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Cyanobacterial blooms alter benthic community structure and parasite prevalence among invertebrates in Florida Bay, USA

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ABSTRACT: Many marine habitats are at risk due to increasing frequency, intensity, and persistence of harmful algal blooms. Repeated cyanobacterial harmful algal blooms (cyanoHABs) in Florida Bay, USA, kill sponges, resulting in reduced filtration and loss of shelter for benthic species. The loss of these key ecosystem functions can impact disease dynamics if fewer pathogens are filtered from the water column (dilution), if shelter loss increases host density in remaining shelters and a directly transmitted disease is present (host regulation), or if shelter loss changes species distributions and foraging patterns (trophic exposure). We show persistent impacts to hard-bottom communities relative to non-impacted communities 2 yr after a significant cyanoHAB. We compared benthic structure, invertebrate epibenthic/infaunal community composition, and parasitism among macroinvertebrates, stone crab *Menippe mercenaria*, and Caribbean spiny lobster *Panulirus argus*. On sites degraded by cyanoHABs, we found more, smaller sponges, indicating regrowth. Despite this evidence of recovery, epibenthic/infaunal invertebrate communities were distinct and more diverse on unimpacted sites. Additionally, there were fewer, smaller bivalves on impacted sites. The bivalve *Tucetona pectinata*, prey for stone crabs, was nearly absent on impacted sites, resulting in decreased prevalence of the apicomplexan gregarine *Nematopsis* sp., which is trophically transmitted from *T. pectinata* to *M. mercenaria*. *Panulirus argus* virus 1 also appears to be affected by cyanoHABs, as it was absent on impacted sites but present in 26.5% of spiny lobster on unimpacted sites. Impacts remain evident 2 yr after significant cyanoHABs, which does not bode well for these areas considering the frequent reoccurrence of blooms.

KEY WORDS: Habitat degradation · Harmful algal bloom · HAB · Florida Bay · Benthic invertebrate community

1. INTRODUCTION

Habitat degradation due to anthropogenic and natural disturbance is a key issue affecting marine environments worldwide (McCauley et al. 2015) and undermining the ecosystem services they provide (Costanza et al. 1997, Smale et al. 2019). In areas with increased nutrient load (i.e. eutrophication) and certain climate change impacts, such as ocean acidification and warming waters, the frequency, intensity, and persistence of harmful algal blooms (HABs) is on the rise (Fu et al. 2012). These blooms, both toxic and nontoxic, can directly and indirectly harm wildlife (Fire & van Dolah 2012, Capper et al. 2013, Gravinese et al. 2018), humans (Carmichael 2001, Ibelings et al. 2014), and ecosys-

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tems (Sunda et al. 2006, Paerl & Huisman 2008). Additionally, HABs that impact foundational species can lead to cascading ecosystem consequences (Butler et al. 1995).

There are also many ways that environmental change can interact with disease to affect host populations (Lafferty et al. 2004, Behringer & Duermit-Moreau 2021). Susceptibility to parasitism and disease can vary ontogenetically (Behringer 2012), by sex (Zuk & McKean 1996), habitat (Altizer et al. 2011), and with a myriad of other factors that are influenced by environmental change (Nunn et al. 2003, Luis et al. 2013). Specifically, environmental stressors that are linked to habitat degradation, such as increased water temperature (Karvonen et al. 2010), pollution (Khan 1990), malnutrition (Beck & Levander 2000), and eutrophication (Lafferty 1997), have also been linked to an increased susceptibility to parasites in a variety of habitats (Holmes 1996). Changing environmental conditions can also directly impact parasites and disease-causing agents, leading to changes in virulence (Braid et al. 2005), abundance/activity (Groner et al. 2014), new emergence/outbreak (Travers et al. 2009), and range shifts (Burge et al. 2014). These interactive effects alter the host–pathogen–environment triad in ways that can result in net positive or net negative outcomes for any given host species.

Florida Bay, USA, is home to an expansive limestone hard-bottom marine habitat, covering approximately 30% of the shallow water environment (Bertelsen et al. 2009). These locations are designated as 'Essential Fish Habitat' for several commercially fished teleosts and invertebrates (NOAA 2021). This limestone hard-bottom habitat is dominated by sponges, which provide structural complexity to an otherwise low-relief habitat (Behringer & Butler 2006). Over 60 species of sponges found in this habitat are essential in driving benthic–pelagic coupling of nutrients by filter-feeding (Valentine & Butler 2019) and as shelter for numerous species (Westinga & Hoetjes 1981).

In addition to being important habitat features, sponges are also extremely efficient filter-feeders responsible for linking benthic macrofauna with nutrients in the water column by filtering microbes and assimilating dissolved organic carbon and particulate organic carbon (Reiswig 1971, Valentine & Butler 2019). They effectively remove pathogenic bacteria from the water column (Maldonado et al. 2010) and may gain significant nutrition from filtering viruses (Hadas et al. 2006). This filtration may significantly lower disease-causing agents in areas with dense sponge populations.

These ecosystem functions are severely impaired after periodic cyanobacterial blooms, which result in sponge die-offs (Butler et al. 1995, Peterson et al. 2006). The non-toxic but mucilaginous *Synechococcus* spp. cause these cyanobacteria harmful algal blooms (hereafter referred to as cyanoHABs), reduce light penetration, and appear to smother sponges (Puls 2015), resulting in extreme habitat degradation (Butler et al. 1995). Such die-offs have occurred periodically since 1990, with varying intensity (Cannizzaro et al. 2019). The most recent bloom resulting in documented habitat degradation occurred between 2016 and 2017 (Cannizzaro et al. 2019). A bloom in 2007 degraded sponge communities over 500 km^2, resulting in the loss of over 90% of sponges at severely affected sites (M. Butler & D. Behringer unpubl. data). These die-offs reduce filtration capacity that can lead to further decreases in water quality and increases in turbidity (Peterson et al. 2006), resulting in a negative feedback loop that further degrades the environment and nearby seagrass beds (Glibert et al. 2009, Hall et al. 2016).

There are 3 main pathways in which degradation of the hard-bottom habitat in Florida Bay can directly and drastically increase exposure to harmful parasites. First, in the 'dilution' pathway (Keesing & Ostfeld 2021) the diminished filtration of bacteria and viruses by sponges can lead to greater proliferation of these harmful organisms (Hadas et al. 2006, Maldonado et al. 2010). Second, in the 'susceptible host regulation' pathway (Keesing et al. 2006), the loss of sponge shelters can artificially increase population density in remaining shelters, thereby increasing the potential for direct transmission of diseases (Hughes et al. 2002). Finally, in the 'trophic' pathway (Wood et al. 2010), prey availability may decrease with shelter loss (Butler et al. 2016), which could impact foraging habits (Sigler et al. 2009) or result in consumption of suboptimal prey (Amélineau et al. 2019) and thereby expose individuals to new parasites.

