Does the benthic invertebrate community reflect disturbances in the central Indian River Lagoon?

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Abstract The Indian River Lagoon (IRL) is home to numerous species of plants and animals, including sessile benthic invertebrates. In addition to being an important component of the ecosystem, sessile benthic organisms may be of use to detect disturbances within the lagoon. This paper presents data from a long-term monitoring program of benthic invertebrate communities at a test site in the central lagoon since 2008. Over this time, these organisms endured the declining health of the IRL along with natural disturbances (i.e., cold snaps, algal blooms, tropical cyclones). Seasonal community composition was similar to what has previously been recorded, indicating that the health of the lagoon has not caused any long-term damage to benthic invertebrate community. However significant impacts were observed with barnacle and encrusting bryozoan cover as a result of various disturbances. Of the three types of disturbances investigated, the cold snap had no effect, the hurricane only had short-term impacts (weeks) and algal blooms had short- and long-term (months) impacts. Barnacle cover was severely reduced by algal blooms and at the same time the encrusting bryozoan cover increased. As algal blooms and anthropogenic disturbances become more frequent in the IRL, barnacles and encrusting bryozoans may be used as an indicator taxa for decreases in habitat quality.

Introduction

While the Indian River Lagoon (IRL) has often been referred to as one of the most biodiverse estuaries in North America (Gilmore 1985), the first effort to put together a comprehensive species inventory was not undertaken until 1994 (Swain et al. 1994). The report provides a baseline of 2493 species present in the lagoon at some stage in their life cycle. Subsequent surveys can compare to this baseline to understand how community composition may change through time within the lagoon.

Included on the first species inventory are many taxa of sessile benthic invertebrates that attach to hard surfaces, including barnacles, oysters, tubeworms and bryozoans. Mook (1976) reported the first in-depth study of the benthic invertebrate community found on hard substrates within the Indian River Lagoon, noting a total of eighteen species. This work was expanded to seventy-two when a wider region of the lagoon was studied (Mook 1983a). More recently, forty sessile benthic invertebrates were identified on oyster reefs in the northern lagoon,

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including several new organisms not identified in 1983 (Boudreaux et al. 2006). Based on these previous studies, it is apparent that temporal variation is prevalent in the benthic community (Mook 1976, Mook 1983a, Boudreaux et al. 2006). The benthic organisms can be placed into two broad categories based on when they are most abundant. One group is comprised of widely distributed species present in the lagoon all year or only during the cooler months, e.g., ivory barnacle (*Amphibalanus eburneus*) or bushy bryozoan (*Bugula neritina*), and the second group is comprised of stenothermic tropical species present only during the warm months, e.g., the encrusting bryozoan *Schizoporella floridana* (Mook 1976).

A solid baseline of benthic invertebrate community composition is useful for assessing impacts of natural and anthropogenic disturbances. Benthic invertebrates, typically infaunal communities, are often used to monitor ecosystems for human-induced impacts because they are sedentary and are representative of conditions of one area (Li et al. 2010). The infaunal community of the Indian River Lagoon has been used to monitor the anthropogenic impacts of increases of freshwater inflow, nutrients and sedimentation within the southern lagoon (Borja and Tunberg 2011). On hard substrates, predation disturbance has been the focus of research (Mook 1981, Mook 1983b, Swain et al. 1998) with the removal of predation pressure having the greatest influence on community structure (Mook 1981). The impacts of other natural and human-induced disturbances on benthic invertebrate communities on hard substrates have not been studied for the lagoon, although impacts from hurricanes (Walters et al. 2007) and an algal bloom (Walters et al. 2021) have been reported for the reef-forming oyster *Crassostrea virginica*. Over its history, the area surrounding the lagoon has been increasingly used for agriculture and urbanized leading to increases in runoff (Kim et al. 2002), thus increasing the load of pollutants and nutrients (Sigua et al. 2000). The decrease in lagoon water quality has led to a loss of biological integrity indicated by the decrease in seagrass coverage (Sigua et al. 2000), which has only continued in recent years (IRL2011C 2015). Given these decreases in lagoon health, it is important to determine whether the benthic invertebrate community has been impacted.

This study takes advantage of a long-term data set to address three important goals. The first goal was to reassess the community composition of sessile benthic invertebrates in the central Indian River Lagoon and to evaluate if community composition changes through time. The second and third goals were to determine if the benthic invertebrate community reflects disturbances, both natural and human-induced, that have occurred in the lagoon, and if any individual taxon could be used as indicator organisms. The benthic community or specific taxon may provide another tool for managers to detect ecological changes in the lagoon.

Materials and Methods

The benthic invertebrate community was monitored in the Central Indian River Lagoon from 2008 to 2019 via settlement panels immersed at a floating test platform. Throughout this time, the test platform has been moored at three different locations. From 2008 until October 2016, it was located at a site approximately 5 km north of Sebastian Inlet (27°53′59.03″ N, 80°28′28.25″ W). Hurricane Matthew destroyed the dock at the Sebastian test site, therefore the platform was moved to a temporary location (28°2′4.93″ N, 80°32′56.52″ W) from October 2016 to February 2017. The data at the temporary

Table 1. Summary of the major disturbances that occurred during the study and were investigated for potential impacts on the benthic community.

