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Abiotic factors control sponge ecology in Florida mangroves

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ABSTRACT: It is well documented that biotic effects play an important role in determining the distribution and abundance of sponges on Caribbean coral reefs: predation by fishes restricts some species to refugia, and allelopathic interactions result in a competitive hierarchy for space. Recently, it has been proposed that biotic effects are similarly important in mangrove habitats; specifically, that sponges common to mangrove habitats grow fast and rapidly out-compete species otherwise found in reef habitats for prop-root space. To begin to test this hypothesis, 9 species of common reef sponges were transplanted to prop roots at 3 mangrove sponge sites with different flow regimes (as measured with plaster clods) near Key Largo, Florida. Reef sponges transplanted to all 3 mangrove sites declined in health and died, most within 60 d, while those back-transplanted to a reef site survived and grew. Reef sponge decline was most rapid at sites with the lowest flow during periods of the month with the least tidal flux, when a combination of freshwater input, high temperature and turbidity were likely responsible for their demise. We conclude that some mangrove sites that support sponge growth do so because the species found there can endure the abiotic conditions of mangrove habitats, and not because of competitive dominance over species otherwise found on the reef.

KEY WORDS: Physical effects · Flow regime · Mangrove · Fouling community · Temperature-salinity stress · Predation

INTRODUCTION

Sponges are an important component of tropical marine ecosystems. On Caribbean coral reefs, sponges rival or exceed hard and soft corals in diversity and abundance (Suchanek et al. 1983, Schmahl 1991, Alcolado et al. 2004). While much less diverse or abundant, sponges are also important members of the fouling communities that grow on the prop roots of the Caribbean mangrove *Rhizophora mangle* (Kathiresan & Bingham 2001). These habitats exhibit different abiotic and biotic regimes that affect sponge ecology, but the relative importance ascribed to each has had an interesting history.

For coral reef sponge assemblages, the importance of biotic effects was not recognized until fairly recently (Pawlik 1997, 1998). Predation on sponges by fishes was initially dismissed as playing an insignificant role, because available evidence indicated that spongivorous fishes used a 'smorgasbord' feeding strategy that diluted their predatory effect over a large number of sponge species (Randall & Hartman 1968, Wulff 1994). It was subsequently discovered that predation by fishes eliminates some sponge species from reefs, restricting them to refuge habitats (Dunlap & Pawlik 1996, 1998, Pawlik 1997, 1998, Wulff 2005). Moreover, reef fishes do not prey on chemically defended sponge species, but on a category of palatable species that appear to persist on the reef despite constant grazing (Pawlik et al. 1995, Pawlik 1998). On reefs, biotic factors other than predation appear to be less important in structuring the sponge community, although some sponges are competitively dominant over others through allelopathic interactions (Engel & Pawlik 2005a). Abiotic factors are less likely to differentially structure the reef sponge community because coral

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reef habitats are tied to relatively constant, oligotrophic conditions.

For Caribbean mangrove sponge assemblages, as for mangrove fouling communities in general, the conventional view has been that abiotic factors play a key role in determining distribution and abundance (Bingham & Young 1995, Farnsworth & Ellison 1996). In addition to constraints imposed by variable conditions of salinity, temperature and sedimentation, sponge growth is restricted to the subtidal portion of mangrove prop roots between the mean high water line and the sediment surface (Rützler 1995). Not surprisingly, diversity of sponges in mangroves is much lower than on reefs (Engel & Pawlik 2005a,b), but several species (e.g. *Tedania ignis, Geodia gibberosa*) take refuge there from the sponge-eating fishes found on reefs, where they otherwise can only grow in protected interstices (Dunlap & Pawlik 1996, Pawlik 1998).

