http://isurus.mote.org). While bleaching prevalence (proportion of colonies showing signs of bleaching) was high in Florida in 2005 (19% of all colonies of the 11 species selected exhibited signs of bleaching), the lowest PRM values of any summer survey were recorded during that same year (0.41%; Fig. 2A). PRM values in 2007 were elevated (0.57%) compared to the overall mean (0.49%, all years combined), but the highest PRM values were recorded in 2006 (0.64%), when no significant bleaching was predicted or recorded.

In Florida, no significant relationship was found between PRM and bleaching prevalence (correlation analysis, $p > 0.1$) when data were grouped for all years and habitats. However, when the data were analyzed at a higher resolution, sites that experienced bleaching had significantly higher levels of PRM (0.62%) than those sites not experiencing bleaching (0.45%) (t-test, $p < 0.05$). Bleaching prevalence was positively correlated with PRM at the site level (generalized linear regression, $p < 0.05$). Colonies that exhibited

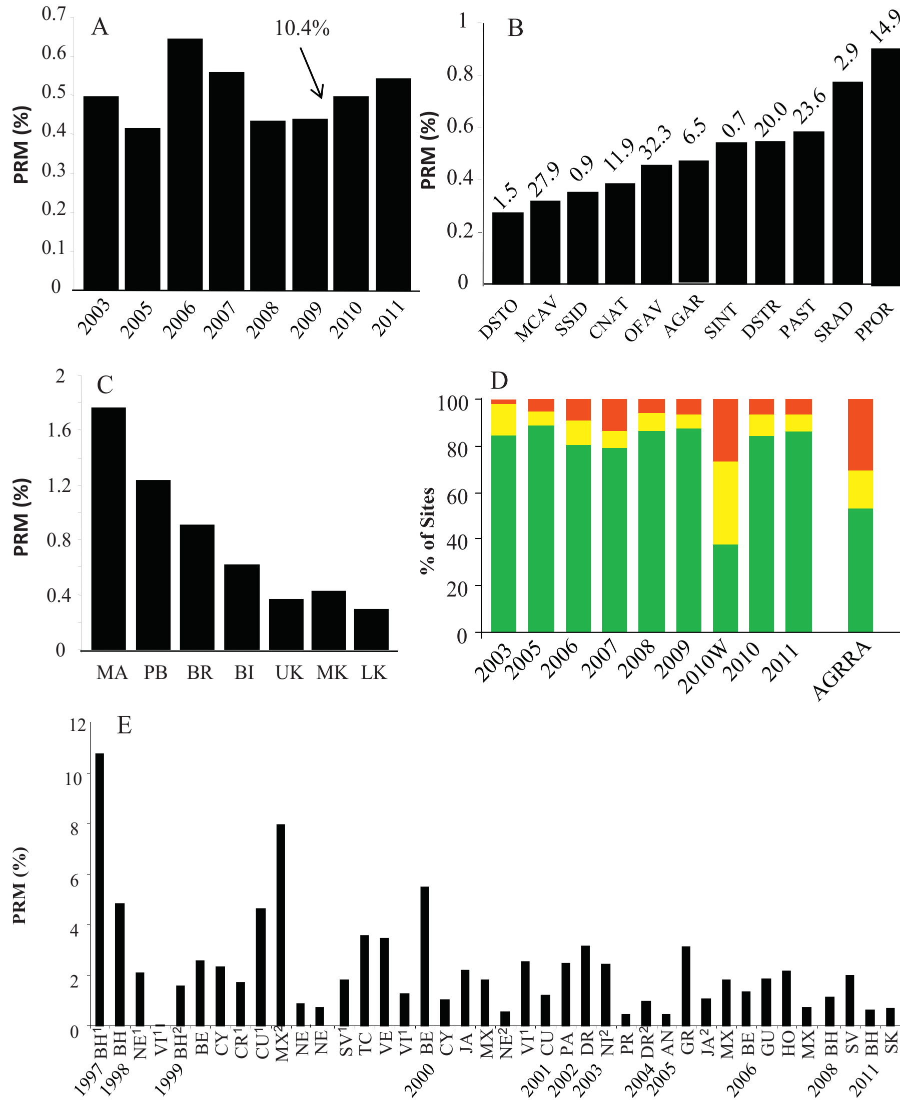

Fig. 2. (A) Percent recent mortality (PRM) for stony corals grouped by year for summers 2003–2011 in the Florida reef tract. The arrow shows the timing of the January 2010 cold-water event (PRM = 10.4%). (B) PRM by species (all years and habitats combined) from summer surveys. The numbers above each bar are the PRM values recorded for each species during the 2010 cold-water event. (C) PRM values for the different regions along the Florida reef tract (all species and years combined, only summer surveys included). MA = Martin County, PB = Palm Beach County, BR = Broward County, BI = Biscayne region (Miami-Dade County), UK = Upper Florida Keys, MK = Middle Florida Keys, LK = Lower Florida Keys. (D) Percent of reef sites that exhibited different levels of PRM during summers and the 2010 cold water anomaly (2010W), and in the Caribbean (AGRRA, all sites and surveys combined). White (Green in the web version) = <1.0% PRM, Grey (Yellow in the web version) = 1–2% PRM, Black (Red in the web version) = >2% PRM. (E) PRM from Caribbean countries sampled using the AGRRA protocol from 1997 to 2011. BH = Bahamas, NE = Netherland Antilles, VI = US Virgin Islands, BE = Belize, CY = Cayman Islands, CR = Costa Rica, CU = Cuba, MX = Mexico, GU = Guatemala, HO = Honduras, SV = St. Vincent, GR = Grenada, TC = Turks and Caicos, VE = Venezuela, JA = Jamaica, PA = Panama, DR = Dominican Republic, NI = Nicaragua, PR = Puerto Rico, AN = Antigua, SK = St