Journal of Experimental Marine Biology and Ecology 503 (2018) 92–99

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

The effects of water quality on back-reef sponge survival and distribution in the Florida Keys, Florida (USA)

Mark J. Butler IV[a,*], Jeremy B. Weisz[b], Jack Butler[a,c]

[a] Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA
[b] Department of Biology, Linfield College, McMinnville, OR 97128, USA
[c] Marine Physical Laboratory, Scripps Institution of Oceanography, La Jolla, CA 92093-0205, USA

ARTICLE INFO

Keywords:
Sponge
Salinity
Temperature
Florida
Water quality

ABSTRACT

For decades, water quality in Florida Bay and the shallow, back-reef areas of large portions of the Florida Keys (Florida, USA) have varied dramatically as a consequence of climatic conditions and water management strategies in the adjacent freshwater marshes of the Everglades. The resulting fluctuations in water quality have led to die-offs of seagrass and sponges in hard-bottom habitats, transforming the ecosystem. In this study, we examined the implications of water quality on sponge community structure in two ways. First, in laboratory experiments we tested the tolerance of five prominent sponge species to salinities ranging from 15 psu to 45 psu at typical summer and winter temperatures. We then compared sponge distributions at 32 sites in the Florida Keys with regional patterns in water quality. Our experiments showed that during the summer the loggerhead sponge (*Speciospongia vesparium*) and glove sponge (*Spongia cheiris*) were the most tolerant of sustained changes in salinity, but most species died at higher rates at salinities other than 35 psu. Salinity-associated mortality declined in the winter, but was again higher at salinities < 35 psu. A pulsed change in salinity at summer temperatures yielded idiosyncratic results depending on the species. Analysis of the field data showed that some species such as *Ircinia variablis* and *Cinachyrella alloclada* grow in most environments, whereas the occurrence of most species declines when salinity is variable and at high nutrient concentrations. These results provide a more detailed picture of the species-specific environmental tolerance of several shallow-water Caribbean sponges, and suggest that changes in environmental conditions are likely to significantly impact their distribution and species composition with potentially drastic impacts on ecosystem function.

1. Introduction

Benthic suspension feeders are a key component controlling benthic-pelagic coupling in shallow coastal ecosystems via removal of planktonic dissolved and particulate organic matter (Gili and Coma, 1998; Peterson, 2004; Jiménez and Ribes, 2007). When sufficiently dense, suspension feeders (e.g., bivalves, ascidians, bryozoans, polychaetes, cnidarians, echinoderms, and sponges) can exert strong top-down control of planktonic communities and influence biogeochemical cycling of nutrients, oxygen concentration, and turbidity in shallow marine ecosystems from tropical to polar seas (Hily, 1991; Dame and Olenin, 2005; Grebmeier and Barry, 1991; Orejas et al., 2000). Via these dramatic effects on water quality, suspension feeders are considered important "ecological facilitators" that help shape environmental conditions in ways that promote more diverse and resilient communities (Cardinale et al., 2002). Despite their sway over water column characteristics, suspension feeders are not immune to abiotic conditions that can alter their demography and distribution.

Sponges, for example, provide an array of ecosystem services (e.g., bioerosion, benthic-pelagic coupling, biogeochemical cycling, provisioning of habitat) with appreciable effects on environmental conditions that structure other animal and plant species (reviewed in Diaz and Ruetzler, 2001; Bell, 2008). They also directly support human commercial enterprises in the form of dried sponges for medicinal, bath, and artisan purposes, as well as bioactive chemical compounds for medicine and industry (Witzell, 1998; Pronzato, 1999; Duckworth, 2009; Pawlik, 2011; Butler et al., 2017b). Yet, sponges in the Mediterranean, Caribbean, and elsewhere have long been subject to episodic mass die-off events due to changing water quality conditions (Galstoff et al., 1939; Vicente, 1989; Maldonado et al., 2010; Cebrian et al., 2011) and, in some cases, to an emergence of diseases (Webster, 2007; Gochfeld et al., 2012) that also plague other marine species (Harvell et al., 2004). The virulence of some sponge diseases is linked to high seawater temperatures (Smith, 1941; Hummel et al., 1988; Vacelet