It has recently been suggested that biotic factors play a much more important role in mangrove habitats than previously recognized (Wulff 2005). Reciprocal transplantation experiments corroborated the importance of fish predation in structuring reef sponge ecology (previously demonstrated by Pawlik 1998), but transplants of reef sponges to an offshore mangrove habitat revealed faster growth rates of mangrove species than reef species, and led the author to conclude '…that typical faunas of mangroves and reefs are not tied to these habitats by abiotic factors. Greater sponge species diversity on the reef does not necessarily indicate superior conditions for sponges. Instead reefs may be a refuge for species that grow too slowly to coexist with typical mangrove species.' Further, the author summarized that '…spongivorous predators excluded typical mangrove sponges from reef sponge assemblages, and reef sponges were excluded from mangrove sponge assemblages by competition' (Wulff 2005, p. 313).

The purpose of this study was to test the hypothesis that reef sponges are excluded from mangrove sponge assemblages in coastal mangrove habitats near Key Largo, Florida. Nine species of reef sponges were transplanted from an offshore patch reef to cleaned mangrove prop roots at 3 sites (representing a cline of tidal flow) that supported a pre-existing mangrove sponge assemblage. If competition excludes reef sponges from mangrove sponge habitats, reef sponges should be able to survive and grow in these habitats in the absence of competition.

MATERIALS AND METHODS

The survival of reef sponges in mangrove sponge habitats was examined at sites near Key Largo, Florida in the summer of 2005. Mangrove transplant sites in Florida Bay were chosen that (1) supported resident sponge populations on prop roots of the red mangrove, *Rhizophora mangle* (see community description in Engel & Pawlik 2005b), and (2) experienced a cline of tidal flow based on their geography and past observations. Jewfish Creek (25° 11.083′ N, 80° 23.3′ W) is a relatively wide channel that connects Barnes and Blackwater Sound; Shady Creek (25° 7.989′ N, 80° 25.276′ W) is a narrow mangrove creek that connects to Dusenbury Creek and winds through the mangroves to a shallow basin where it branches into 2 shallower creeks, one of which is Shady Cove. Dry Rocks Reef (25° 7.850′ N, 80° 17.521′ W), a shallow patch reef at ~7 m depth with a high diversity of typical Caribbean coral reef fauna, served as a sponge collection and control site (see maps in Engel & Pawlik 2005a,b).

The dissolution of plaster clods was measured to determine if daily tidal flux differed between the chosen sites (Thompson & Glenn 1994). Hemispherical plaster clods were attached to prop roots at each mangrove site with cable ties. At Dry Rocks Reef, clods were fastened to the top of 0.4 m cubes of 2 cm^2 vexar mesh that were firmly attached to the limestone substratum at ~7 m depth. Three clods were deployed at each site for a period of 24 h on 27 May 2005 and again on 13 June 2006, corresponding to a period of high and low tidal flux, respectively, based on tide predictions by the US National Oceanic and Atmospheric Administration. Initial and final masses of clods were determined after drying at 50°C for 12 h. Percent change in mass was compared across sites and tidal regimes using a 2-way ANOVA. Data were arcsine transformed to meet the assumptions of ANOVA, and multiple comparisons between sites for each tidal regime and between tidal regime for an individual site were conducted using a Bonferroni-adjusted multiple comparison test, with $\alpha = 0.0031$. All statistics were conducted using SAS v9.1 (SAS Institute).

Nine reef sponge species were collected for transplantation: 6 having a rope-like morphology (*Aplysina cauliformis*, *Amphimedon compressa*, *Aplysina fulva*, *Callyspongia armigera*, *Iotrochota birotulata*, and *Niphates erecta*) and 3 having a vasiform morphology (*Callyspongia vagnalis*, *Niphates digitalis*, and *Aplysina archeri*). For each rope species, 16 straight lengths of 15 cm were cleanly cut with scalpels from larger sponges (width = 2 to 4 cm). For each vase species, 8 sponges ~15 cm in height were similarly cut from their bases (width = 4 to 8 cm). Cut sponges were transferred to 100 l containers of aerated seawater and transported to mangrove sites. During transport, each sponge piece was uniquely tagged and provided with a cable tie for later attachment. Four sponge pieces of each rope species were