Hard-bottom degradation from cyanoHABs may also decrease exposure to parasites through these pathways. If degraded habitat is less attractive to hosts, decreasing host density, the susceptible host regulation pathway would lead to a decrease in directly transmitted parasites. The trophic pathway may lead to a decrease in trophically transmitted parasites that are present in healthy hard-bottom habitat if intermediate hosts are negatively impacted by shelter loss or other effects of cyanoHABs. In these scenarios, parasite prevalence may be an indication of ecosystem health (Hechinger & Lafferty 2005, Johnson et al. 2016). Restoration projects are increas-

Table 1. Known parasites in dominant decapod crustaceans in Florida Bay hard-bottom habitat, namely Florida stone crab *Menippe mercenaria* and Caribbean spiny lobster *Panulirus argus*. Transmission and exposure pathways influence the expected outcomes of degradation by cyanobacterial harmful algal blooms on parasite prevalence in these host species

Host	Parasite	Type	Transmission	Impact	Exposure pathway	Expected outcome of degradation to parasites
Menippe mercenaria	*Nematopsis* sp.	Apicomplexan gregarine	Trophic	Unknown	Trophic	(1) ↑ if bivalve density increases (2) ↓ if bivalve density decreases
	Hematodinium sp.	Dinoflagellate	Environmental	Mortality	Dilution	(1) ↑ if sponges filter pathogen
Panulirus argus	PaV1	DNA virus	Direct	Mortality	Dilution	(1) ↑ if sponges filter pathogen
					Susceptible host regulation	(1) ↑ if host density increases due to shelter limitation (2) ↓ if host density decreases due to habitat quality
	Ameson herrnkindi	Microsporidian	Direct	Unknown	Susceptible host regulation	(1) ↑ if host density increases due to shelter limitation (2) ↓ if host density decreases due to habitat quality

ingly using prevalence of parasites with complex life cycles as a measure of success (Huspeni & Lafferty 2004, Moore et al. 2020).

These exposure pathways have the potential to impact a wide range of hard-bottom dwellers, including the Florida stone crab *Menippe mercenaria* and the Caribbean spiny lobster *Panulirus argus*. As 2 dominant benthic predators and scavengers that compete for sponge shelter (Behringer & Hart 2017), they could be heavily affected by habitat degradation and loss of sponge habitat. These decapods are known hosts of viral and protistan parasites with distinct transmission and exposure pathways that are expected to be impacted in different ways by habitat degradation (Table 1).

We took advantage of a natural experiment to examine how habitat degradation caused by cyanoHABs impacts benthic community structure in Florida Bay, and how these changes may affect parasite diversity and prevalence in Florida stone crabs and Caribbean spiny lobsters. We first established the differences in the benthic coverage and structure between sites impacted by the periodic cyanoHABs and unimpacted sites to determine whether there are habitat differences that would support changes in parasitism due to dilution and/or susceptible host regulation pathways. Next, we examined epibenthic and infaunal invertebrate communities on these sites, to see whether and how they were impacted by the blooms to test the trophic exposure pathway. Finally, we screened *M. mercenaria* and *P. argus* and several prey species for parasites to determine whether exposure pathways and expected outcomes of cyanoHABs and degradation align. Additionally, we screened sympatric decapods of similar size in search of potential sinks and sources of parasites.

2. MATERIALS AND METHODS

2.1. Habitat

Five hard-bottom sites were surveyed in the Florida Keys (3 'unimpacted' and 2 'impacted') in July and September 2019 (Fig. 1). Sites were chosen based on known history of cyanoHABs and sponge mortality, as well as sufficiently high stone crab density to allow for collections. At each site, benthic coverage and habitat were characterized to quantify any differences between impacted and unimpacted habitats. Within each site, 4 non-overlapping 2 m × 25 m belt transects were used to record the number and size (diameter and height) of structures (sponges, solution holes [small pits in karst limestone], coral heads, and rocks). All structures larger than 10 cm × 5 cm were identified and counted along the belt transect, and the measurements from the first 10 on each transect were recorded. Benthic substrate coverage was assessed along the same transect using the point intercept method along each 25 m transect (Alvarez-Filip et al. 2011). The percent cover of benthic substrate (sponge, seagrass, coral, soft coral, red macroalgae, green macroalgae, brown macroalgae, or sand) was estimated every 25 cm along the transect for a total of 100 estimates per transect.

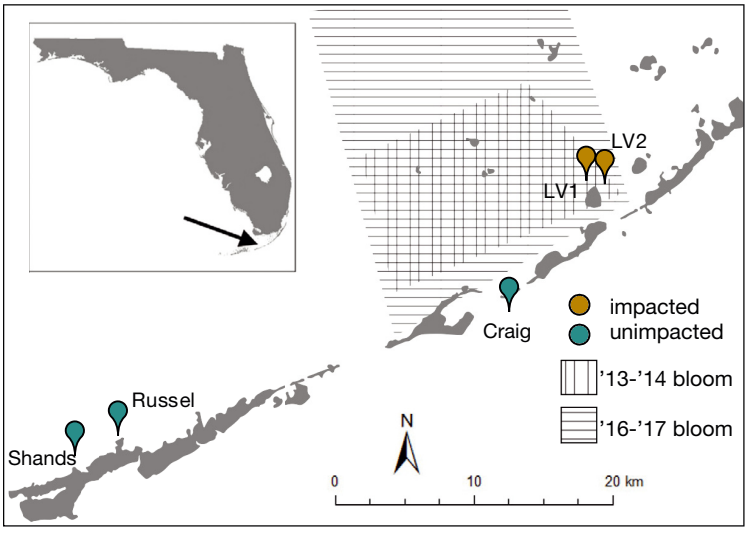

Fig. 1. Sampling sites (n = 5) in Florida Bay, USA: from south to north, the 3 unimpacted sites are Shands, Russel, and Craig Keys and the 2 impacted sites are Lignumvitae Key 1 (LV1) and Lignumvitae Key 2 (LV2). Hatching shows extent of the 2 most recent major cyanobacterial harmful algal blooms that occurred in 2013–2014 and 2016–2017. Inset map shows the state of Florida, with arrow indicating the location of Florida Bay

2.2. Benthic community

We then sampled each site for epibenthic and infaunal organisms, to assess differences in prey availability and overall invertebrate communities among the sites and between hard-bottom and seagrass within sites. Sampling was conducted using a Venturi suction sampler (Orth & van Montfrans 1987) with a 1 mm^2 mesh sieve. At each site, 0.25 m^2 plots (n = 5 within hard-bottom and 5 within seagrass) were sampled for 5 min or until all sediment had been removed, whichever came first. Samples were then frozen at −20°C for later identification of all invertebrates to the lowest possible taxonomic level. We weighed the first 5 individuals of each species in a sample individually, and the remaining were counted and weighed collectively by species.

2.3. Parasite communities

At each site, we collected stone crabs (n = 20–25) and spiny lobsters (n = 15–20) for parasite profile analysis. Additionally, we collected 3 mollusks (n = 5 each of bittersweet comb *Tucetona pectinata*, American star snail *Lithopoma americanum*, and tulip snail *Fasciolaria tulipa*) and 2 sympatric crabs (n ≤ 10 each of blotched swimming crab *Achelous spinimanus* and West Indian spider crab *Maguimithrax spinosissimus*) for parasitology. The mollusks represent potential intermediate hosts of trophically transmitted *Nematopsis* sp. and the sympatric crabs represent potential alternative hosts of *Hematodinium* sp. The mollusk species we collected were presumed to be prey items because the shells from at least 1 of each species were found in or around a stone crab den. Several live *T. pectinata* were collected directly from stone crab dens and crushed shells of this species were frequently observed around their dens. Crustaceans were collected by hand, as were mollusks, although some additional bivalves were collected ad hoc via suction sampling. Each animal was measured and sexed, and the shelter type and any conspecifics sharing shelter were noted for crustaceans.

