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Jack Butler
Florida International University

William C. Sharp
Florida Fish and Wildlife Conservation Commission

John H. Hunt
Florida Fish and Wildlife Conservation Commission

Mark J. Butler
Florida International University

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SPECIAL FEATURE:
HONORING CHARLES H. PETERSON, ECOLOGIST

Setting the foundation for renewal: restoring sponge communities aids the ecological recovery of Florida Bay

JACK BUTLER,^{1,†} WILLIAM C. SHARP,² JOHN H. HUNT,² AND MARK J. BUTLER IV¹

¹*Department of Biological Sciences, Institute of Environment, Florida International University, North Miami, Florida 33181 USA*

²*Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 2796 Overseas Hwy, #119, Marathon, Florida 33050 USA*

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Abstract. Coastal ecosystems are constantly buffeted by anthropogenic forces that degrade habitats and alter ecological processes and functions; in turn, this habitat degradation diminishes the ecosystem goods and services on which humans rely. Within the last few decades, the field of restoration ecology has burgeoned into a discipline that marries scientific rigor with functional restoration practice—an idea championed by Pete Peterson and his research. Here, we describe our efforts to restore the hard-bottom sponge communities of Florida Bay, FL (USA)—a once-diverse subtropical lagoon severely degraded by cyanobacteria blooms—and the scientific and practical lessons learned from those efforts. Sponge community restoration yielded insights into basic sponge biology and ecology (e.g., density-dependent growth rates) and hastened the recovery of ecological processes (e.g., rates of sedimentation, structuring of water column characteristics, soundscape productions). Because the results of our initial restoration efforts were promising, our collaboration among academic researchers, natural resource managers, and non-governmental organizations has begun scaling up restoration efforts to re-establish the sponge communities over large areas of degraded hard-bottom to “jump start” the ecological recovery of Florida Bay. Though our efforts show promise for ecological recovery, restoration will require a concerted effort by scientists, resource managers, and citizens to stem the anthropogenic drivers of ecological degradation of this unique South Florida ecosystem.

Key words: ecological recovery; Florida Bay; habitat restoration; Special Feature: Honoring Charles H. Peterson, Ecologist; sponge biology.

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† **E-mail:** jbutler@fiu.edu

INTRODUCTION

Human activities alter and degrade terrestrial, aquatic, and marine habitats (e.g., Colin et al. 2018, Hall-Spencer and Harvey 2019, Palmeirim et al. 2020), but anthropogenically driven habitat degradation disproportionately affects coastal marine ecosystems (Lotze and Milewski 2004). Examples of habitat degradation from iconic

coastal habitats (e.g., mangrove forests [Polidoro et al. 2010, Goldberg et al. 2020], seagrasses [Waycott et al. 2009, Chefaoui et al. 2018], or coral reefs [Jackson et al. 2001, Pratchett et al. 2014]) showcase the pervasive consequences of human actions (e.g., habitat destruction, pollution, resource overexploitation) that alter the structure and function of coastal ecosystems and shift coastal ecosystems from natural to

anthropogenically modified states (Nordhaus et al. 2018).

The effects of degradation and loss of coastal habitats manifest in many ways. For example, the wholesale physical destruction or selective removal of structure-forming species homogenizes habitats and reduces biodiversity (Thrush et al. 2006). Hydrodynamic models show that the loss of salt marsh habitat results in increased storm surge and reduced wave attenuation along coastlines (Wamsley et al. 2009, Temmerman et al. 2012). Landings of recreational and commercial fish species decline in lockstep with the loss of oyster reefs due to overharvesting, disease, and poor water quality (Peterson et al. 2003). These are but a few examples. Recognizing the severity of the problem, the United Nations General Assembly declared 2021–2030 the “UN Decade of Ecosystem Restoration” (<https://www.decadeonrestoration.org>) and the “UN Decade of Ocean Science for Sustainable Development” (<https://www.oceandecade.org>), urging signatory nations to increase ecosystem restoration efforts to stem habitat loss and revitalize degraded habitats upon which humans rely for food security, clean water, and other ecosystem services (Young et al. 2005).

A recent review found that the number of articles detailing restoration efforts in salt marsh, seagrass, and oyster reef habitats (Zhang et al. 2018) has indeed increased rapidly over the last 15 yr reflecting the public will and scientific attention now devoted to coastal habitat reclamation. Yet, as scientists and resource managers design and implement habitat recovery and restoration efforts, they face complex and difficult challenges. Understanding how to best rebuild and maintain ecosystem attributes and functions is typically system-dependent, as are policy and management goals. Pete Peterson recognized and dealt with such challenges in his own work and was committed to the notion that successful ecological restoration must marry scientific rigor with technical restoration practice (e.g., Peterson et al. 2003). To honor his memory and achievements in restoration ecology, we here consider how that same perspective has permeated our own restoration work on sponge-dominated hard-bottom habitat in south Florida.

FLORIDA BAY: A CASE STUDY IN ECOLOGICAL RESTORATION

Florida Bay is a shallow, subtropical coastal lagoon, lying between the southern tip of Florida (USA) and the Florida Keys (Fig. 1). The subtidal coastal environment is typified by a patchwork of seagrass meadows, sandy softbottom, and sponge-dominated hard-bottom dotted by mangrove-fringed islands. The habitats of the estuary are noted for their productivity, biological diversity, and roles as nursery habitats for many marine organisms (Holmquist et al. 1989, Thayer and Chester 1989, Butler et al. 1995, Behringer and Butler 2006, Behringer et al. 2009). Sponges, octocorals, ahermatypic stony corals, and macroalgae all inhabit hard-bottom, but large sponges (e.g., the loggerhead sponge *Spherospongia vesparium* and the vase sponge *Ircinia campana*) create the dominant vertical structure found in these communities (Chiappone and Sullivan 1994, Butler et al. 1995).

These large sponges provide shelter and habitat for myriad fishes and invertebrates, including the economically valuable spiny lobster, *Panulirus argus*. Yet the sponges that dominate hard-bottom animal biomass afford more than biogenic structure; they are prolific biological filters. Peterson et al. (2006) estimated that the sponge community of Florida Bay could filter the water column every three days, making it the intrinsic link between the benthos and water column (Gili and Coma 1998). Furthermore, the microbial communities found within these large sponges exert powerful influence over biogeochemical cycling and water column characteristics (Hoer et al. 2018, 2020, Valentine and Butler 2019). Sponges also harbor soniferous animals whose cacophony of snaps and rumblings produce a distinctive and loud soundscape used by larvae to orient to these sponge-dominated hard-bottom areas (Butler et al. 2016, 2017b).