Kitts. PRM for the AGRRA data were calculated for each site using all colonies of the same 11 coral species selected for Florida, and averaged for each survey. Each AGRRA survey contains multiple sites, ranging from 2 to 153. AGRRA data included here were provided by K. Marks. AGRRA surveys with an "1" included coral colonies ≥25 cm, surveys with a "2" included coral colonies ≥10 cm. All other surveys included colonies ≥4 cm.

bleaching had significantly higher levels of PRM (1.10%) compared to those without bleaching (0.42%) (t-test, $p < 0.05$).

3.2. PRM under disturbance conditions (impacts of the 2010 cold snap)

PRM remained generally <1% at the majority of sites even under elevated bleaching prevalence (2005, 2007). On the other hand, the 2010 cold-water event (January–February 2010) provided an extreme test of impacts for the proposed stress indicator. During this event, described in detail by Lirman et al. (2011), Kemp et al. (2011), and Colella et al. (2012), sea temperatures reached lethal levels (<16 °C) for periods of tens to hundreds of hours, causing significant stress to the Florida reef tract.

A total of 3470 colonies were surveyed within 76 reef sites during winter 2010 along the Florida reef tract (Fig. 2S). PRM levels during and shortly (<4 weeks) after the extreme event (10.4%) were >20 times higher than the average PRM recorded during all summer surveys conducted between 2003 and 2011 (0.49%) (Fig. 2A). PRM was >1% at less than 20% of sites surveyed during the summers, but PRM exceeded 1% at 62.5% of sites during the cold snap (Fig. 2D). While none of the 11 species examined exceeded, on average, 1% PRM during summer surveys, during the cold-water event 9 of the 11 species had PRM levels well above 1%. Average PRM exceeded 20% for four species, *D. strigosa*, *P. astreoides*, *M. cavernosa*, and *O. faveolata* during this event. All 11 species showed significant increases in PRM between the summer surveys (all summers combined) and those recorded during the cold-water event ($p < 0.05$ for all comparisons) (Fig. 2B).

PRM correlated with spatial low-temperature patterns, with shallow inshore patch reef habitats exhibiting PRM levels > 50 times higher than deeper fore-reef habitats in the same region (12.5% for patch reefs compared to 0.25% for fore-reefs). These habitats of the Florida Keys, especially those located in the Lower and Middle Keys, had the lowest recorded temperatures in the region due to their shallow nature and connections to lagoonal habitats (Lirman et al., 2011).