All individuals were euthanized and necropsied within 24 h of capture. For molecular diagnostics, skeletal muscle, hepatopancreas, gill, and antennal gland were biopsied and fixed in 1 ml of 99% ethanol. Skeletal muscle, hepatopancreas, gonad, gill, heart, midgut, antennal gland, and epithelial tissue were biopsied for histological processing and were submerged in Davidson's saltwater fixative (Hopwood 1969) for 24–48 h, then rinsed in tap water and transferred to 70% ethanol. Fixed samples were processed for hematoxylin and alcoholic eosin (H&E) staining using standard methods (Feldman & Wolfe 2014). Disease screening was conducted using an Olympus BH-2 light microscope. Screening was conducted by viewing one entire section of each organ at various magnifications (4–100×).

All *M. mercenaria*, *A. spinimanus*, and *M. spinosissimus* were additionally screened for *Hematodinium* sp. infection via conventional PCR (Bojko et al. 2018), and all *P. argus* were screened for *Panulirus argus* virus 1 (PaV1) and *Ameson herrnkindi* microsporidia infections using conventional PCR (Baker et al. 1994, Montgomery-Fullerton et al. 2007, Ovcharenko et al. 2010, Moss et al. 2012). DNA was extracted from gill, hemolymph, and muscle tissue for *Hematodinium* sp., PaV1, and *A. herrnkindi*, respectively, using Qiagen DNeasy blood and tissue extraction kits according to manufacturer's protocols. PCR reactions consisted of 1.25 U of *Taq* polymerase, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 1 µmol of each primer, and 3 µl of DNA template (10–100 ng $µl^{-1}$) in a 50 µl reaction volume (Table A1 in the Appendix). Amplicons were visualized on a 2% agarose gel (120 V, 60 min) and appropriately sized bands were extracted from the

gel, purified, and sent for forward sequencing (Eurofins genomic sequencing services; www.eurofins.com). Sequence data were compared with other isolates in GenBank using NCBI BLASTn.

2.4. Statistical analyses

To assess any differences between shelter availability, which would affect the susceptible host regulation exposure pathway, at impacted and unimpacted sites number and size of (1) all shelters, (2) all sponge shelters, (3) loggerhead sponge shelters, and (4) solution holes encountered on belt transects were compared. Loggerhead sponges *Spheciospongia vesparium* were singled out because of their importance as habitat for spiny lobster and stone crab. We used Kruskal-Wallis rank sum *H*-tests (hereafter KW tests) with Bonferroni correction to account for data with non-homogeneous variances that did not meet the assumptions of parametric statistics. We approximated sponge biomass density to assess filtration and dilution capabilities by multiplying the average sponge area (diameter × height) per transect by percent of sponge coverage for that transect and compared impacted to unimpacted sites using a KW test. To assess habitat quality, which could also impact parasitology through the susceptible host regulation pathway, we used KW tests to compare the percent coverage of each bottom type from the transects (abiotic, macroalgae, corals, seagrass, and sponges) between impacted and unimpacted sites.

To characterize differences in invertebrate communities, average mass and abundance of invertebrates per sample and biomass and abundance of phyla (with Mollusca split into Bivalvia, Gastropoda, and Polyplacophora, and Arthropoda split into Decapoda and Isopoda) were compared between site types using KW tests, only including species found on both impacted and unimpacted sites to remove bias in species size. To determine if there were differences in epibenthic and infaunal invertebrate community composition, and thus prey availability, at impacted and unimpacted sites, a Bray-Curtis distance matrix (Bray & Curtis 1957) was calculated in the 'vegan' package in R (Oksanen et al. 2019) using the counts of species found in each sample. A principal coordinates analysis (PCoA) was used to visualize the similarity in overall species composition found among samples and permutational multivariate analysis of variance (PERMANOVA) with 1000 permutations to compare impacted and unimpacted sites. Biodiversity was compared between site types using KW tests on the Shannon diversity index (Shannon 1948), species richness, and species evenness (Simpson 1949). To determine which benthic species are characteristic of impacted and unimpacted sites, respectively, an indicator species analysis from the 'labdsv' package (Dufrene & Legendre 1997, Roberts 2019) was applied to the species abundance by sample matrix. This analysis accounts for invertebrate site fidelity and relative abundance to identify species that preferentially occur at impacted and unimpacted sites, respectively.

To test for differences between the prevalence of parasites or diseases observed at impacted and unimpacted sites, chi-squared tests with Yates continuity correction were used in instances where expected values were <5. For significant chi-squared results with multiple comparisons (e.g. 5 sites), pairwise chi-squared tests with Bonferroni correction were used. All data were analyzed in RStudio (Version 1.0.153, R version 4.1.2).

3. RESULTS

3.1. Habitat

Most shelters encountered were sponges (mean ± SD = 13.1 ± 8.0 per 25 m transect), although solution holes (0.69 ± 0.8), rocks (0.63 ± 1.8), and coral heads (0.5 ± 0.8) were also found along transects. Unimpacted sites had significantly fewer overall shelters than impacted sites, and fewer sponge shelters in particular (Fig. 2a–c; shelters: $H = 4.5$, $p = 0.03$; sponges: $H = 5.7$, $p = 0.02$); however, there were no differences between the number of loggerhead sponge shelters ($H = 1.6$, $p = 0.20$) or solution holes ($H = 0.02$, $p = 0.89$). The mean size of all shelters, sponge shelters, and loggerhead sponge shelters at unimpacted sites was larger than at impacted sites (Fig. 2b–d; shelters: $H = 50.5$, $p < 0.001$; sponges: $H = 49.2$, $p < 0.001$; loggerhead sponges: $H = 49.2$, $p < 0.001$). Sponge biomass density did not significantly differ between impacted (18.0 ± 29.1 cm^2) and unimpacted sites (11.0 ± 8.2 cm^2; $H = 0.18$, $p = 0.67$).

At unimpacted sites, benthic coverage was dominated by red macroalgae *Laurencia* spp. (35.7 ± 33.9%), sand (34.3 ± 16.9%), and various green macroalgae (e.g. *Halimeda* spp., *Udotea* spp., and *Penicillus* spp.; 23.2 ± 16.6%). The impacted site benthos was dominated by sand (60.5 ± 18.0%), turtle grass *Thalassia testudinum* (19.9 ± 27.6%), and green macroalgae (15.2 ± 16.7%). Other coverage encountered along transects included the sponges *Ircinia*