Unfortunately, over the past three decades, the diverse biotic communities of Florida Bay and the nearshore waters of the Florida Keys have experienced substantial ecological changes. Die-offs of the seagrass, *Thalassia testudinum*, in the late 1980s (Zieman et al. 1999) precipitated expansive cyanobacterial blooms in large portions (>500 km²) of southern Florida Bay (Butler

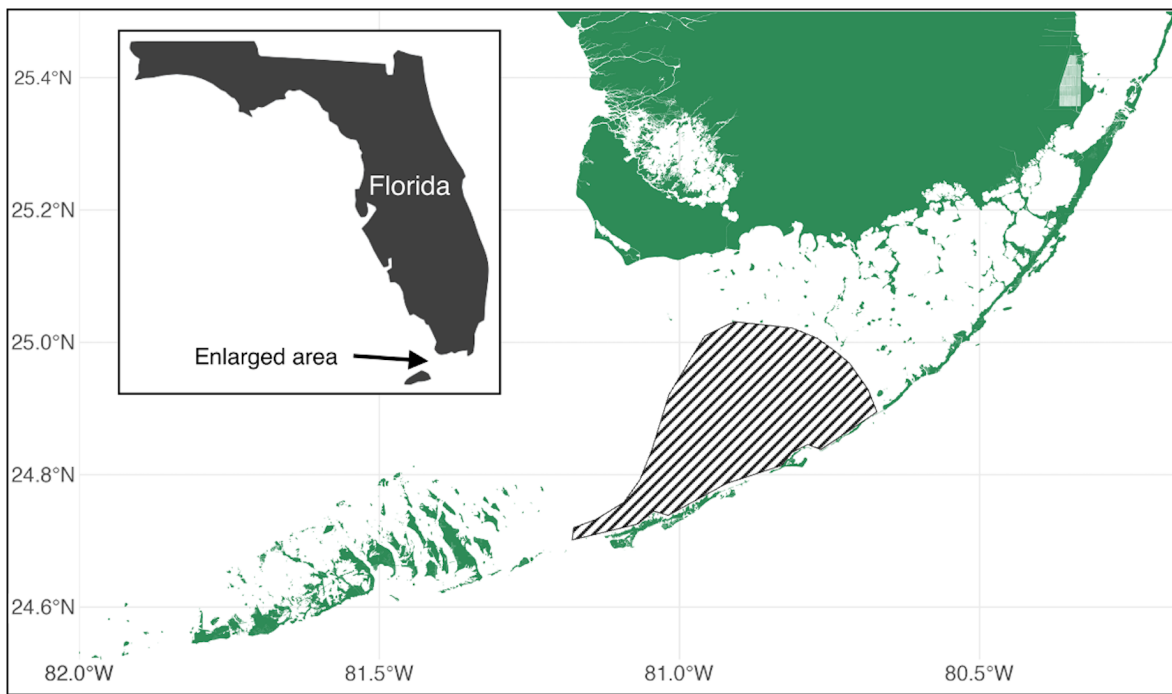


Fig. 1. Map of Florida Bay and the Florida Keys, including the extent of the hard-bottom area degraded by cyanobacteria blooms highlighted by the hashed polygon (adapted from Butler et al. 1995). Inset shows the entire state of Florida.

et al. 1995, Boyer et al. 1999). The first reported cyanobacterial bloom began in November 1991 and lasted until February 1992 and reduced the visibility of the normally clear waters of Florida Bay from ~8 m to less than half a meter (Butler et al. 1995). Sponge communities on hard-bottom areas engulfed in the cyanobacteria blooms suffered widespread mortality, with some species exhibiting >90% mortality (Butler et al. 1995). Subsequent cyanobacteria blooms have occurred sporadically throughout the 1990s and 2000s, hindering natural recovery of sponge communities in these degraded areas (Stevely et al. 2011).

The extensive habitat degradation of Florida Bay demanded a recovery effort, but at the same time offered a unique opportunity to use the “blank slate” of barren habitat to test ecological theory. In this respect, our approach to ecological recovery efforts mirrors that championed by Pete Peterson: that basic science must underpin and accompany environmental restoration if those efforts are to yield satisfactory results. The biology of the target organisms and their functional

role in natural communities should be clear and that knowledge should serve as the foundation for restoration. The latter is best done not only with a plan for post-restoration monitoring of key ecological attributes but also within an experimental framework that yields even more information about the system and the efficacy of restoration. Another similarity in our approach to that of Pete Peterson is the decades-long collaborative nature of our work that has joined university researchers with state resource managers resulting in a larger, more comprehensive, and more practical restoration enterprise.

Our collaboration was cemented following the unique and massive sponge die-off that first swept through hard-bottom communities in Florida Bay in the early 1990s. Although hard-bottom habitat covered an estimated 40% of the seafloor in Florida Bay (Herrnkind et al. 1997, Zieman et al. 1999), those sponge-dominated communities had been little studied especially in comparison to those on nearby coral reefs. Yet, what became clear to us early on is that the

factors controlling the structure of sponge communities in shallow coastal waters (e.g., recruitment limitation, competition for planktonic resources [Valentine 2019], temperature/salinity extremes [Butler et al. 2017]), their contribution to ecosystem processes (benthic–pelagic coupling [Valentine and Butler 2019], soundscapes [Butler et al. 2016], habitat structure [Herrnkind et al. 1997]), and their response to inshore selective pressures (e.g., absence of alleopathy, dependency on microbial symbiosis [Weisz et al. 2007], low species diversity) were quite different from sponge communities on coral reefs. In short, we faced the challenge of restoring a habitat about which little was known.

More than 60 species of sponge are found in the shallow, hard-bottom habitats (<3 m) of Florida Bay and the Florida Keys; many more species occur on the region's coral reefs (Pawlik 2011). Sponges on the hard-bottom communities of Florida Bay dominate the animal biomass in undisturbed areas, averaging over 47,000 sponges/ha with a total mean volume of approximately 17 m³/ha (Table 1; Fig. 2). Those species range in size from diminutive taxa <50 cm³ to the large loggerhead sponge (*S. vesparium*) can reach greater than a meter in diameter. Although large species (i.e., >50 cm diameter) make up only 10% of the total sponge density, they dominate the total sponge community biomass (~60%; Table 1). Our research and restoration efforts have

largely focused on these dominant, large sponge species.