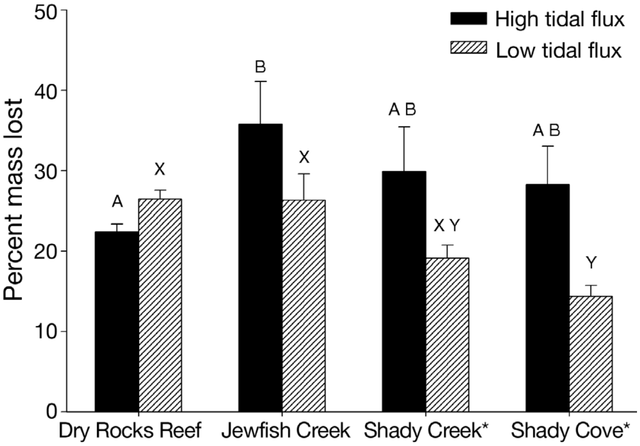

Fig. 1. Percentage mass (mean + SD) lost by dissolution for plaster clods deployed for 24 h at experimental sites near Key Largo, Florida, during a period of high and low tidal flux (N = 3). Similar letters above bars indicate sites for which differences between means are not significant for either high or low tidal flux. *: significant difference in clod dissolution between tidal regimes (2-way ANOVA: Site, Tidal flux, Interaction $p < 0.01$; Bonferroni-adjusted multiple comparisons, $\alpha = 0.0031$)

haphazardly attached to 4–5 cleaned prop roots at each mangrove site. Reef sponges were transplanted onto prop roots so that they occupied the same vertical range as mangrove sponges on adjacent roots, with positions at ~15, 30, 45, 60 and 75 cm below the water surface. For each vase species, 4 sponges were transplanted to the Shady Creek site only. As a control for transport and manipulation, after deploying sponge pieces at all the mangrove sites, 4 replicate pieces of all 9 rope and vase species were transported back to Dry Rocks Reef and attached to the top of 0.4 m cubes of 2 cm^2 vexar mesh that were firmly attached to the limestone substratum.

Sponges at all sites were monitored weekly for the first month, and then every 2 wk. For rope sponge pieces, necrosis progressed linearly along the length of the sponge, leaving the sponge skeleton; therefore, the length of remaining live tissue was measured. Vase sponges were qualitatively scored as good, fair and dead.

For the experimental period, daily rainfall data were obtained from the National Climatic Data Center for the John Pennekamp State Park weather station, Key Largo, Florida. Tidal discharge data (a measure of tidal flux) and sea surface temperature data (recordings every 15 min) were provided by the United States Geological Survey Integrated Coastal Monitoring Network for Jewfish Creek (site 251105080231800), Key Largo, Florida.

RESULTS

Plaster clod dissolution at the 4 sites revealed that flow was significantly greater during predicted periods of high tidal flux than low tidal flux at both Shady Creek and Shady Cove, but not at Jewfish Creek or the reef site (Fig. 1). Based on clod dissolution, Shady Creek and Shady Cove sites experienced 36 and 49% less flow, respectively, during low tidal flux than during high tidal flux. During high tidal flux, mangrove sites were found to have similar flow, with flow at Jewfish Creek significantly higher than at Dry Rocks Reef. During low tidal flux, Dry Rocks Reef and Jewfish Creek had similar flow, Shady Cove had significantly less flow than either Dry Rocks Reef or Jewfish Creek, and Shady Creek had intermediate flow that was not significantly different from any of the other sites (Fig. 1).

For the 6 species of rope sponges combined, the average length of living tissue increased at Dry Rocks Reef, but steadily declined at all 3 mangrove sites, with the most rapid decline occurring at the Shady Creek and Shady Cove sites (Fig. 2). The typical mangrove sponge assemblage (primarily *Chondrilla nucula, Lissodendoryx isodictyalis*, *Tedania ignis* and *Halichondria* sp.) of adjacent prop roots at all 3 mangroves sites was normal and healthy throughout the experimental period, except for the last data point (16 August 2005), when some sponges at the Shady Creek and Shady