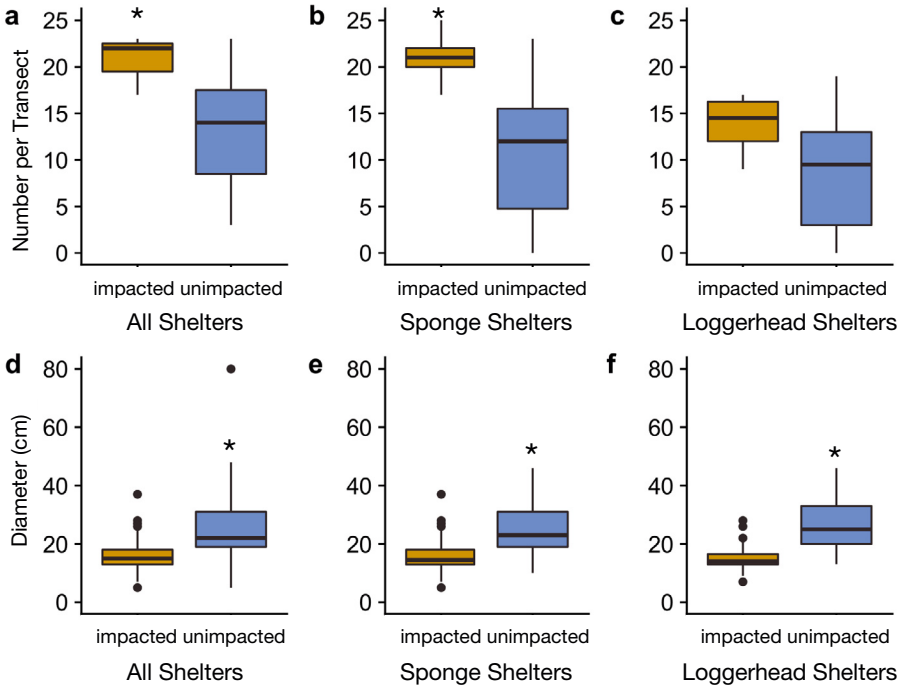

Fig. 2. Number of (a) shelters, (b) sponge shelters, and (c) loggerhead sponge shelters per transect and the diameter in cm of (d) shelters, (e) sponges, and (f) loggerhead sponges at impacted and unimpacted sites surveyed. The horizontal lines indicate the means, the box dimensions include the 25th and 75th percentiles, and the whiskers extend to the minimum and maximum, with outliers shown as closed circles. Asterisks indicate shelters at a given site that are significantly greater in number or size based on Kruskal-Wallis *H*-tests

strobilina and *I. campana*, golfball coral *Favia fragum*, the sea fan *Gorgonia ventalina*, and the brown macroalgae *Sargassum* spp. Pairwise comparisons of benthic coverage revealed greater macroalgal coverage on unimpacted sites ($H = 7.7$, p = 0.005), greater abiotic coverage on impacted sites ($H = 5.7$, p = 0.017), and no differences in corals ($H = 0.11$, p = 0.74), seagrass ($H = 0.44$, p = 0.51), or sponge benthic coverage ($H = 0.02$, p = 0.88; Fig. 3).

3.2. Benthic community

We identified 1734 individual invertebrates from 102 taxa (Table 2) belonging to the phyla Mollusca, Arthropoda, Echinodermata, Annelida, and Sipunculida. Neither the number of individuals ($H = 0.22$, p = 0.64) nor total biomass per sample ($H = 0.24$, p = 0.63) differed between unimpacted (n = 40.3 ± 34.1; biomass = 7.03 ± 6.40 g) and impacted (n = 34.2 ± 27.2; biomass = 5.92 ± 4.40 g) sites. There were more sipunculids in samples from impacted (n = 7.1 ± 6.9) vs. unimpacted sites (n = 3.3 ± 3.9; $H = 5.56$, df = 1, p = 0.02). All other phyla and major taxonomic groups showed no differences between the number of individuals per sample at impacted vs. unimpacted sites. When comparing just species found at both impacted and unimpacted sites, there were differences in the mass of the major taxonomic groups at each site type; individual bivalves ($H = 13.3$, p < 0.001) were on average 5.5× heavier on unimpacted (0.93 ± 1.27 g) than impacted sites (0.17 ± 0.17 g), and chitons ($H = 4.5$, p = 0.03) were on average 2.5× heavier on unimpacted (0.02 ± 0.01 g) than impacted (0.009 ± 0.006 g) sites. No other phyla or major taxonomic groups were significantly different in mass between impacted and unimpacted sites.

The centroids and dispersion of epibenthic and infaunal communities differed between impacted and unimpacted sites (PERMANOVA $R^2 = 0.078$, p = 0.001) and between seagrass and hard-bottom (PERMANOVA $R^2 = 0.037$, p = 0.03), but there was no interaction between site type and bottom type (PERMANOVA $R^2 = 0.018$, p = 0.65; Fig. 4a). No differences in community structure metrics were identified at seagrass vs. hard-bottom habitats (diversity: $H = 0.71$, p = 0.40; richness: $H = 0.23$, p = 0.63; evenness: $H = 3.0$, p = 0.08); therefore, these bottom types were combined for the remaining analyses.

Communities at unimpacted sites had higher species diversity ($H = 9.4$, p = 0.002; Fig. 4b), richness ($H = 4.3$, p = 0.04; Fig. 4c), and evenness ($H =$

5.0, p = 0.03; Fig. 4d). At unimpacted sites, *Tucetona pectinata* and Atlantic oyster drill *Urosalpinx cinerea* were identified as indicator species (Dufrene & Legendre 1997), whereas indicator groups on impacted sites included sipunculids, flyspeck cerith *Cerithium muscarum*, stocky cerith *C. litteratum*, and Morton's egg cockle *Laevicardium mortoni*.

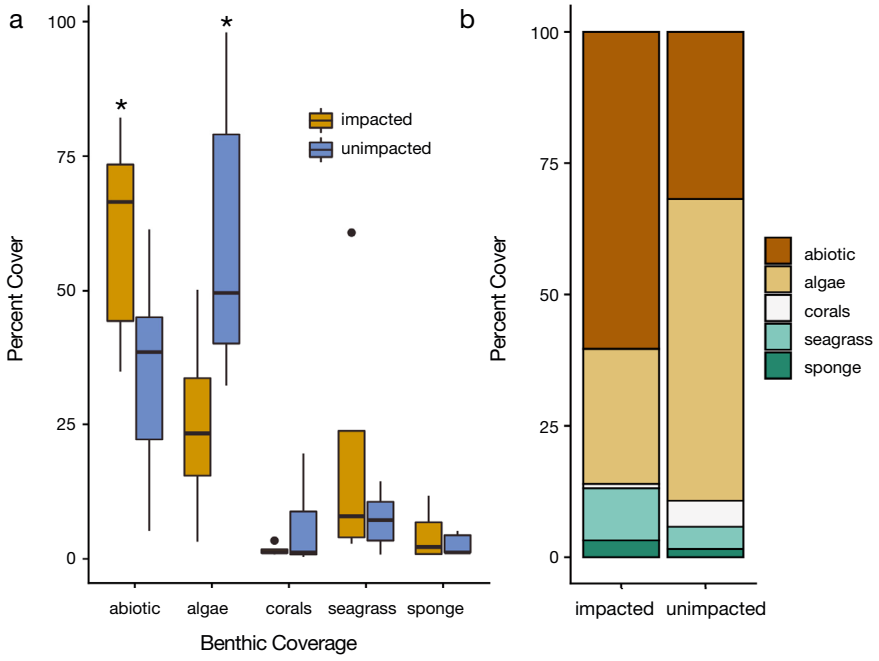

Fig. 3. Benthic coverage was assessed using the point-intercept methods on 25 m transects (n = 4) per site. (a) Percent cover by coverage type, colored by site type. Boxplot limits as in Fig. 2. Asterisks indicate significance based on Kruskal-Wallis *H*-tests. (b) Total percent coverage by site type