Scientific beginnings

Prior to the first sponge die-offs, we had already begun to appreciate the importance of sponge-dominated hard-bottom as critical nursery habitat for juvenile spiny lobsters (Forcucci et al. 1994, Butler and Herrnkind 1997, Behringer et al. 2009)—the basis for one of the most economically important fisheries in Florida and the Caribbean. That realization laid the foundation for our early inter-agency partnership and studies of demographic bottlenecks to lobster recruitment driven by the abundance of large, shelter-forming sponges (Butler and Herrnkind 1997, Herrnkind et al. 1997, Bertelsen et al. 2009). The relationship between sponge community structure and lobster recruitment continues to be a driving force behind public and agency support for sponge restoration efforts. Sponges themselves support small, but important artisanal sponge fisheries in Florida and the Caribbean serving the cosmetic, medical, and art communities. The effects of this commercial fishery on sponge communities are sustainable at current harvest levels (Cropper and DiResta 1999, Butler et al. 2017) but are themselves devastated by sponge die-offs. Economic concerns associated with sponge die-offs were therefore an important component of public support for sponge restoration.

Sponge biology and restoration implications

Like corals, sponges are clonal animals that reproduce both sexually and asexually through breakage and reattachment of fragments or by budding (Maldono and Uritz 1999). This clonal life history favors the creation of sponge transplants via “cuttings”: transplantable sponge fragments cut from wild or nursery stocks without sacrificing the original animal that can be left to heal and regrow (Stevely and Sweat 1985). Our initial trials revealed that creation of sponge cuttings is best accomplished when water temperatures are low (generally October–May when monthly average water temperatures are below 26°C [NOAA National Centers for Environmental Information–Peterson Key Weather Station]) and healing of cut sponges and attachment to calcium carbonate brick baseplates takes

Table 1. Summary of natural shallow hard-bottom sponge community characteristics in the Florida Keys prior to sponge die-offs.

Species	Mean no./ha	Percentage of total abundance	Percentage of total volume
Loggerhead <i>Spherospongia vesparium</i>	850	1.8	32.8
Brown Branching <i>Ircinia felix</i>	1643	3.4	11.2
Yellow Rope <i>Aplysinia fulva</i>	1340	2.8	8.9
Vase <i>Ircinia campana</i>	681	1.4	5.2
Commercial <i>Hippospongia lachne</i> <i>Spongia barbara</i> <i>Spongia barbara dura</i> <i>Spongia graminea</i>	331	0.7	1.8
Stinker <i>Ircinia strobilina</i>	109	0.2	2.6
All others	42,832	89.7	37.5

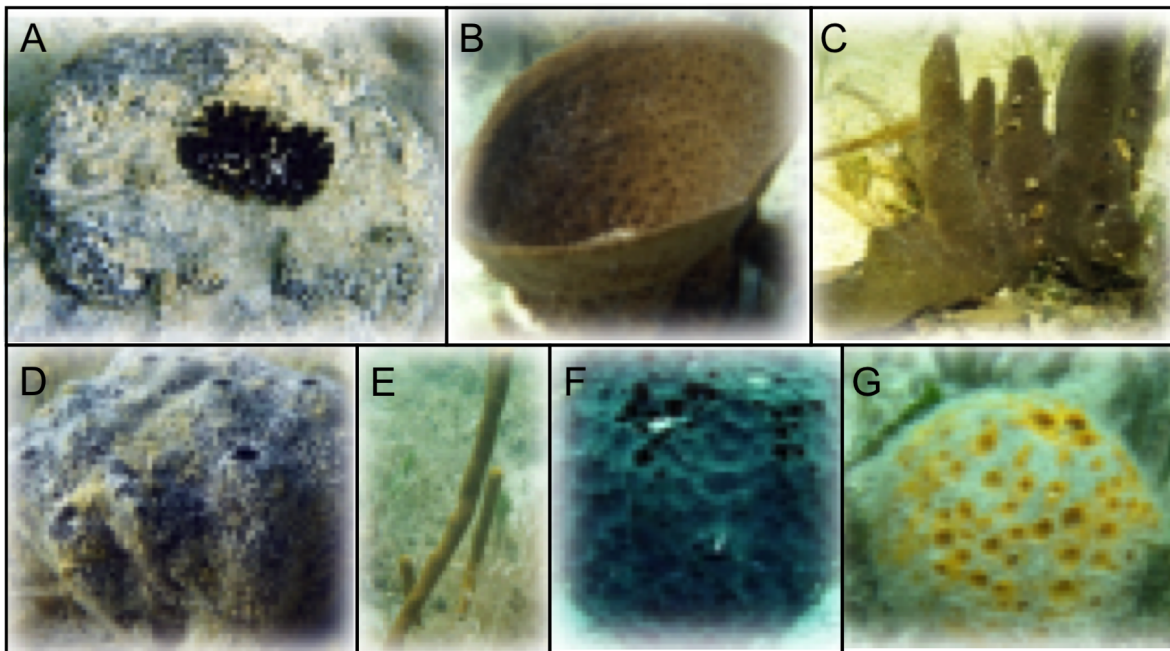


Fig. 2. Representative photographs of common sponge species found in Florida Bay and the Florida Keys. (A) Loggerhead sponge, *Spheciospongia vesparium*; (B) Vase sponge, *Ircinia campana*; (C) Brown branching sponge, *Ircinia felix*; (D) Sheepswool sponge, *Hippospongia lachne*; (E) Yellow rope sponge, *Aplysinia fulva*; (F) Stinker sponge, *Ircinia strobilina*; (G) Golfball sponge, *Cinachyra* sp.

2–3 months depending on the species (Fig. 3), similar to rates of reattachment of detached wild sponges (Butler et al. 2017). Although ideal for restoration, the approach begs a few simple questions that are important to the development of a successful restoration methodology and therefore drove our first set of studies (Table 2). These initial questions were based on well-established evolutionary theory concerning the trade-offs between size/age, growth, and reproduction of animals (Gadgil and Bossert 1970, Kozlowski 1992).

Sponges can be monocious or dieocious, depending on the species. For many species, brooded ciliated larvae are released into the water column in an advanced stage of development, so they are competent to settle within a few hours or days and therefore have low dispersal capabilities (Lindquist et al. 1997, Maldonado 2006). For example, Kaye and Reiswig (1991) found that larvae of a commercially harvested sponge (*Hippospongia lachne*) were competent to settle 1–2 d after release. However, other species such as the Clionoids (of which the dominant

structure-forming on hard-bottom communities the Loggerhead sponge *Spheciospongia vesparium* is a member) are oviparous—that is, these sponges broadcast both sperm and eggs into the water column—and fertilization and larval development occur in the environment (Ereskovsky 2018). Larval duration of Clionaid sponges is estimated to be ~10 d (Mariani et al. 2000). As a consequence of their short planktonic larval duration, sponge populations tend to show strong genetic structure over distances as short as tens of kilometers (Griffiths et al. 2020a, b) although there is also evidence of periodic longer dispersal events (DeBiasse et al. 2010).