3.3. AGRRA data

The AGRRA data considered here included >47,000 colonies surveyed from 1179 sites from 21 Caribbean countries or territories from 1997 to 2011. PRM for all surveys combined was 2.2% (±2.0), with highest levels recorded in the Bahamas in 1997 (10.7%) and 1998 (4.8%), Mexico in 1999 (7.9%), and Belize in 2000 (5.5%) (Fig. 2E). For those countries where surveys were done in multiple years (Bahamas in 1997, 1998, 1999, 2008, and 2011; Mexico in 1999, 2000, 2005, and 2006), PRM decreased over time, with highest levels observed during or shortly after the 1997–1998 mass bleaching event (Wilkinson, 2000) and Hurricane Mitch (Steneck and Lang, 2003) and lowest levels in the most recent surveys. Of the 41 AGRRA surveys included in this study, only five had mean PRM levels lower than the mean PRM values recorded during the summers in Florida between 2003 and 2011. Seventy-eight percent of AGRRA surveys (32 out of 41) had PRM values >1%. Only one AGRRA survey (Bahamas in 1997, 10.7%) exceeded the PRM value recorded in Florida during the 2010 cold-water event (10.4%). Lastly, PRM was >1% at 46% of reef sites surveyed by the AGRRA program from 1997 to 2011, compared to no more than 21% of reef sites in Florida in background stress years and 62.5% of reef sites during the cold snap (Fig. 2D).

3.4. Prevalence of recent mortality

The prevalence of recent mortality (i.e., percentage of colonies with any level of recent mortality) remained <5% during the 2003–2011 summers in the Florida reef tract when all colonies from the 11 species selected were evaluated (Fig. 3A). Prevalence of recent mortality was 19.9% during the 2010 cold-water anomaly and 14.1% for all the AGRRA surveys combined. Prevalence was <5% for 9 out of the 11 species assessed in Florida during the summer surveys, with only *O. faveolata* (6.4%) and *P. porites* (7.0) exceeding this benchmark. Prevalence values increased 200–1700% during the 2010 cold-water event (Fig. 3B).

The prevalence of partial mortality was consistently higher in the AGRRA surveys than in Florida. In contrast with the Florida summer surveys, only two AGRRA surveys (US Virgin Islands in 1998 and the Bahamas in 2011) had prevalence values <5% (Fig. 3C). Moreover, the percentage of sites with >10% of colonies showing signs of partial mortality in the AGRRA surveys (70% of sites) far exceeded the percentage of sites with >10% of colonies showing signs of partial mortality during the 2010 cold-snap in Florida (48% of sites) (Fig. 3D). Finally, in Florida, 48% of sites had no colonies with recent mortality (i.e., zero prevalence) during all the summer surveys combined, compared to 41% of sites without partial mortality during the 2010 cold-water event, and 20% of sites without partial mortality in the AGRRA surveys.

4. Discussion

Establishing thresholds and benchmarks for indicators requires extensive data collected under both unperturbed and stressful conditions. The reef monitoring data collected in Florida since 2003 provided a unique opportunity to test the application of a coral reef stress metric. Here, we propose percent recent mortality (PRM) and prevalence of partial mortality of stony corals as a potential metric of coral species and coral community status and a reliable indicator of recent stress that fulfill the criteria outlined by Nuttle et al. (2011) for selection of ecological indicators for south Florida as part of the MARES project (Table 1S).

Recent mortality is an early indicator of unfavorable and stressful environmental conditions on reefs. While corals are expected to exhibit background levels of partial mortality due to low-level, chronic disturbance, high PRM levels or high prevalence of partial mortality are indicative of conditions where growth and regeneration rates are not able to keep up with mortality. In Florida, we documented differences in PRM and prevalence among species and habitats, but these differences were relatively small within and among years when no major disturbances were recorded. Low variability among years in the absence of a major disturbance is considered a desirable attribute for a robust indicator (Fisher et al., 2008). When a metric varies widely in the absence of significant stress, the detection power for disturbance events is greatly diminished (Cooper et al., 2009; Bradley et al., 2010).