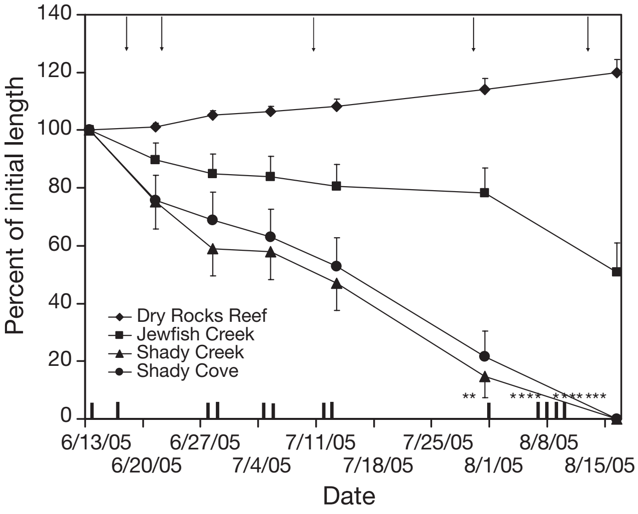

Fig. 2. Percentage change (±SE) of initial live tissue length of 15 cm pieces of 6 species of rope sponges transplanted from Dry Rocks Reef to experimental sites near Key Largo, Florida (N = 24). Vertical arrows at top of graph indicate days when daily rainfall ≥2.5 cm was recorded. Small bars above *x*-axis indicate days when daily tidal flux was in lowest quartile relative to the mean for the experimental period. Asterisks above *x*-axis indicate days when daily sea surface temperatures were in highest quartile relative to the mean for the experimental period, Date: mm/dd/yy

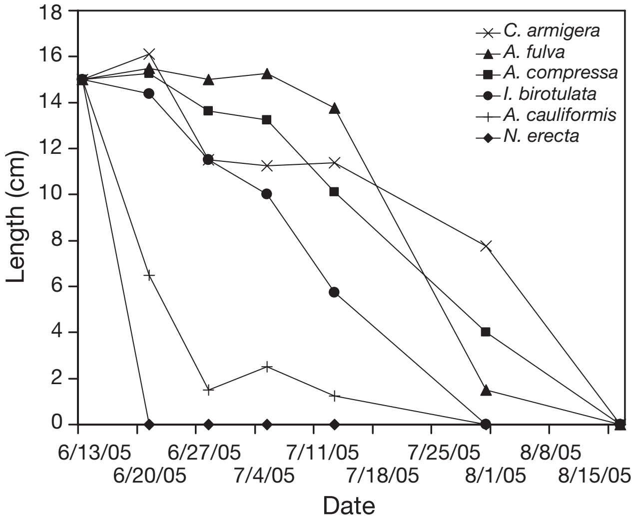

Fig. 3. Change in mean length of live tissue of rope sponges transplanted from Dry Rocks Reef to Shady Creek mangrove site near Key Largo, Florida (N = 4). Variance not displayed for clarity. Date: mm/dd/yy

Cove sites exhibited a white surface film and others were observed detached and floating at the water surface.

During the experimental period, there were 5 rainfall events in excess of 2.5 cm (max = 5.6 cm on 18 June 2005) and 13 events of mean daily tidal flux that were in the lowest quartile relative to the mean for the experimental period (Fig. 2). Mean daily tidal flux for the experimental period was 37.7 m^3 s^{-1}, with minimum daily tidal flux of 26.9 m^3 s^{-1} on 5 July 2005. Four of the low tidal flux events occurred near the end of the experimental period, when there were also 13 d in which mean daily sea surface temperatures were in the highest quartile relative to the mean for the experimental period (Fig. 2). Mean sea surface temperature for the experimental period was 31.0°C, with maximum mean daily temperatures of 32.8°C reached on 4 and 15 August 2005.

By mid-August, 2 mo after the beginning of the experiment, sponges at Dry Rocks Reef had grown by nearly 20%, while sponges had lost a mean of ~50% of living tissue at Jewfish Creek and all were dead at Shady Creek and Shady Cove. When the sites were next checked, 10 wk after the end of the experimental period, the remaining rope sponges at Jewfish Creek were also dead.