An unusual aspect of sponge biology that should be considered during restoration planning is the presence of sponge gemmules. These gemmules are persistent sponge tissues that remain invisible under the substrate and undergo diapause until environmental conditions improve (Loomis 2010). This type of recovery is easily distinguished from larval recruitment because the regrowth of tissue, albeit slow, stems from the original sponge footprint creating a large halo of



Fig. 3. Photograph of a researcher placing recently created sponge cuttings in species-specific arrays on the seafloor to begin the healing and attachment process (2–3 months) before eventual transplantation. Cuttings are attached to cement bricks via cable ties; some species first shrink in size before attachment (e.g., *Spheciospongia vesparium*) so are also temporarily enclosed in mesh to retain them on the brick baseplate.

Table 2. Summary of the scientific and practical questions addressed in our sponge restoration studies and their effects on population and ecosystem responses that were measured.

Question	Sponge population response	Ecosystem response	Citation
Size of transplant?	Mortality; growth; reproduction	Habitat provisioning	This paper
Timing of transplantation?	Mortality; growth		Donahue (2008); Butler and Valentine (<i>unpublished data</i>)
Transplant species?	Mortality; growth; reproduction	Filtration; soundscape; benthic scouring	This paper; Valentine and Butler (2019); Butler et al. (2016, 2017); Donahue (2008)
Transplant biomass?	Growth	Filtration; habitat provisioning	This paper; Valentine and Butler (2019)
Transplant diversity?		Filtration; soundscape	Butler and Valentine (<i>unpublished data</i>); Butler et al. (2016)

tissue rather than a single point that is characteristic of larval recruitment. The activation of this natural method of sponge recovery after mass sponge die-offs is not uniform among sites or species but is an unexplored contributor to the recovery process.

These aspects of sponge biology have important implications for the restoration of sponge communities over large scales. First, it means that genets from which transplants are derived should come from nearby populations so as to not disrupt the natural, patchy population structure of sponge communities. The limited dispersal of sponge larvae and slow regrowth of gemmules also suggest that natural recovery of sponge communities will be slow, requiring decades depending on the size of the disturbance and sponge species (Stevley et al. 2011). Hence, it was likely that the >500 km² region of Florida Bay absent of sponges following recent die-offs would only repopulate gradually from the edges via larval recruitment or asexual fragmentation unless modified by restoration. Our initial restoration work was predicated on

this hypothesis. Therefore, rather than focusing our efforts on a few, large restoration areas, we instead established over 30 smaller restoration sites (25 m × 25 m in area) throughout the region so as to “jump start” larval recruitment from numerous locations within the zone vacant of sponges. This approach was subsequently verified by monitoring of sponge recruits in restoration areas and unrestored negative control areas (Fig. 4).

Survival of sponge transplants on these initial hard-bottom restoration sites varied among species, with high survival of six of the nine species that we attempted to transplant: Three species were poorly suited to transplantation (*Tedania ignis*, *Aplysinia fulva*, *Cinachyrella alloclada*). We also hypothesized that transplantation of smaller sponge cuttings (~500–1000 cm³) as opposed to entire sponges (1500–6500 cm³) would be logistically easier and result in more out-plantings. Within a species, whole sponge transplants and cuttings generally survive equally well (Fig. 5), ranging from 60% to 88% survival two years

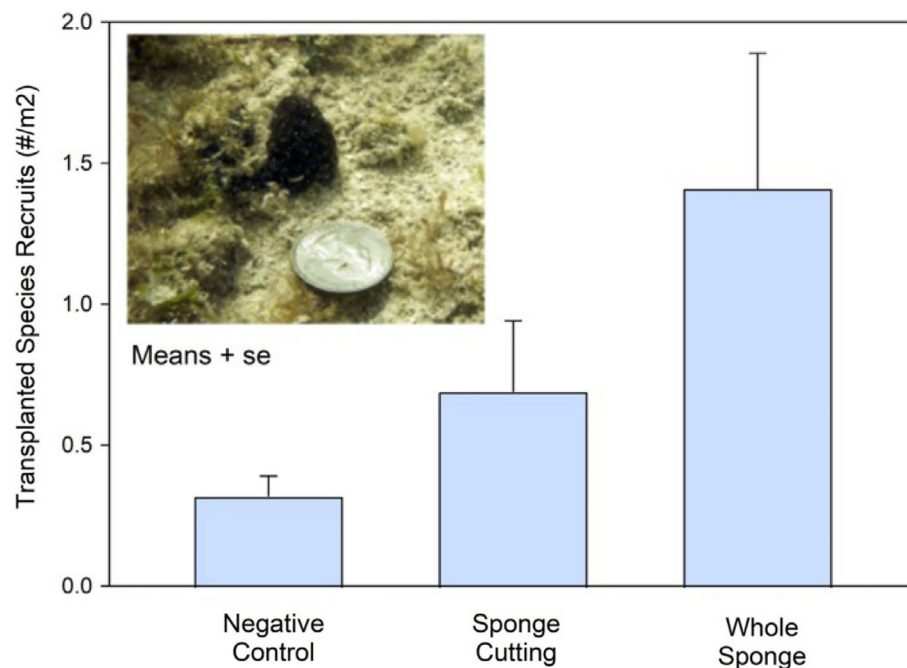


Fig. 4. Comparison of sponge recruitment (number of recruits/m²) of transplanted sponge species two years after transplantation on three types of restoration sites: unmanipulated negative control sites, sites on which sponge cuttings were transplanted, and sites on which whole sponges were transplanted. *N* = 4 experimental sites/treatment. (Inset) Photograph of a sponge recruit (*Spongia graminea*) on one of the sites.

after transplantation. However, based on possible growth/reproductive trade-offs, we predicted that the size of sponge transplants would affect subsequent recruitment with smaller transplants directing more energy into growth rather than

reproduction. Those predictions were generally confirmed, although results were species-dependent. To estimate growth of sponges, we measured their diameter and height and used these measures to calculate the volume of