Disturbance	Date	Impact on Water Quality	Reference
Cold Snap	January 2-13, 2010	Water temperatures below 10°C	Roberts et al. 2014
Algal Bloom	July-November, 2011	Green algae and cyanobacteria with cell densities exceeding 1×10^6 cells ml^{-1}	Phlips and Badylak 2012
Brown Tide	June-August, 2012	*Aureoumbra lagunensis* with cell densities exceeding 3×10^6 cells ml^{-1}	Phlips and Badylak 2012
Hurricane Irma	September 10-11, 2017	Sustained winds of of ~80.5 km/h with peak gust of 151.3 km/h; 25-38 cm of rain; lowest salinity of ~10	Hanisak and Davis 2018; NOAA 2020

location were not included in analyses due to the short duration at and the lower quality of the test site. After a new long-term site was found in Grant, FL (27°55′47.32″ N, 80°31′32.15″ W) the test platform was moved in February 2017 where it remained for the rest of the study (until December 2019). An analysis of similarities (ANOSIM) indicated that the community composition was similar between the Sebastian and Grant test sites (ANOSIM-R < 0.1, p = 0.6), therefore the data were pooled for all analyses.

Community data were collected from August 2008 to December 2019 using 25.4×30.5 cm panels made of either polyvinyl chloride (PVC) or PVC panels coated with gray epoxy paint. PVC panels were utilized from September 2008 to May 2017 and epoxy-coated panels were used from January 2013 to December 2019. An ANOSIM indicated that substrate type did not influence the benthic invertebrate community (ANOSIM-R < 0.1, p = 0.6), therefore the data were analyzed together. Every month two double-sided panels, allowing for four surfaces, were deployed on frames to ensure panels remained at 0.5 m below the surface (ASTM D3623 2012). Panels remained in the water for three months, after which they were visually assessed in the field for organisms that could be identified by the naked eye and were directly attached to the surface (ASTM D6990 2011). Cover of each functional group, which are based on morphology (e.g., barnacles, tubeworms, tunicates), was estimated using cover analysis (ASTM D6990 2011). When organisms were overlapping, only those organisms attached directly to the panel were included in the analysis.

A literature review was conducted to identify major natural and human-influenced disturbances that have occurred during the same period as the benthic invertebrate monitoring (Table 1). Four disturbances were chosen based on their impact to other organisms in the lagoon, including a cold snap, two algal blooms and one major tropical cyclone. In 2010, Florida experienced a historic cold snap with the coldest period occurring January 2-13. In central-east Florida, daily temperatures were 8-11°C below normal and nearshore water temperatures dropped below 10°C (Barlas et al. 2011, Roberts et al. 2014). A major bloom of picoplankton green algae and cyanobacteria occurred from July to November 2011 (Phlips and Badylak 2012). A major brown tide event occurred from June to August of 2012, which was the first observation of *Aureoumbra lagunensis* since monitoring began in 1997 (Phlips and Badylak 2012). Both blooms were recorded in the Mosquito Lagoon, northern Indian River Lagoon and Banana River. Water clarity visibly changed at the test site during the blooms (K. Hunsucker pers. obs.), but no quantitative measurements are available. The tropical cyclone was Hurricane Irma, which passed over central Florida September 10-11, 2017.

All statistical tests were conducted in R (R Core Team 2020, version 4.0.2), and the R package vegan was utilized to perform all multivariate analyses. Permutational multivariate analyses of variances (PERMANOVA) were used to determine if benthic community composition differed by season, month and year. Pair-wise comparisons were made for significant terms, and the *p*-value was adjusted using a Bonferroni correction. Similarity percentages (SIMPER) were used to determine which functional groups contributed to any differences detected during the pair-wise comparisons. A natural logarithm

transformation was applied to cover data for all multivariate analyses to reduce the influence of functional groups with high total cover.

The cover of significant groups determined by the SIMPER analysis were used to determine if the disturbances impacted the benthic community. Mean cover values were then calculated for each month and used to compare between years with the disturbances and years without the disturbances. A Shapiro-Wilk test and a Bartlett's test determined if the assumptions of normality and equal variances were met by the data. Either a Student's *t*-test or a Mann-Whitney *U* test was used to compare data between disturbance and non-disturbance years for the cold snap and the tropical cyclone. An analysis of variance (ANOVA) and a Tukey's test for pair-wise comparisons were used to determine if the benthic community response differed between the two algal blooms as well as years with no algal blooms. Data from visual assessments that occurred during the disturbances were used to test for impacts on mature communities. Data from visual assessments occurring three months following the disturbances, thus the panel that was deployed during the disturbance, were used to determine if community development was impacted by each disturbance. When significant differences in cover were detected between disturbance and non-disturbance years, indicator species analyses were conducted using the multipatt function in the R package indicspecies (De Cáceres and Legendre 2009).