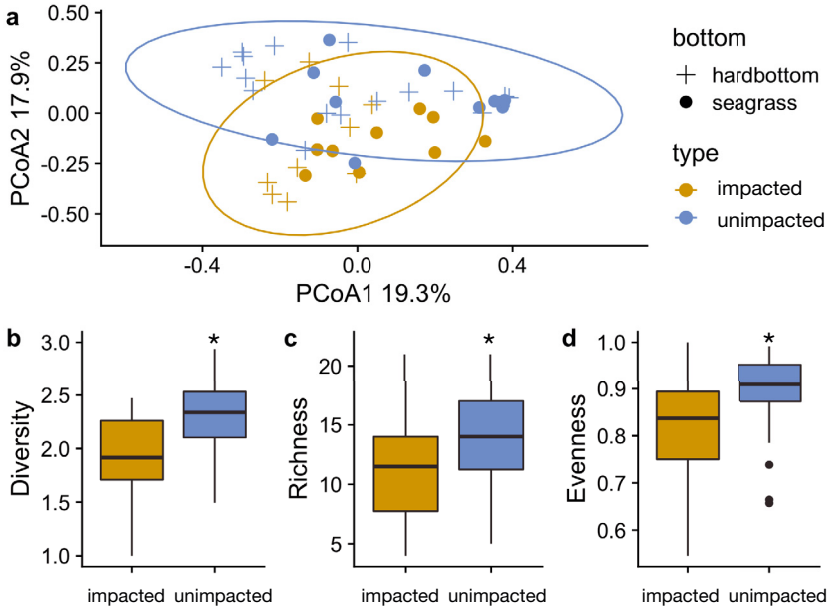

Fig. 4. Epibenthic and infaunal invertebrate communities were assessed through suction sampling and species identification. Using (a) principal coordinates analysis (PCoA), which calculates the similarity between entire suction samples, we show that invertebrate communities differ between impacted and unimpacted hardbottom. Invertebrate communities on healthy hardbottom have higher (b) Shannon Diversity index, (c) species richness, and (d) species evenness. Boxplot limits as in Fig. 2. Asterisks indicate significance based on Kruskal-Wallis *H*-tests

Table 2. Individual invertebrates identified from suction samples collected at impacted and unimpacted sites, listed to lowest taxon identified. Indicator values from indicator species analysis, calculated based on site fidelity and relative abundance, are listed. Significant indicator species are denoted with asterisks (*p < 0.05; **p < 0.01; ***p < 0.001)

Taxon	Impacted	Unimpacted
Annelida		
Amphinomidae	0.00	0.12
Diopatra cuprea	0.00	0.04
Nereididae	0.21	0.45
Polychaeta	0.11	0.11
Polynoidae	0.00	0.04
Sabellidae	0.04	0.09
Syllidae	0.08	0.50
Terebellidae	0.03	0.34*
Arthropoda		
Achelous floridanus	0.00	0.12
Achelous gibbesii	0.00	0.04
Achelous spinicarpus	0.00	0.04
Achelous spinimanus	0.00	0.04
Alpheus christofferseni	0.13	0.01
Alpheus floridanus	0.15	0.00
Alpheus packardii	0.26	0.22
Alpheus sp.	0.02	0.09
Alpheus verrilli	0.00	0.04
Anomura	0.05	0.00
Anthuridae	0.01	0.09
Brachycarpus biunguiculatus	0.00	0.04
Calappa flammea	0.05	0.00
Callinectes sp.	0.05	0.00
Caridea	0.06	0.02
Coryrhynchus sidneyi	0.00	0.04
Cymothoidae	0.00	0.04
Decapoda	0.05	0.00
Ebalia sp.	0.03	0.02
Epialtus elongatus	0.01	0.12
Erichsonella floridana	0.03	0.02
Euryplax nitida	0.05	0.00
Grapsidae	0.00	0.04
Latreutes fuscorum	0.00	0.12
Leptochela sp.	0.00	0.04
Lysmata rathbunae	0.00	0.04
Neogonodactylus bredini	0.00	0.04
Omalacantha bicornuta	0.01	0.20
Paguristes sp.	0.20	0.10
Pagurus sp.	0.04	0.07
Palaemonidae	0.00	0.04
Panopeus herbstii	0.00	0.08
Paracerceis caudata	0.02	0.05
Penaeidae	0.03	0.03
Penaeus aztecus	0.05	0.00
Penaeus setiferus	0.00	0.08
Periclemenes sp.	0.08	0.05
Pitho lherminieri	0.25	0.26
Portunus sayi	0.05	0.00
Precessa sp.	0.00	0.04
Rimapenaus constrictus	0.00	0.04
Stenopus sp.	0.00	0.08
Tyche emarginata	0.00	0.04
Xanthidae	0.17	0.16

Taxon	Impacted	Unimpacted
Echinodermata		
Amphiuridae	0.20	0.41
Holothuroidea	0.00	0.08
Ophiuridae	0.01	0.20
Oreaster reticulatus	0.00	0.04
Mollusca		
Acanthochitona pygmaea	0.03	0.02
Acanthopleura pygmaea	0.00	0.15
Americardia media	0.03	0.02
Anadara sp.	0.00	0.04
Bivalvia	0.00	0.04
Bostrycapulus aculeatus	0.00	0.12
Bulla striata	0.07	0.20
Cerithium eburneum	0.26	0.24
Cerithium litteratum	0.33**	0.00
Cerithium muscarum	0.59*	0.13
Cerithium sp.	0.30*	0.00
Cerodrillia thea	0.03	0.03
Chama congregata	0.00	0.04
Chione cancellata	0.00	0.15
Columbella mercatoria	0.00	0.12
Conasprella jaspidea	0.15	0.06
Conus sp.	0.00	0.04
Costoanachis avara	0.00	0.08
Cylindrobulla beauii	0.00	0.08
Drilliidae	0.00	0.04
Eoacmaea pustula	0.00	0.08
Favartia cellulosa	0.02	0.05
Fulvia laevigata	0.18	0.04
Gastropoda	0.00	0.08
Ischnochiton papillosus	0.00	0.08
Laevicardium mortoni	0.53***	0.00
Laevicardium pictum	0.05	0.00
Limaria pellucida	0.00	0.08
Lithopoma phoebium	0.00	0.15
Lottia antillarum	0.00	0.04
Mitrella dichroa	0.00	0.04
Modulus modulus	0.16	0.21
Natica tedbayeri	0.02	0.02
Niveria quadripunctata	0.05	0.00
Olivella sp.	0.00	0.08
Olivella watermani	0.00	0.12
Parvilucina crenella	0.02	0.25
Phrontis vibex	0.02	0.02
Polyplacophora	0.05	0.10
Prunum apicinum	0.05	0.13
Tegula fasciata	0.01	0.16
Tellina sp.	0.08	0.20
Tucetona pectinata	0.00	0.44***
Urosalpinx cinerea	0.02	0.50**
Vermicularia spirata	0.10	0.00
Vokesimurex rubidus	0.00	0.04
Sipunculida	0.67***	0.16

3.3. Parasite communities

There was no difference in size between lobsters collected at unimpacted (mean ± SD carapace length [CL] 47.9 ± 14.7 mm; n = 49) versus at impacted sites (52.4 ± 17.4 mm CL; n = 22; $H = 1.1$, p = 0.31). There was no evidence of *Ameson herrnkindi* infection via PCR. One lobster exhibited gross signs of PaV1 infection during necropsy, and 18.3% of *Panulirus argus* were positive for PaV1 via PCR. Significantly more lobsters from unimpacted sites (26.5%) were infected with PaV1 than those collected from impacted sites (0%; $\chi^2 = 5.5$, df = 1, p = 0.02).

Menippe mercenaria (n = 65) measured 68.1 ± 20.7 mm in carapace width (CW) at unimpacted sites and 69.0 ± 13.2 mm CW (n = 44) at impacted sites, which did not differ significantly ($H = 0.0002$, p = 0.99). *M. mercenaria* were collected from solution holes at unimpacted (56.9%) and impacted (95.5%) sites; however, more crabs were collected from living shelters, such as sponges and coral heads, on unimpacted (26.2%) vs. impacted sites (4.5%). There was no evidence of *Hematodinium* sp. infection via histopathological screening, and all PCR assays were negative for *Hematodinium* sp.