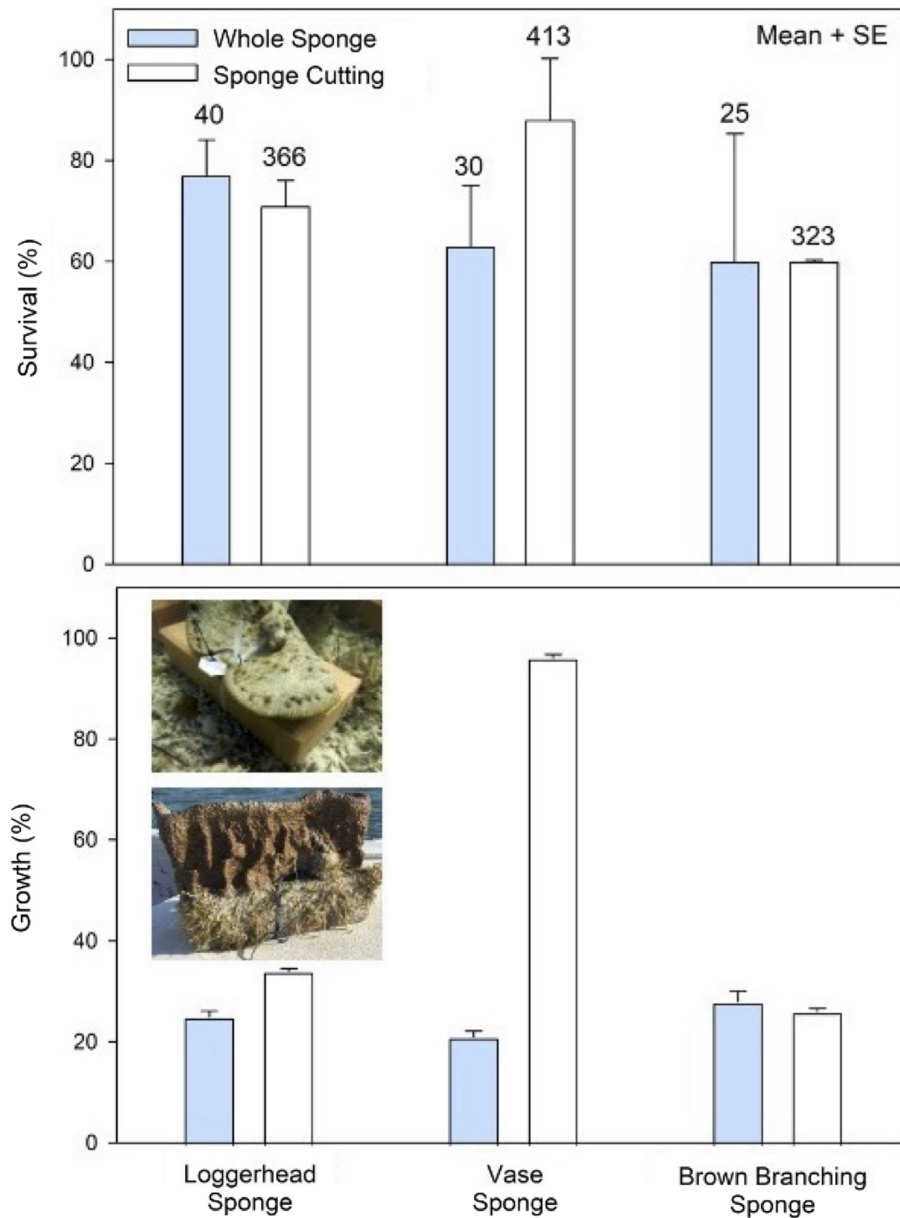


Fig. 5. Survival (top panel) and growth (bottom panel) of whole sponges and sponge cuttings of three species (Loggerhead sponge, *Spherospongia vesparium*; Vase sponge, *Ircinia campana*; Brown Branching sponge, *Ircinia felix*) two years after transplantation onto sponge restoration sites. Number of sponges is listed above histograms. (Insets) Photographs of an *I. campana* cutting when transplanted (top) and two years later (bottom) showing representative changes in size.

cylinder as a proxy for sponge biomass. Differences in growth between cuttings and whole sponge transplants over a 2-yr period ranged from negligible to cuttings surpassing the growth of whole sponges by more than a three-fold margin (Fig. 5). Just the opposite was true for reproduction during that same timeframe. New sponge recruits on restoration sites provisioned with whole sponges (representing ~10-fold increase in biomass over sponge cuttings) were two times higher than on restoration sites populated solely with cuttings, which in turn were two times higher than in unrestored control areas (Fig. 4). However, in a separate study in which we varied the biomass of sponge cuttings on restoration sites, we discovered that a five-fold increase in the biomass of sponge cuttings (achieved by increasing the number of cuttings placed on a site) only resulted in a 12% increase in the recruitment of the targeted (i.e., transplanted) sponge species. These results are informative for development of a strategy and standard methodology for restoration and indicate that levels of recruitment are not only a function of biomass but of the size/age status of individual sponges.

Other studies that we conducted revealed the surprising result that picoplankton and DOC concentrations in the water column (i.e., sponge “food”) are inversely proportional to the natural background density of sponges. Moreover, sponge cuttings of three species (*I. campana*, *S. barbara*, *S. graminea*) and of the same genotypes transplanted into hard-bottom areas that differed in natural sponge abundances grew at rates inversely proportional to local sponge density (Valentine 2019). This is a clear indication that sponges in shallow, hard-bottom habitats compete for and deplete planktonic food resources. Although a remarkable ecological discovery that runs counter to the previous notion that sponges are not food limited (based mostly on studies of reef sponges [e.g., Pawlik et al. 2015]), such results again help steer restoration design (see the *Scaling up sponge restoration* section below).

These experimental findings on sponge biology inform us how to improve the success of large-scale sponge restoration efforts:

1. Production of sponge cuttings is a logistically superior methodology that results in

numerous outplants with no trade-off in survival, enhanced post-transplant growth, and an acceptable delay in the production of new recruits as compared to transplantation of whole sponges.

2. Many but not all species are amenable to transplantation based on cuttings.
3. Sponge densities in nurseries must be kept below median natural densities to ensure their rapid growth.

Sponge biology and restoration effects on ecosystem processes

Sponges can have powerful effects on ecosystem processes in shallow tropical marine ecosystems. They drive benthic–pelagic coupling by filtering dissolved and particulate organic matter from the water column (Reiswig 1974, Gili and Coma 1998, Petersen et al. 2006, Jiménez and Ribes 2007, Riisgård and Larsen 2010, de Goeij et al. 2013), alter water chemistry in association with their symbiotic microorganisms (Weisz et al. 2007, Webster and Taylor 2012, Fiore et al. 2013, Archer et al. 2017), increase habitat structural complexity (Herrnkind et al. 1997, Henkel and Pawlik 2005, McMurray et al. 2008), and harbor soniferous animals that contribute to underwater soundscapes (Butler et al. 2016, 2017a, b). Moreover, most of these effects vary among sponge species and species combinations highlighting the importance of biodiversity for sponge restoration efforts.