* Corresponding author.
E-mail address: mbutler@odu.edu (M.J. Butler).

https://doi.org/10.1016/j.jembe.2018.03.001
Received 13 September 2017; Received in revised form 5 February 2018; Accepted 8 March 2018
Available online 15 March 2018
0022-0981/

et al., 1994), but not all sponge die-offs can be traced to disease (Butler et al., 1995;Vicente, 1989; Cebrian et al., 2011). Several sponge mass mortalities that occurred in the Mediterranean and Caribbean, for example, were correlated with phytoplankton blooms (Butler et al., 1995; Maldonado et al., 2010).

Recent studies of sponge mass mortalities have focused on possible changes in the association between sponge hosts and their symbionts in response to increased seawater temperature and eutrophication. For example, the composition and diversity of symbiotic archaeal communities associated with pollution-tolerant sponge species in Brazil varies among populations separated by just a few kilometers, yet subject to different levels of eutrophication (Turque et al., 2010). Sponge mass mortalities in the Mediterranean Sea also correlate positively with elevated temperatures, but effects are more severe for sponges that host both phototrophic and heterotrophic microsymbionts as compared to sponges harboring only heterotrophic bacteria (Cebrian et al., 2011). In the same study, a laboratory experiment confirmed that the photosynthetic efficiency of cyanobacteria within sponge hosts was reduced at high temperatures, and that cyanobacterial decay could be involved in sponge mortality. Other studies of sponge-microbe associations indicate that microbial communities are stable within sponges when subject to high temperatures and nutrient concentrations (Simister et al., 2012; Pita et al., 2013; Thomas et al., 2015). Thus, the effect of environmental stressors on the complex symbiotic relationship between sponge hosts and microbial endosymbiont communities, sponge diseases, and sponge mass mortality events remains unresolved.

This is especially true in Florida Bay (Florida, USA) where environmental change has been dramatic and mass die-offs of whole sponge communities are increasingly common (Butler et al., 1995; Peterson et al., 2006; Stevely et al., 2011; Butler IV et al., 2015; Butler IV and Dolan III, 2017). The shallow, hard-bottom sponge communities of the Florida Keys are dominated by species that harbor diverse and abundant microbial communities and are referred to as high microbial abundance (HMA) sponges, as opposed to low microbial abundance (LMA) sponges that are more common on many coral reefs (Hentschel et al., 2003). HMA sponges have low pumping and particle clearance rates, thus much of their energy is derived from high rates of nutrient fixation by symbiotic microbes (Weisz et al., 2007).

1.1. Environmental change and the decline of sponge communities in Florida Bay

The nearshore, backreef habitats of the Florida Keys and Florida Bay (USA) lie at the southern terminus of the Florida Peninsula, just "downstream" of one of the world's largest, and most substantially altered wetlands - the Everglades (Light and Dineen, 1994; McIvor et al., 1994). Construction during the early 1900's of the "overseas railway" and later the highway that links the islands of the Florida Keys, along with major water management projects upstream within the Everglades ecosystem has significantly altered the hydrology of this large estuary (Swart et al., 1996; Marshall et al., 2008). Because of the resultant decrease in freshwater runoff and groundwater flow, combined with longer water residence times in this subtropical estuary, Florida Bay now experiences highly variable salinity and temperature regimes (Fourqurean and Robblee, 1999; Lee et al., 2006; Kearny et al., 2015). In turn, those stressors have reconfigured the ecosystem and spawned episodic blooms of cyanobacteria, seagrass die-offs, and mass mortalities of sponge communities (Butler et al., 1995; Butler IV et al., 2015; Butler IV and Dolan III, 2017; Fourqurean and Robblee, 1999; Phlips et al., 1999; Stevely et al., 2011; Blakey et al., 2015). Further changes to the ecosystem and species distributions are projected due to climate-related alterations in temperature and weather (Cook et al., 2014; Kearny et al., 2015), among them being significant reconfiguring of sponge-dominated hard-bottom communities.