Supported by the analysis of colony-based data from >50,000 colonies from 11 stony coral species and nearly 1400 sites, we propose <1.0% PRM and a prevalence of partial mortality of <5% of colonies as representative of pre-disturbance background conditions for the Florida reef tract. PRM levels exceeding 1.0% and prevalence levels exceeding 5% can be used as early warning indicators of degrading conditions. PRM values that exceed 2.0% are indicative of increasing stress levels. Finally, PRM values considerably higher than 2.0% should be considered to reflect significant stressful conditions to coral communities. These could also be interpreted as likely warning signals of potential major coral mortality as evidenced by average PRM levels of >10% and prevalence levels of nearly 20% as a consequence of the 2010 cold-water event (Lirman et al., 2011; Kemp et al., 2011; Colella et al., 2012).

While these thresholds are proposed for the entire Florida reef tract, when monitoring data are collected following a robust probability-based sampling design that accounts for habitat-specific characteristics of both disturbances and response, habitat or species-specific thresholds and benchmarks can be established with increased levels of precision and lower detection levels (Bradley et al., 2010; Smith et al., 2011a). For example, while <1% PRM would be an indicator of favorable pre-disturbance conditions for most of Florida, PRM levels were commonly >1% in both Palm Beach and Martin Counties. Thus, for these two northern counties (marginal reef environments due to extreme temperature fluctuations) the benchmark PRM level may need to be adjusted to <2%. The same applies to species-specific benchmarks if susceptible species have different thresholds than more resistant taxa as was the case for *O. faveolata* and *P. porites* that showed levels of recent mortality prevalence that exceeded the 5% benchmark during background years.

PRM values from coral reefs of the Florida reef tract compared favorably with those recorded in the Caribbean and the Mesoamerican reef region, where a benchmark of 2% PRM was proposed for pre-disturbance conditions (Kramer, 2003; McField and Kramer, 2007). Values of PRM above this benchmark in the AGRRA database were directly related to major acute disturbances like disease outbreaks, temperature anomalies, and hurricanes. During background years, corals of the Florida reef tract exhibited PRM values well below the regional benchmark, further suggesting the need to develop habitat and region-specific benchmarks. Similarly, the prevalence of recent mortality did not exceed 5% during any of the summer surveys from 2003 to 2011. In contrast, only two AGRRA surveys (US Virgin Islands in 1998 and the Bahamas in 2011) had prevalence values <5%, and 28 out of 40 surveys exceeded 10% prevalence. Finally, while nearly 20% of colonies exhibited partial mortality in Florida during the 2010 cold-water event, this extreme