Following the initial sponge die-offs in the early 1990s, we observed the rapid sedimentation of hard-bottom areas when in proximity to seagrass meadows, likely because seagrasses attenuate water currents and allow sediment to settle out of the water column (M. Butler, *personal observation*). Within a few years, those patches of hard-bottom disappeared, filled in by sediments and seagrass. We hypothesized that the former presence of large sponges had previously increased local turbulence and scouring, reducing sedimentation and thus contributing to the maintenance of hard-bottom habitat. Our subsequent experiments on two large sponge species (*S. vesparium*, *I. campana*) and their effects on local rates of scouring in comparison to rocks of a similar size and open areas confirmed our hypothesis with the added caveat that effects

varied among species and current velocity (Donahue 2008). Hence, restoration of sponge communities where sedimentation rates are high is likely to benefit from a mixed approach to sponge transplantation that includes whole sponge transplants.

Studies conducted in mesocosms have demonstrated that high sponge biomass, especially where current velocities are lower, greatly reduce chlorophyll-*a*, ammonium, and dissolved organic carbon in while increasing concentrations of nitrites, nitrates, and phosphates (Valentine 2019, Valentine and Butler 2019). But sponge species identity had idiosyncratic effects on water-column constituents (i.e., different sponge species affected water chemistry differently), indicating the importance of sponge biomass and biodiversity, as well as species-specific filtration on nutrient cycling. These findings highlight how changes in the abundance and diversity of sponges in coastal ecosystems can drastically alter water-column properties, thus emphasizing the importance of sponge biodiversity in the design of sponge restoration projects.

It is not surprising that large sponges (e.g., *S. vesparium*, *I. campana*, *I. strobilina*) and those with complex architectures (e.g., *I. felix*, *A. varians*) provide refuge to juvenile fishes and invertebrates as reflected at experimental restoration sites that included these shelter-provisioning sponge species (Fig. 6). Those data were based on diver surveys (four 25 m long \times 2 m wide transects on each site) conducted on negative control sites (i.e., unmanipulated sites subject to sponge die-offs), sites restored via small sponge “cutting” transplants, and sites restored via transplantation of whole sponges ($N = 4$ of each site type). These results emphasize the need to include structure-providing species in restoration efforts so as to promote recruitment of fish and invertebrates, including commercially important taxa such as the Caribbean spiny lobster (*Panulirus argus*). Some sponge species also shelter infaunal animal taxa (e.g., snapping shrimp, polychaetes, and ophiroids) that dwell within the complex network of internal canals inside sponges. Indeed, colonies of the only known marine eusocial animals are inhabitants of sponges such as *S. vesparium* (Duffy et al. 2000). This feature of sponge ecology is also species-dependent and largely a function of canal diameter (Butler et al. 2017), again underscoring

consideration of sponge diversity in restoration projects. Some of the animal species associated with sponges—whether epifaunal or infaunal—are also soniferous.

The sponge mortality caused by the widespread cyanobacteria blooms and the concomitant loss of shelter and habitat that sponges provide diminished the hard-bottom soundscape. The diverse assemblage of fishes and invertebrates that inhabited the sponge communities of Florida Bay had once produced a rich, complex acoustic environment, characterized by the unending snap, crackle, and pop of snapping shrimp and the “hoots” of toadfish. Conversely, acoustic recordings of hard-bottom areas denuded of sponges revealed a much quieter soundscape, lacking the acoustic features prominent in the soundscape of healthy hard-bottom areas (Fig. 7) (Butler et al. 2016). The larvae and juveniles of many marine organisms use underwater soundscapes as a cue to find appropriate habitat, and the loss of the rich sonic environment once present on these hard-bottom communities also lead to diminished recruitment of larval fishes and invertebrates (Butler 2016, Anderson et al. 2021).

The most conspicuous acoustic features absent from the degraded soundscape are snapping shrimp snaps, and because many species of snapping shrimp are obligate sponge-dwellers, we hypothesized that the loss of large sponges with intricate internal canals also meant the loss of snapping shrimp populations in these hard-bottom areas. Using acoustic modeling and distance sampling techniques, we estimated that snapping shrimp populations in degraded hard-bottom areas were one to two orders of magnitude lower density and abundance than in healthy hard-bottom areas (Butler et al. 2017). Acoustic monitoring of our early sponge community restoration sites revealed that our efforts aided the recovery of the hard-bottom soundscape (Fig. 7). Three years after establishment, the soundscapes emanating from these small, restored areas were indistinguishable from the soundscapes of healthy hard-bottom areas (Butler et al. 2016). Hence, provisioning restoration sites with sponge taxa that harbor soniferous infauna can restore underwater soundscapes indicative of healthy hard-bottom, attracting hard-bottom-associated fishes and invertebrates