Histopathological screening identified the trophont stage of a trophically transmitted apicomplexan gregarine, *Nematopsis* sp., in the gut of 20.2% of *M. mercenaria* (Fig. 5a). No significant difference in the percentage of infected crabs between unimpacted (23.1%) and impacted sites (15.9%; $\chi^2 = 0.45$, df = 1, p = 0.50) was observed; however, there was a site effect ($\chi^2 = 12.9$, df = 4, p = 0.01), and 1 unimpacted site (Russel Key) had significantly lower prevalence (4.0%) than the other 2 unimpacted sites: Craig Key (31.6%; $\chi^2 = 4.2$, df = 1, p = 0.05) and Shands Key (38.1%; $\chi^2 = 6.4$, df = 1, p = 0.005). When site was removed from the comparison, unimpacted sites (35.0%) had significantly higher prevalence of the gregarine infection relative to impacted sites (11.4%; $\chi^2 = 5.4$, df = 1, p = 0.02; Fig. 5c).

Putative prey species collected for parasite screening included *Lithopoma americanum* (n = 2), *T. pectinata* (n = 12), and *Fasciolaria tulipa* (n = 4). Through histopathological analysis, the oocyst stage of a *Nematopsis* sp., was observed in the gills of *T. pectinata* (Fig. 5b), as well as a trematode in the digestive gland. Prevalence of *Nematopsis* sp. was 91.7%; however, no *T. pectinata* were found and necropsied at impacted sites (Table 3).

Maguimithrax spinosissimus (n = 7) (CW = 41.5 ± 20.7 mm) and *Achelous spinimanus* (n = 4) (CW = 52.7 ± 12.0 mm) were also collected. Histopathological analysis revealed a trematode encysted in the primary gill filament of 1 *M. spinosissimus* (Fig. 6a) and a systemic infection of *Hematodinium* sp. in the

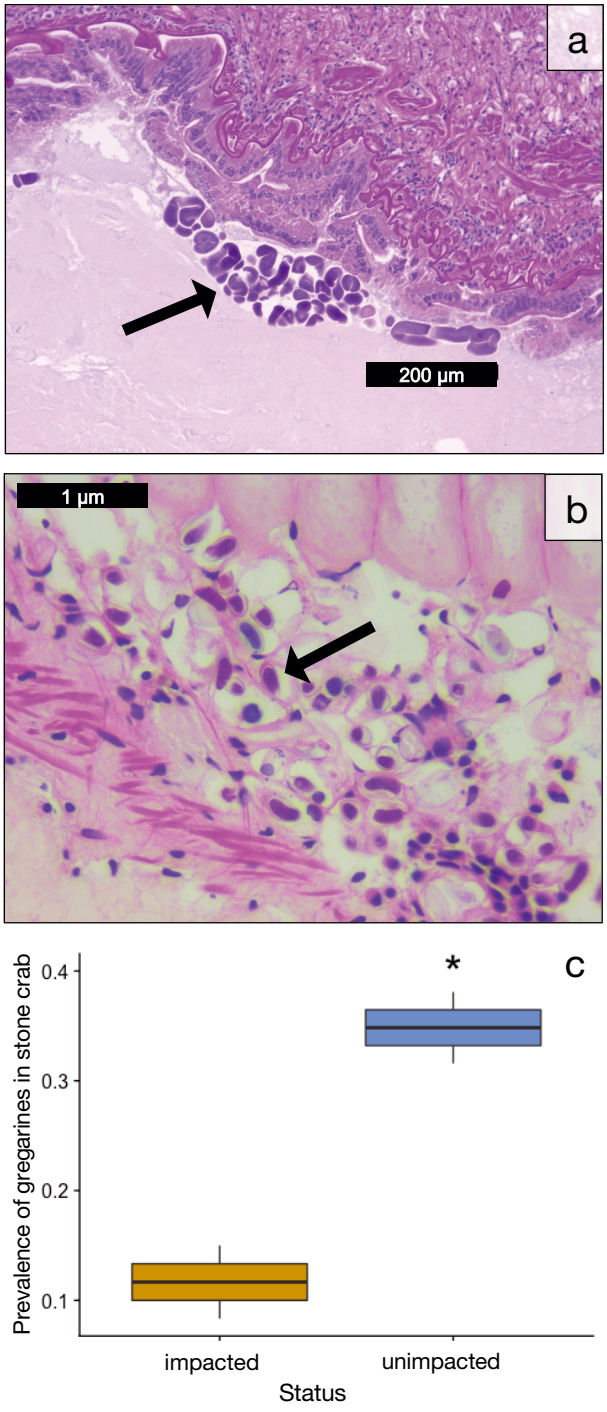

Fig. 5. *Nematopsis* sp. gregarine apicomplexan (a) trophont stage infecting stone crab *Menippe mercenaria* hindgut tissue and (b) oocyte stage infecting *Tucetona pectinata* primary gill filament. (c) Prevalence of *Nematopsis* sp. infecting *M. mercenaria* on impacted and unimpacted sites. Boxplot limits as in Fig. 2

Table 3. Percent prevalence of identified parasites in *Menippe mercenaria*, *Panulirus argus*, *Tucetona pectinata*, and *Maguimithrax spinosissimus*. For size measurements, carapace width is given for *M. mercenaria* and *M. spinosissimus*; carapace length is given for *P. argus*, and shell width is given for *T. pectinata*. Prevalence of *Hematodinium* sp., *Panulirus argus* virus 1 (PaV1), and *Ameson herrnkindi* detected via conventional PCR. Prevalence of *Nematopsis* sp. detected via histopathology. nd: data were not available; na: not applicable

Site type	Sex distribution (M:F)	n	Size (mm) (mean ± SD)	*Hematodinium* sp.	*Nematopsis* sp.	PaV1	*Ameson herrnkindi*
Menippe mercenaria							
Unimpacted	35:30	65	68.1 ± 20.7	0	35.0[a], (23.1)	na	na
Impacted	18:26	44	69.0 ± 13.2	0	11.4	na	na
Panulirus argus							
Unimpacted	23:26	49	47.9 ± 14.7	na	na	26.5	0
Impacted	11:11	22	52.4 ± 17.4	na	na	0	0
Tucetona pectinata							
Unimpacted	nd	12	17.9 ± 4.3	na	91.7	na	na
Impacted	nd	0	na	na	0	na	na
Maguimithrax spinosissimus							
Unimpacted	5:0	5	41.2 ± 25.3	20	0	na	na
Impacted	2:0	2	42.4 ± 1.9	0	0	na	na

[a]*Nematopsis* sp. prevalence given without crabs collected at site Russel Key (prevalence with Russel Key in parentheses)

hepatopancreas, muscle, and gill of another *M. spinosissimus* (Fig. 6b). The *Hematodinium* internal transcribed spacer (ITS) sequence obtained via PCR from this *M. spinosissimus* in the Florida Keys (GenBank accession no. OM913495) showed 100% similarity to *H. perezi* isolated from *Callinectes sapidus* in Texas, USA (accession KX244634, e-value = 1×10^{-162}) and environmental water samples in Maryland (accession KF727429, e-value = 7×10^{-162}) (Li et al. 2010, Pagenkopp Lohan et al. 2012, 2013). This is the first report of *H. perezi* in *M. spinosissimus*.