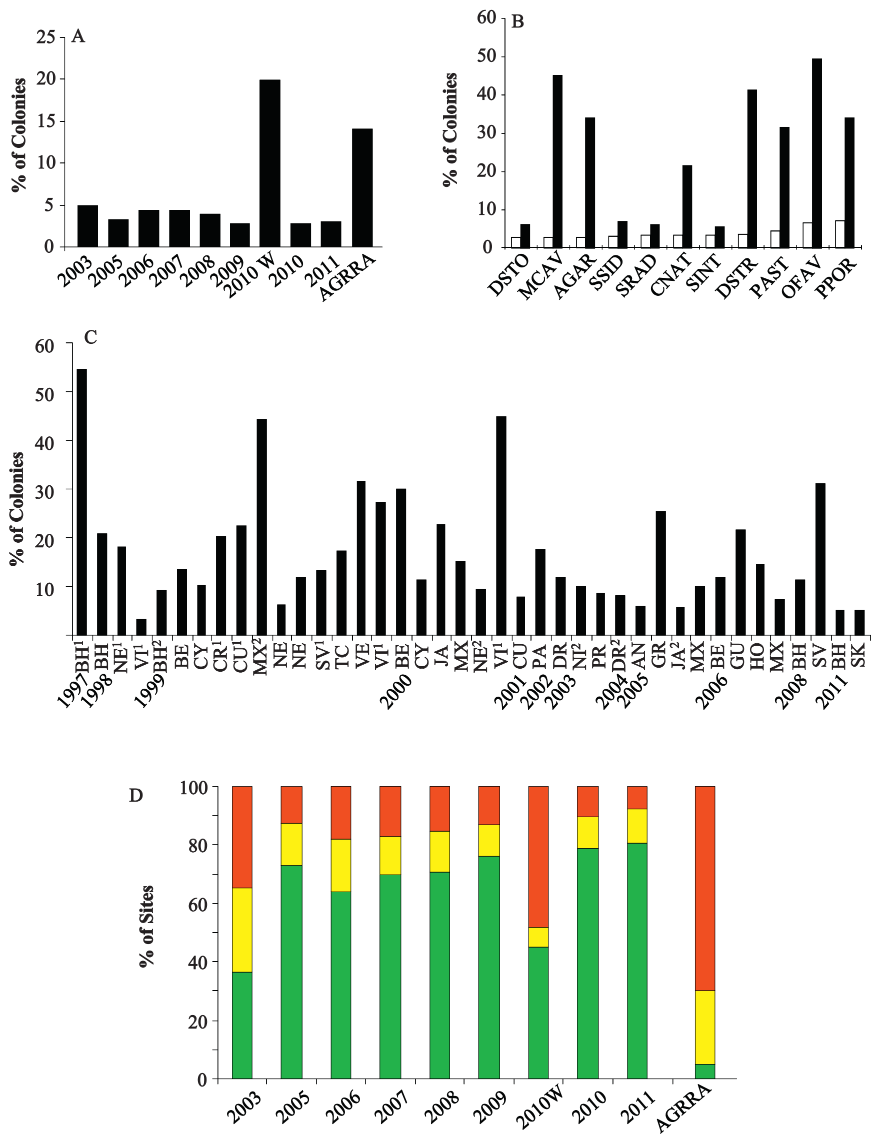

Fig. 3. (A) Prevalence (percentage of colonies with any level of recent mortality) for stony corals grouped by year for summers 2003–2011 in the Florida reef tract and the AGRRA region. (B) Prevalence of partial mortality by species (all years and habitats combined) from the summer surveys (white bars) and the 2010 cold-water event (black bars). (C) Prevalence of partial mortality for surveys conducted in the Caribbean and Mesoamerican regions by the AGRRA Program. The site codes appear in the legend for Fig. 2. (D) Percentage of sites that exhibited different levels of prevalence of recent mortality during summers and the 2010 cold water anomaly (2010W) in Florida, and in the Caribbean and Mesoamerican regions (AGRRA, all sites and surveys combined). White (Green in web version) = <5.0% prevalence, Grey (Yellow in web version) = 5–10% prevalence, Black (Red in web version) = >10% prevalence.

level was exceeded at 13 of 40 sites in the Caribbean from 1997 to 2011. These findings highlight the favorable status of corals of the Florida reef tract and support the need to establish higher benchmarks levels for PRM (2–4%) and prevalence of recent mortality (10–20%) for the Caribbean and Mesoamerican regions. Specific benchmarks for sites within these regions can only be established after each site has been surveyed under background and disturbance conditions as in the Florida reef tract.

Because recent mortality is collected at the colony level, different sites can exhibit different levels of PRM simply based on differences in community composition. For example, sites with a high abundance of species susceptible to stress would tend to have higher levels of PRM for the same level of a physical stress (e.g., temperature anomalies) as compared to sites dominated by highly resistant species. The disproportionate contribution of species with distinct morphologies (e.g., branching vs. mounding), growth patterns (e.g., fast vs. slow), and resistance-to-stress levels (e.g., susceptible vs. resistant) is a problematic attribute of community-level ecological indicators like coral cover. When one species' response overwhelms the level of a given indicator and that particular species is unevenly distributed among sites, comparisons among sites lose power and validity. The selection of PRM as an indicator of status on coral reefs overcomes this limitation by providing a colony-based metric. Thus, comparisons among sites can be made based on the PRM of targeted coral species or groups of species that are abundant on both sites of interest. Single-species metrics can be further aggregated at the community level by concentrating on a number of abundant species that are shared by all sites of interest.