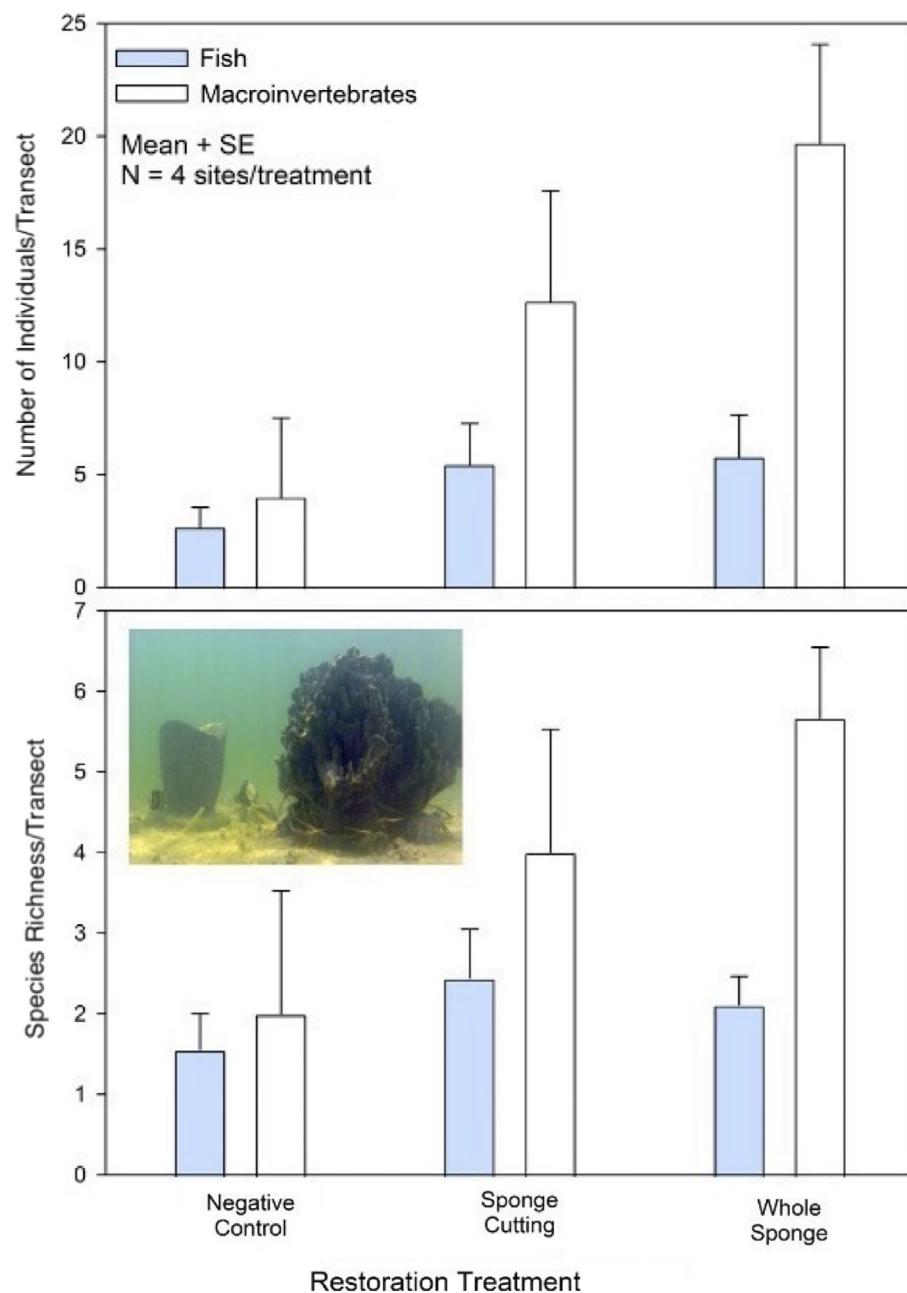


Fig. 6. Mean number of fish and macroinvertebrates (top panel) and species richness of fish and macroinvertebrates (bottom panel) observed in replicated diver transects (50 m^2 ; 25 m long \times 2 m wide; three transects per site) two years after site establishment on three types of sponge restoration treatment sites: negative control sites (unmanipulated sites subject to sponge die-off), sites restored with sponge cuttings of seven sponge species, and sites restored with whole sponges of seven sponge species. (Inset) Photograph of a whole sponge restoration site inhabited by fish and lobsters six months after establishment.

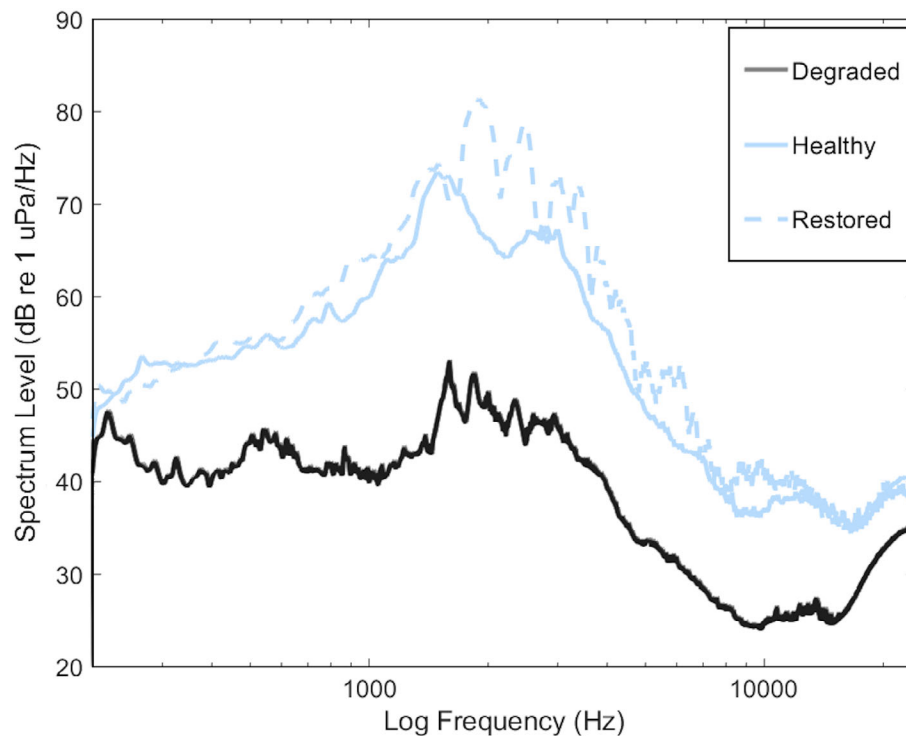


Fig. 7. Soundscape comparisons among healthy (solid blue line), restored (dashed blue line), and degraded (solid black line) hard-bottom areas three years after the establishment of hard-bottom restoration sites (adapted from Butler et al. 2016).

and contributing to the recovery of the community.

Scaling-up sponge habitat restoration

The encouraging results of the experimental scale sponge propagation and translocation efforts led us to the next logical step in the sponge restoration process: Can these methods support restoration efforts at a scale sufficient to return the ecological function and resiliency throughout the extensive areas of now sponge-depauperate hard-bottom habitat throughout Florida Bay. With that vision, we began evaluating a sponge restoration strategy that would initially entail testing and refining our established propagation process to ensure we could produce ecologically functional sponges in the numbers required to support larger scale restoration efforts. Once we had created sufficient sponge biomass, they would be out-planted within an experimental framework (e.g., to test how the distance between

restoration sites affects sponge sexual reproduction and larval recruitment) and paired with annual monitoring that would allow us to test sponge restoration site designs and methodologies best suited to initialize a positive ecological feedback loop that would drive recovery of these degraded communities.

Our initial restoration work relied on collecting donor material from naturally occurring sponges; however, it became clear that producing sponges solely by this method was unlikely to provide the sponge biomass necessary for restoration at larger scales. Attempting to produce large numbers of sponges from naturally occurring sponges was also likely to compromise the ecological function of those sponge communities that served as “donor” areas. To address these issues, we began evaluating the efficacy of using in situ sponge nurseries to create sponge biomass to support larger scale restoration efforts. Based on the “gardening” concept now widely employed to support coral restoration

activities (Rinkevich 1995, Lirman and Schopmeyer 2016), sponge cuttings were cloned from a diversity of naturally occurring sponges and allowed to heal and grow. Once large enough, these clonal sponges were propagated to produce another set of sponge cuttings for transplantation into degraded areas, thus relieving the natural sponge communities of the effort to produce sponges for restoration.