Among the 6 species of rope sponges, there were differences in the rate of necrosis observed at the mangrove sites (Fig. 3 for Shady Creek). Least tolerant of mangrove conditions was *Niphates erecta,* followed by *Aplysina cauliformis* and *Iotrochota birotulata*, with *Aplysina fulva*, *Amphimedon compressa,* and *Callyspongia armigera* the last to succumb. At Dry Rocks Reef, all species grew with the exception of *A. compressa*, which neither gained nor lost length.

For the 3 species of vase sponges transplanted to Shady Creek, all rapidly declined in health and died within 45 d, while those transplanted back to Dry Rocks Reef remained healthy until the end of the experimental period. Among the 3 species, *Aplysina archeri* declined the most rapidly at Shady Creek, and all replicates were dead within 15 d. Transplants of *Callyspongia vaginalis* and *Niphates digitalis* were dead after 45 d, corresponding to the time frame that marked the most rapid decline of the rope sponges. For both rope and vase sponges, there was no evidence that tissue loss was due to any biotic factor, such as predation by fishes or invertebrates, or competition with other fouling organisms. There was also no evidence of sponge-specific pathogenesis, because mangrove sponges on adjacent prop-roots were healthy until the last day of the experimental period.

DISCUSSION

This study was prompted in part by a more qualitative experiment that was conducted by one of us (J.R.P.) in July 1992 at Sweetings Cay, a series of offshore mangrove islands separated by tidal cuts on the uninhabited east end of Grand Bahama Island (26° 33.451′ N, 77° 52.88′ W). Reef and mangrove sponges were reciprocally transplanted onto 0.5 m^2 horizontal plates 0.1 m above the bottom at 1.5 m depth below mangrove prop roots populated by a typical mangrove sponge community. Reef sponge species used in this experiment were *Iotrochota birotulata* and *Aplysina cauliformis* (rope-like), *Callyspongia vaginails* (vasiform), and *Ectyoplasia ferox* (mound-forming), with 4 pieces of each sponge attached to each of 3 replicate plates. After only 15 d, all reef sponges transplanted to the mangrove site were dead, except for some living sponge tissue remaining at the center of pieces of *E. ferox*, while reef sponges back-transplanted to the reef site were healthy and mangrove sponges back-transplanted to the mangrove site were healthy (*Tedania ignis, Dysidea etheria, Lissodendoryx isodictyalis, Chondrilla nucula*).

In the present study, none of the 9 species of common reef sponges from Dry Rocks Reef survived transplantation to prop roots at mangrove sponge habitat sites, and most were dead within 60 d. Clearly, if these reef species cannot survive in these mangrove sponge habitats, they could not compete for space with existing mangrove sponges, in contrast to the recent conclusion that reef sponges are excluded from mangrove sponge assemblages by competition (Wulff 2005). Of the 9 reef species used in the present study, 3 were also used by Wulff (2005)—*Amphimedon compressa, Aplysina fulva* and *Iotrochota birotulata*—and these survived and grew over a period of 7 mo at mangrove transplant sites on Twin Cays, Belize. Of the remaining 3 reef species used by Wulff (2005), 2 did not survive transplantation to Twin Cays (*Desmapsamma anchorata, Monanchora arbuscula*) while the other (*Mycale laevis*) survived and grew, but none of these 3 species were common at Dry Rocks Reef and they could not be transplanted in the present study.

For mangroves in the Florida Keys, abiotic factors are particularly stressful for mangrove sponge assemblages during the late summer, when temperatures and rainfall events peak. We observed necrosis of mangrove sponges at the Shady Creek and Shady Cove sites on 16 August 2005 (primarily *Lissodendoryx isodictyalis*, *Tedania ignis*, and *Chondrilla nucula*) after a period of high sea surface temperatures and low tidal flux (Fig. 2), and have observed similar events in late summer and early fall in past years. Despite these seemingly catastrophic losses, mangrove sponge populations recover rapidly, either from the growth of surviving sponge remnants or from recruitment (Bingham & Young 1995).