4.1. Caveats and limitations

PRM is a suitable indicator of short-term environmental stress that is based on the proportion of a colony having experienced recent tissue mortality. It is, however, not a cumulative indicator of stress, which precludes its use for the documentation of long-term trends in coral condition. If environmental or biological conditions are adequate over the weeks to months preceding a particular survey, PRM will report a favorable status even if major tissue losses took place at a site in the more distant past. Thus, PRM only documents the status of the tissue present shortly prior to the survey, ignoring previous losses. This was evidenced in the Florida surveys conducted in the summer of 2010 (6–8 months after the cold snap) when PRM returned to pre-disturbance levels even when a significant amount of tissue had been lost due to the cold-water event (Colella et al., 2012). Similarly, diseases or space competitors that kill coral tissue very slowly may progress without leaving a PRM signal. With the loss of tissue, the exposed skeleton is eroded or overgrown by algae or sponges and thus is not "available" for recent mortality to take place. Thus, a coral reef community with 50% coral cover may have the same level of PRM as a community with only 5% coral cover if recent conditions are equally favorable at both sites. This shortcoming of PRM as a long-term, cumulative indicator of coral reef status highlights the need to include multiple metrics in comprehensive monitoring programs. In Florida, long-term patterns of decline in coral cover have been documented effectively using annual surveys of permanent transects (Porter et al., 2002; Colella et al., 2012) and remote sensing tools (Palandro et al., 2008). In addition, demographic parameters (e.g., coral abundance, size, recruitment, disease prevalence) are commonly measured to supplement PRM and coral cover as additional metrics of coral reef status and trends in Florida (Fisher et al., 2007; Lirman and Fong, 2007; Miller et al., 2013). As PRM may decline with declining coral cover, the proposed benchmarks may need to be further adjusted based on the information provided by other metrics like trends in coral cover. For example, while a 1% benchmark may be adequate for present conditions, further declines in coral cover may prompt the adoption of a lower PRM benchmark as a trigger for management actions. Further adjustments may be needed if average colony sizes change dramatically as PRM can be related to colony size (Lirman et al., 2011).

While a highly desirable attribute of any robust indicator is to provide a diagnostic, causal link to stress factors, direct linkages between stress and response in complex ecosystems like coral reefs rarely exist. Recent mortality in corals is a general response to stress, and it will be difficult to attribute the cause of tissue mortality to a particular stressor unless the sampling intensity and frequency is extremely high or the disturbance event is clearly demarcated, such as was the 2010 cold-water event, the 1997–1998 bleaching event, and Hurricane Mitch in the Caribbean. Establishing direct cause-and-effect relationships for recent mortality will require new research that integrates field and controlled laboratory studies.

5. Conclusion

Recent mortality can be used as an effective indicator of coral colony, population, and coral reef community status. A benchmark level of <1% PRM and <5% prevalence are proposed here for the Florida reef tract based on surveys of >50,000 coral colonies from 11 coral species during periods of background environmental conditions. Average PRM values >2% and prevalence levels >5% are generally indicative of significantly stressful conditions such as those experienced during severe bleaching, cold-water anomalies, and major hurricanes. Recent mortality provides an early-warning indicator of declining environmental conditions. PRM is influenced directly by rates of tissue mortality and recovery. As such, it is directly related to the function and structure of coral reefs ecosystems that provide essential ecological and economic goods and services to human populations. Finally, the status of this indicator can be easily communicated to stakeholders and can trigger management actions like temporary closures to try to prevent the spread of disease or allow for the recovery after disturbances, or perhaps the establishment of more permanent protection such as MPAs.

Acknowledgments

We are grateful to the large number of dedicated divers that spent long hours underwater measuring corals in Florida and the Caribbean. The Florida Reef Resilience program is led and funded by the Nature Conservancy. The AGRRA program is led by R. Ginsburg, J. Lang, and P. Kramer. We are indebted to the Lirman Lab members, C. Drury, R. Santos, B. Huntington, T. Thyberg, and to the TNC project leaders, J. Byrne, M. Johnson, C. Lustic, and K. Marks. This paper is a result of research under the Marine and Estuarine Goal Setting (MARES) for South Florida Project funded by the National Oceanic and Atmospheric Administration Center for Sponsored Coastal Ocean Research (Coastal Ocean Program), under award NA08OAR4320889 to the University of Miami, NA09NOS4780224 to Nova Southeastern University, NA09NOS4780225 to the University of Massachusetts Amherst, NA09NOS4780226 to the National Audubon Society, NA09NOS4780227 to Florida Gulf Coast University, NA09NOS4780228 to Florida International University, and to the NOAA Atlantic Oceanographic and Meteorological Laboratory. We thank the MARES team, W. Nuttle, P. Fletcher, P. Ortner, and C. Kelble for their leadership and reviews of our paper. This manuscript was greatly improved by the comments of two anonymous reviewers.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.10.021.

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