Shallow (< 3 m), hard-bottom communities represent approximately 30% of the benthic marine habitat of Florida Bay and Florida Keys, interspersing with seagrass and sandy bottom. Sponges dominate the sessile animal biomass in these hard-bottom habitats with a mean abundance of > 80,000 sponges/ha represented by over 60 species (Torres et al., 2006;Stevely et al., 2010, 2011,). Many are large sponges (> 20 cm dia.); one of the most common large sponge species (*Spechiospongia vesparium*) can exceed 1 m in diameter.

The abundance of sponges in back-reef hard-bottom areas underscores their seminal importance in a variety of ecosystem processes. For example, they provide physical refugia for numerous obligate and opportunistic species (e.g., snapping shrimp (Duffy, 1992), Caribbean spiny lobster (Herrnkind et al., 1997)) and significantly alter benthic-pelagic coupling in Florida Bay through their filtering of microbes and particulate organic matter (POM), assimilation of dissolved organic matter (DOM), and impact on biogeochemical cycling (Peterson et al., 2006;, Archer et al., 2017). Only a few studies of sponge filtration have been conducted on species that occur in Florida Bay and all have demonstrated that they are efficient filter feeders of picoplankton (Lynch & Phlips, 2000Peterson et al., 2006, Wall et al., 2012). Indeed, sponge filtration capabilities are so great and sponges so numerous in Florida Bay that they are estimated to filter the entire water column within three days (Peterson et al., 2006, Wall et al., 2012). Several sponge species also support an artisanal commercial sponge fishery (Butler et al., 2017b), highlighting their economic as well as ecological importance in the region.

However, sponge communities in Florida Bay experienced mass die-offs caused by blooms of cyanobacteria in 1990–91, 2007, 2013, and 2016 (Butler et al., 1995; Stevely et al., 2011). Each event has occurred in roughly the same portion of Florida Bay, destroying > 90% of the sponge community in an area > 500 km^2 (Butler et al., 1995, Butler IV et al., 2015; Stevely et al., 2010, 2011). Given the foundational role that sponge communities play in tropical hard-bottom communities, it is obvious that the nearly complete loss of sponges in such a large area has deleterious ecological consequences, including the loss of nursery habitat for species such as spiny lobster (Butler et al., 1995; Herrnkind et al., 1997) and a dramatic reduction in water column filtering and biogeochemical cycling (Lynch and Phlips, 2000; Peterson et al., 2006; Wall et al., 2012).

Although changes in cyanobacteria concentrations and clades (Berry et al., 2015) precipitated the massive loss of sponges in the region, the mechanistic cause of the sponge mortality remains unknown. The cyanobacteria blooms and sponge die-offs also coincided with atypical salinities and high seawater temperatures, which are factors that have contributed to sponge die-offs elsewhere in the Caribbean and in the Mediterranean. Thus, knowing the thermal and salinity tolerances of sponges is crucial to understanding the influence of environmental factors on back reef sponge community composition, and the likely outcome of a more variable future environment due to changes in the global climate and regional allocation of freshwater run-off from the Everglades. In this study, we examined how environmental factors may influence sponge distributions by testing the salinity tolerances of five common back reef sponge species during the summer and winter, and by comparing sponge community structure in shallow hard-bottom sites across the Florida Keys in relation to physiochemical characteristics of seawater in those areas. Given that few sponges have adapted to freshwater or estuarine conditions, we hypothesized that regions in the Florida Keys with sustained, low salinity (< 25 psu) would harbor the most depauperate sponge communities followed by locales subject to reverse estuary effects, hence very high salinity (> 45 psu) especially at high summer temperatures. We also predicted that high concentrations of total phosphorous that often spark dense phytoplankton blooms in this phosphorous-limited carbonate system would be associated with less diverse, less dense sponge communities.