Although abiotic factors associated with the late summer were observed to be particularly stressful for mangrove sponges in the present study, it should be noted that the decline in health of reef sponges transplanted to Florida mangrove sponge habitats began in June with the first assessment of transplanted sponges (Fig. 2), when conditions were still favorable and mangrove sponge communities were healthy and growing. Mangrove sponge communities were also healthy during the July 1992 transplant of reef sponges to the offshore mangrove site in the Bahamas, after which reef sponges were mostly dead in only 15 d, while back-transplanted mangrove sponges were healthy. These results suggest that reef sponges cannot survive the abiotic conditions of these mangrove habitats under conditions that are otherwise favorable for the mangrove sponge community.

Why did reef sponges die when transplanted to mangrove sponge habitats in the present study, while those transplanted in Wulff (2005) survived? The most likely explanation is that the Twin Cays site used by Wulff (2005) was an offshore mangrove cay of the Belize Barrier Reef that had much less stressful abiotic conditions. Although 2 of the 6 reef sponge species chosen for transplantation to Twin Cays did not survive the 7 mo experiment conducted in Wulff (2005), the relative growth of the remaining 4 species were used to formulate the general conclusion that biotic factors are more important in structuring mangrove sponge assemblages than abiotic factors. Our results suggest otherwise for coastal Florida and offshore Bahamas mangrove sponge habitats.

Mangroves are predominantly terrestrial, and cover 60 to 75 % of tropical and subtropical coastlines (Lalli & Parsons 1999, Kathiresan & Bingham 2001). The proportion of mangrove habitat that is suitable for sponge growth is extremely small. Only prop roots that extend below the lower intertidal will support sponge growth (Rützler 1995), but the vast majority of these roots are in water that is either too shallow or too stagnant; therefore, mangrove sponge assemblages are restricted to prop roots that hang into the subtidal with bottom depths >1 m. These depths are also accessible by boat and snorkeling, while the remaining intertidal mangrove is not, which may give the impression that sponge-covered prop roots are a common feature of mangrove habitats as a whole. In fact, considering all shallow water habitats in the Florida Keys, those which are occupied by mangrove sponge assemblages represent a very small area compared to the vast stretch of offshore hard-bottom available to reef sponges, or the larger grassbed and lagoon areas available to sponges that grow in these habitats.

Past studies have noted that Caribbean mangrove epifaunal communities may be quite different in terms of stability, despite having very similar species compositions. Bingham & Young (1995) described a much more dynamic community in Florida mangroves than had been described by Sutherland (1980) for mangroves in Venezuela. Offshore mangrove habitats are less likely to be influenced by estuarine conditions of freshwater runoff and sedimentation than coastal mangroves. Ellison & Farnsworth (1992) documented mangrove sponge assemblages at 6 sites in Belize, ranging from 2 coastal sites and extending to the offshore Twin Cays site used by Wulff (2005), and concluded that species richness increased with the lower variability in water temperature and salinity found offshore. Ellison & Farnsworth (1992) also reported that transplants of the sponge *Amphimedon viridis* from prop roots of offshore Lark Cay to coastal Placencia resulted in the death of all transplanted sponges within 4 d; they attributed this to the abiotic effects of temperature and salinity. In the present study, reef sponges did not survive in 3 different coastal mangrove sponge habitats of Florida, nor did they survive in an offshore mangrove sponge habitat in the Bahamas.

While abiotic factors predominate in determining the large-scale distribution of sponge assemblages among Caribbean mangrove habitats, biotic factors likely dominate at smaller scales, particularly at the level of individual prop roots (Engel & Pawlik 2005b). Ultimately, of course, sponge distribution and abundance is tied to a shifting spectrum of abiotic and biotic factors, including water quality, currents, storms, food availability, sunlight, predation, competition, recruitment, and pathogenesis, which varies from mangrove, lagoon and grassbed habitats to patch, barrier, and deep-water reefs.

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