4. DISCUSSION

In this study, we documented for the first time significantly different epibenthic and infaunal invertebrate communities at unimpacted hard-bottom sites and those impacted by repeated cyanoHABs in the Florida Keys. The difference is particularly notable in the relatively greater mass of bivalves at unimpacted sites compared to impacted sites, and the low abundance of the bivalve *Tucetona pectinata* at impacted sites. Furthermore, *T. pectinata* appears to be an intermediate host of the apicomplexan gregarine *Nematopsis* sp., which is more prevalent in the final host, *Menippe mercenaria*, at unimpacted sites vs. impacted sites, possibly because of the near absence of the intermediate host at impacted sites. This relationship supports the trophic exposure pathway and expected outcome of decreased bivalve density. We also document support for the susceptible host regulation exposure pathway of PaV1 via decreased prevalence on impacted sites. Observation of these disease- and community-based differences persisting 2 yr after a major cyanoHAB indicates that the longevity of the impacts these blooms have can be far-reaching and pervasive in multiple ecological systems. While sponge communities appear to be rebounding with a greater abundance of smaller sponges on sites affected by the blooms, the persistent reoccurrence of the blooms threatens the long-term resilience of sponge communities.

4.1. Ecological resilience of invertebrate communities in the Florida Keys

After an intense cyanoHAB in Florida Bay in 1991, Butler et al. (1995) found that more than 40% of loggerhead sponges and 80% of other sponge species had perished, whereas 95% remained healthy on the periphery of the bloom. Our impacted sites were located within the heavily affected area of subsequent blooms from 2013–2014 and 2016–2017 (Cannizzaro et al. 2019, K. Hubbard pers. comm.) These were sampled in 2019, allowing our study to take place just 2 yr after an extensive sponge mortality event. While a time-series or data from immediately before and after the bloom for comparison would be the best way to affirm that sponges are rebounding

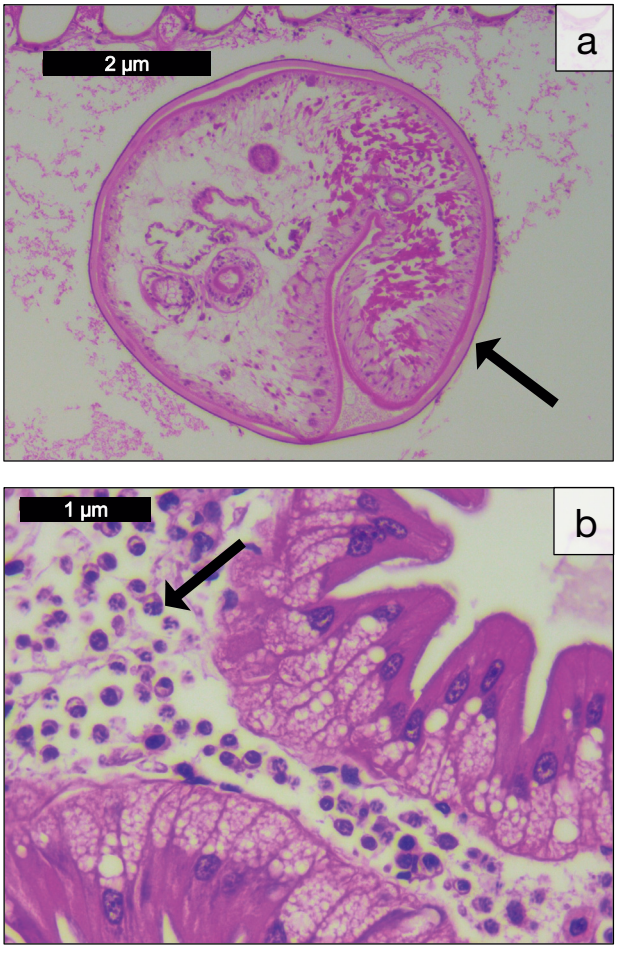

Fig. 6. Parasites (arrows) of *Maguimithrax spinosissimus*: (a) trematode metacercaria encysted in primary gill filament and (b) *Hematodinium perezi* infecting hepatopancreas

between blooms, our data show that more numerous, but smaller, sponges are emerging at degraded sites and represent a good indication of resilience. The nearshore environment of the middle Florida Keys is similar among these sites in terms of depth, water temperature, and habitat (E. Duermit-Moreau unpubl. data). In taking advantage of a natural experiment, we have been able to gather a rich dataset in a natural environment; however, the lack of sampling prior to the blooms may limit our conclusions.

Further evidence of resilience to cyanoHABs is apparent in the overlapping portions of epibenthic and infaunal invertebrate communities at impacted and unimpacted hard-bottom sites. When sponge communities are restored, or environmental conditions allow their regrowth, associated fauna can also return (Butler et al. 2016); however, the overall epibenthic and infaunal communities were distinct and indicative of wider impacts of the cyanoHABs. In particular, the differences in bivalve communities could indicate a direct impact of the blooms on bivalves. Toxin-producing algal blooms affect bivalve larval development (Rolton et al. 2014), clearance rates (Leverone et al. 2007), cellular immunity (Lassudrie et al. 2020), and mortality (Leverone et al. 2006, Griffith et al. 2019). Unlike those HABs, these cyanoHABs do not produce toxins, so we believe the key to this impact is that most bivalves, including *T. pectinata*, are filter feeders, as are sponges. Sponge filtration and water pumping is inhibited by the sticky mucilage produced by *Synechococcus* sp. during high bloom densities (Phlips et al. 1989, Puls 2015) and this mucilage can have a similar effect on bivalves, resulting in direct mortality or inhibiting growth and reproduction and should be examined further.

4.2. Invertebrate biomass and trophic relationships at healthy and degraded sites

Decreased mass of bivalves can have important implications for the health of an ecosystem. In some habitats, such as oyster reefs, they are the dominant filter feeders, capable of increasing water clarity (Beck et al. 2011). They constitute an important prey resource for many vertebrate and crustacean species. *M. mercenaria* are voracious consumers of bivalves (Rindone & Eggleston 2011, Duermit et al. 2015), and we observed extensive evidence of this at unimpacted sites. We specifically observed crushed shells in and around occupied dens and live individuals within dens at sites where this prey item was present.

This trophic link between *M. mercenaria* and *T. pectinata* is likely the transmission pathway for *Nematopsis* sp. (Apicomplexa) found here in the gut and gill of these species, respectively. *N. ostrearum* and *N. prytherchi* have been previously reported in *M. mercenaria* (Sprague 1949, Sprague & Orr 1955); however, no gregarines have been reported in *T. pectinata*. Most apicomplexan gregarines parasitize just a single invertebrate host and have an environmental (free-living or spore) stage, but those in the genus *Nematopsis* have complex lifecycles. Their oocytes can infect bivalves, which act as intermediate hosts, and their trophonts infect decapod crustaceans, the definitive hosts (Sprague & Orr 1955). Molecular identification of this parasite in the oocyte stage has not yet proved successful (Silva et al. 2019), limiting our identification technique. We used a dichotomous key (Clopton 2002) and prior description of the parasite in *M. mercenaria* (Sprague & Orr

1955) to identify the apicomplexan gregarine to genus level for each species in which it was present. There is little evidence in the literature, or in our histological examination, of any pathological effects of *Nematopsis* sp. for either bivalve or stone crab, and there is no indication of zoonosis, so we are not concerned about emergent diseases at this time.