When considering potential locations for sponge nurseries, we considered logistical, ecological, and biological criteria. We envisioned using a network of nursery sites to reduce the risk that an environmental perturbation such as a storm or algae bloom would severely hamper our effort. The nurseries were to be widely placed around the periphery of Florida Bay in areas that had not historically been affected by blooms in order to reduce this risk. Our nursery sites were located on hard-bottom habitat within or adjacent to reasonably healthy sponge communities composed of the species we were targeting for restoration. This facilitated ready access to sponges that would, at least initially, be the source of donor material to begin propagation efforts. Also taken into consideration was the fact that the limited genetic information available suggested that sponges within this region consisted of a homogeneous population (Griffiths et al. 2020a, b).

This scaling-up effort also allowed us to evaluate refinements to our restoration techniques. For example, to reduce the amount of artificial material used to propagate sponges, we tested the efficacy and practicality of using coral rock as substrate to which the sponge cuttings could attach and heal as compared to concrete pavers. We found no difference in sponge mortality or growth based on substrate material; therefore, our future restoration efforts can employ coral rock as substrate and eliminate our placement of man-made substrate into the ocean (FWC, unpublished data).

We also tested whether our sponge “healing time” procedures could be improved by comparing the survival of sponge cuttings allowed to heal on the site from which they were harvested, as compared to cuttings that were immediately transplanted onto degraded hard-bottom sites. Again, there was no difference in survival between sponges allowed to heal in healthy

hard-bottom areas versus sponges immediately transplanted onto degraded hard-bottom sites. Therefore, rather than requiring two distinct field efforts—the first to propagate sponges and the second to transplant those sponges—we can combine the transplant process into a single effort.

Surprisingly, sponge cuttings immediately transplanted into degraded areas not only grew faster than those healed in healthy hard-bottom, but they also developed more internal canal space and therefore harbored a greater density of snapping shrimps. These findings support the competitive release hypothesis put forward by Valentine and Butler (2019), wherein sponges in degraded hard-bottom areas are released from feeding competition and can filter and grow rapidly. Moreover, the increased density of snapping shrimp within sponges immediately emplaced into degraded areas precipitated the return of a natural hard-bottom soundscape (i.e., a soundscape dominated by the crackle of snapping shrimp) and indicates hastened ecological recovery. As we plan the establishment of future sponge nurseries, we should weigh the potential benefits of increased sponge growth rates in degraded hard-bottom versus the potential loss of these nurseries in the face of another harmful algae bloom.

By refining our practical techniques and continuing to couple ecological research with applied restoration, we can hopefully increase the footprint of our efforts to effect change in Florida Bay. Currently, the Florida Fish and Wildlife Conservation Commission, in partnership with The Nature Conservancy, is completing an effort that will transplant 15,000 sponge cuttings onto a degraded site to “jump start” the recovery on a larger scale (i.e., on one-hectare degraded sites rather than the previous 25 m × 25 m sites) than our previous efforts. This project also includes long-term monitoring to evaluate the return of ecosystem function as represented by changes in sponge recruitment, water chemistry changes, and hard-bottom soundscapes. This effort has also closely tracked the costs of all its associated activities to provide resource managers with the economic information so often lacking in coral reef ecosystem restoration efforts (e.g., Edwards et al. 2010) as they

seek to develop a strategy that will effectively support progressively larger scale sponge habitat restoration in Florida Bay.

Finally, the State of Florida will be convening a series of workshops that will bring together this research team with the region's conservation managers to develop a sponge restoration strategy for Florida Bay. We anticipate that the process will integrate not only the ecological and biological work we have described here but also the economic considerations associated with such an undertaking. It is our goal that this process will foster an integration of ideas among these conservation managers to develop clear conservation targets by which to assess restoration efforts and refine them as necessary. Florida Bay is managed by multiple management agencies with varying conservation philosophies. Further, such an effort will require the support of public stakeholders (i.e., the people that rely on the hard-bottom ecosystem for its recreational and commercial value) to succeed. Accordingly, the development of this restoration strategy will include a robust public outreach effort that builds upon incorporating stakeholder volunteers to aid in sponge nursery establishment and sponge transplantation efforts. We believe it fundamental to our efforts that stakeholders become aware of the benefits of ecological restoration and become invested in the success of these restoration efforts. Our vision is that this process will yield a comprehensive sponge restoration strategy for Florida Bay whose implementation will increase the resilience of Florida Bay to future perturbations.

CONCLUSIONS

The practice of restoration ecology is often idiosyncratic to the system or habitat being restored. This is certainly the case in our work on hard-bottom sponge communities of Florida Bay, where many of the hypotheses regarding restoration methods were predicated on the biology and ecology of sponges. Yet we hope that our work can help inform restoration practice in other systems and ecological theory in general. For example, our initial restoration efforts focused on generating material for transplantation (i.e., sponge cuttings) from naturally occurring sponges before transplantation into degraded

areas; however, further research showed that these sponge cuttings actually grow quicker when immediately placed into degraded habitat where they were released from competition for planktonic food resources. This highlights the importance of integrating ecological theory with restoration practice. Furthermore, using often overlooked ecological processes (e.g., soundscape production or biogeochemical processing) in addition to other easily measured parameters (e.g., growth and reproduction) provides a more holistic view of restoration success.

Perhaps the biggest paradox facing restoration practitioners, however, is that ecological restoration often proceeds despite the threat of future community-altering events (e.g., red tides, fires, hurricanes, climate change). Modulating large-scale environmental stressors such as those that plague Florida Bay (i.e., cyanobacteria blooms, salinity, and temperature extremes) remains beyond experimental manipulation, which begs the question as to whether restored systems will be resilient enough to withstand future disturbances. If not, is restoration a waste of effort? The answer to that depends as much on philosophy and economics, as science. We believe that studies of species-specific tolerances and community resilience to such stressors are key to the design of successful restoration programs and a prerequisite for predictions of future outcomes in the face of continued environmental stressors. Indeed, studies of the basic biology and environmental tolerances of different sponge species were crucial to our development of predictive models of future sponge, lobster, and fish community outcomes in Florida Bay in response to environmental change (Butler 2005, Butler et al. 2005, Kearney et al. 2015, Butler and Dolan 2017). No one entity can restore the mosaic of habitats of Florida Bay and the coastal waters of the Florida Keys alone. Ultimately, a collaboration of scientists, resource managers, non-governmental organization, and local, state, and federal agencies are needed that coordinate and mobilize their unique abilities toward the common goal of restoring economically and ecologically important habitats of Florida Bay. Pete Peterson shared this perspective as exemplified in his life's work integrating basic and applied science for the betterment of coastal ecosystems.

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DATA AVAILABILITY

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.16826296.v1>