4.3. Parasite community structure across healthy and degraded sites

With the evidence of the trophic exposure pathway and suppressed bivalve density at impacted sites, there is potential for the gregarine to be used as an indicator of ecosystem health to further understand stone crab foraging. Stone crabs sampled from impacted habitats have altered stable isotope signatures, indicating a change in the base of the food web and a broadening of their diet, with some individuals feeding at lower trophic levels (D. Pharo & D. Behringer unpubl.). The decrease in size and abundance of bivalves, a preferred prey item, at impacted sites may be the cause of these trophic changes, requiring stone crabs to feed on less preferred prey (such as annelids and small gastropods). Due to the high prevalence of gregarines in *T. pectinata* (91.7%), gregarines in the gut of stone crab could be an indication of crabs that are feeding on this species of bivalve and are therefore foraging in healthier hard-bottom habitat.

Spatial variation in parasite pressure can be due to the environmental requirements of the parasite (Owens 1983), but for parasites with complex life cycles, spatial variation can depend on the presence of one or more hosts (Jokela & Lively 1995). This pattern has led to increased work in the field of environmental parasitology (Lafferty 1997, Gagne et al. 2022), which argues that thorough knowledge of parasites within food webs can be used as indicators for anthropogenic impacts (Gilbert & Avenant-Oldewage 2021, Pravdová et al. 2021), habitat degradation (Sitko & Heneberg 2020), and the success of habitat restoration or conservation efforts (Moore et al. 2020, Braicovich et al. 2021). Moore et al. (2020) found that parasite abundance and richness mirrored that of free-living species following oyster reef restoration and that both measurements resembled those collected for healthy reefs after 16 mo.

A second association noted between parasitism and habitat in our study included PaV1, a member of the *Mininucleoviridae* (Subramaniam et al. 2020), which was absent in lobsters collected from impacted sites, relative to a 26.5% prevalence of the virus in lobsters from healthy sites. PaV1 can cause nearly 100% mortality in juveniles over 2–8 wk of infection (Shields & Behringer 2004). In the interim, it is directly transmitted between conspecifics, which are gregarious, sharing shelters in rocks, coral heads, and large sponges (Behringer et al. 2018). A loss of large sponges at impacted sites, resulting in shelter limitation, has been shown to regulate susceptible hosts via increased density of lobsters in the few remaining shelters and thus possibly greater infection transmission (Butler et al. 2015). Despite this increase in density, the prevalence of PaV1 does not appear to increase at impacted sites because healthy lobsters are able to detect and avoid diseased conspecifics (Behringer et al. 2006, Butler et al. 2015). We found fewer lobsters overall at impacted sites; however, they were present at similar densities within dens to those found on unimpacted sites. This observation differs from previous studies that found lower densities of lobsters at degraded sites (Butler et al. 2015).

Contrary to previous studies, we found a relatively high prevalence of PaV1-infected lobsters at unimpacted sites. PaV1 can vary in space and time (Davies et al. 2020) so this snapshot of disease prevalence could simply indicate an irregular fluctuation. The prevalence of PaV1 at unimpacted sites could also be indicative of susceptible host regulation via a more attractive settlement habitat for postlarval and early benthic juvenile lobsters, the latter of which are most susceptible to PaV1 (Moss et al. 2012). Unimpacted sites in our study were dominated by macroalgae, with the red macroalgae *Laurencia* spp. being particularly common, whereas impacted sites had less macroalgal cover and more barren sand and rock. The presence of *Laurencia* is an important settlement cue for competent postlarvae, so this could be attracting more potentially infected and susceptible individuals to unimpacted sites.

In contrast to the trophic and susceptible host regulation exposure pathways, we did not find support for the dilution pathway in this system. We saw similar sponge biomass density among the sites, suggesting that filtration of pathogenic bacteria and viruses may be similar, thus not diluted on unimpacted sites. Another way that environmental change is predicted to affect host–pathogen dynamics is by altering host susceptibility (Harvell et al. 2002, 2004). For example, warming water temperatures have been shown to increase prevalence and severity of epizootic shell disease in American lobster *Homarus americanus* (Tlusty et al. 2007, Groner et al. 2018). While we did

not explore this prediction in the present study, it could play a role in this system.

We also screened for *Hematodinium* sp. in *M. mercenaria*, *Maguimithrax spinosissimus*, and *Achelous spinimanus*, which is the cause of various decapod diseases and a significant mortality driver for many crustacean species globally (Stentiford & Shields 2005, Stentiford et al. 2012). *Hematodinium* sp. can negatively impact crab populations and fisheries and is of great interest to fishers and fisheries managers (Small 2012). Despite finding no molecular or histological evidence of *Hematodinium* sp. infection in *M. mercenaria*, we did find molecular evidence of an *H. perezi* infection in 1 *M. spinosissimus* individual, which establishes the presence of this pathogen in the nearshore hard-bottom habitat of the Florida Keys that is shared with *M. mercenaria*. The isolate found here is very similar to that found in stone crab in Georgia, USA (Sheppard et al. 2003). This pathogen can survive as a free-living stage in the environment outside a host (Pitula et al. 2012). It is also capable of being transferred between host species (Li et al. 2021), so it is important to continue to monitor stone crabs for infection using molecular techniques that allow for identification of specific isolates (Bojko et al. 2018).

4.4. Conclusions

We have documented several important ecological changes associated with the periodic cyanoHABs occurring in Florida Bay. Invertebrate communities differ between impacted and unimpacted hard-bottom sites, and the loss of bivalves at impacted sites could be triggering bottom-up trophic changes, particularly for stone crabs. The apicomplexan gregarine *Nematopsis* sp. is present in stone crabs and their prey, *T. pectinata*, and could be used as an indicator of ecosystem health because it is less prevalent in stone crabs found at impacted sites. Evidence of resilience in the hard-bottom ecosystem is apparent, due to the presence of many small sponges at impacted sites, indicating regrowth since the major bloom 2 yr prior. *Hematodinium* sp. was not detected from stone crabs at either site, despite being identified in another crab species. A high prevalence of PaV1 in lobsters from unimpacted sites could be an indication of better settlement habitat for postlarval spiny lobsters. Future studies should examine the direct impacts of these cyanoHABs on bivalves and whether sponge restoration could help mitigate the impacts reported here.

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Appendix

Table A1. Forward and reverse primer sequences used for the amplification of pathogen groups via PCR from genomic template, extracted from host and pathogen tissues. Each PCR run included an initial 5 min denaturation step and a 5 min final extension step, according to the first and final temperatures, respectively, noted in the thermocycler (Tc) settings. The amplification stage consisted of 35 cycles of all 3 temperatures in the Tc settings, with each temperature being held for 1 min or as detailed below. Dir.: direction

Infection	Primer			Tc settings	Amplicon	Reference
	Dir.	Name	Sequence (5′–3′)	(°C)	size (bp)	
PaV1						
	Fwd	45aF	TTC CAG CCC AGG TAC GTA TC	94–63–72	499	Montgomery-Fullerton et al. (2007), Moss et al. (2012)
	Rev	543aR	AAC AGA TTT TCC AGC AGC GT	(45s–45s–1min)		
Ameson herrnkindi						
	Fwd	V1F	CAC CAG GTT GAT TCT GCC TGA C	94–52–72	1100	Baker et al. (1994), Ovcharenko et al. (2010)
	Rev	MC3R	GAT AAC GAC GGG CGG TGT GTA CAA			
***Hematodinium* sp.**						
1st round	Fwd	2009ITS1F	AAC CTG CGG AAG GAT CAT TC	94–60–72	500	Bojko et al. (2018)
	Rev	2009ITS1&2R	TAG CCT TGC CTG ACT CAT G			
2nd round	Fwd	2009ITS1F	AAC CTG CGG AAG GAT CAT TC	94–60–72	350	
	Rev	2009ITS1R	CCG AGC CGA GGC ATT CAT CGC T			

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