Results

There were eleven functional groups of organisms found attached to the surfaces that fell into three categories. The first category were groups that covered relatively little of the surface (<15%) throughout the entire study, such as algae, sea anemones, sedimentary tubeworms and sponges. The second category, (calcareous tubeworms, hydroids, molluscs and tunicates), were the functional groups that more often covered a small portion of the surface (<20%), but occasionally had increases in total cover. This second category included species such as the eastern oyster *Crassostrea virginica* and potentially several *Hydroides* sp. tubeworms. The final category were the functional groups that were present for the majority of the study and had several instances where they covered >50% of the surface. These included arborescent bryozoans, barnacles and encrusting bryozoans. The majority of barnacles present were *Amphibalanus eburneus*, but *A. amphitrite* and *Balanus trigonus* were also present. Total cover remained relatively high (>85% cover) all year with the lowest cover (>40%) often occurring from February to April (Figure 1).

There were seasonal differences in community structure ($F_{3,671} = 41.5$, p = 0.001) with post hoc analysis indicating all seasons had a unique community composition (p < 0.05 for all comparisons). The seasonal differences were reflected by various functional groups having peaks around the same time every year (Figure 1). Barnacles had the highest cover and dominated panels in late spring to fall with the largest peaks occurring in July-November. In winter, arborescent bryozoans tend to dominate the panels with peaks occurring around February. The benthic community was also different by month ($F_{11,671} = 16.1$, p = 0.001) and year ($F_{11,671} = 18.1$, p = 0.001), however the post hoc analysis was not powerful enough to determine which months or years are significantly different.

Interannual variation was reflected in encrusting bryozoans, where there was an irregular cycle in peaks. As well as large increases in percent cover by less common functional groups, such as a peak in calcareous tubeworms in spring 2014. These
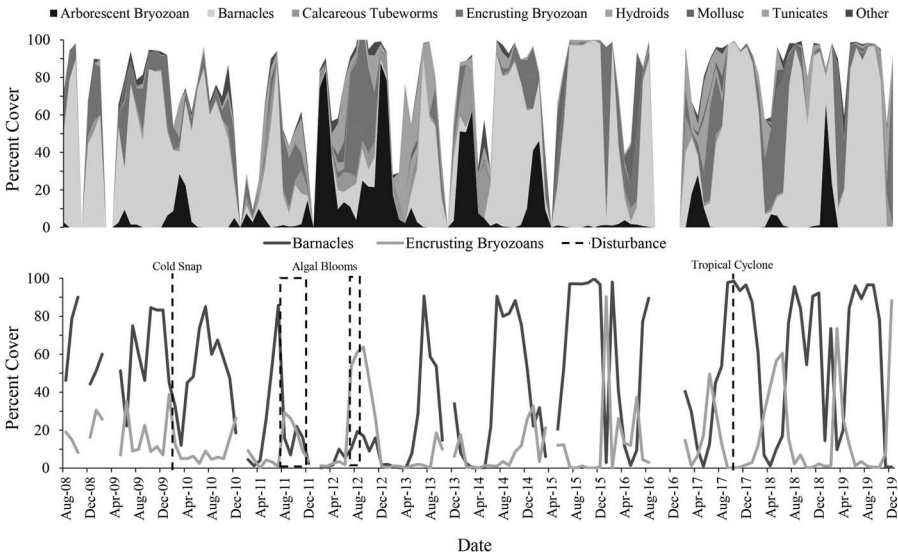
Figure 1. (Top) Benthic invertebrate community composition on settlement panels after a three-month immersion in the central Indian River Lagoon from August 2008 to December 2019. The "other" grouping is comprised of functional groups that covered less than 15% of the surface for the entire study (algae, sea anemones, sedimentary tubeworms and sponges). (Bottom) Mean total cover by barnacles (dark gray line) and encrusting bryozoans (light gray line) during the same time period. The dotted lines on the bottom figure indicate the timing of the disturbances. Gaps in the data are months when panels could not be visually assessed or when the platform was located at the temporary site (October 2016-February 2017).

peaks in less dominant functional groups often occur when there was a lower cover of barnacles.

Barnacles contributed the most to community differences between spring and winter (20.2%), summer (22.5%) and fall (24.1%), as well as winter and fall (20.8%). Encrusting bryozoans contributed the most to community differences between winter and summer (19.6%), as well as summer and fall (22.6%). Therefore, mean barnacle and encrusting bryozoan cover were used as metrics to determine if the benthic community was influenced by the various disturbances (a cold snap, algal blooms and a tropical cyclone).

The cold snap in January 2010 did not impact the mature benthic community nor the benthic community that developed on the panel deployed during the cold period (all p-values ≥ 0.05; Table 2). The mean cover of barnacles was reduced by the algal blooms in the mature community ($F_{2,109} = 33.0$, $p < 0.001$) and the community that developed during the blooms ($F_{2,97} = 10.9$, $p < 0.001$; Table 2). The barnacle cover did not differ between the two algal blooms for both time points ($p > 0.1$). Barnacle cover during the summer of 2011 and 2012 dramatically decreased ($< 25\%$) compared to all other summers (Figure 1). Encrusting bryozoan cover was also impacted in both the mature community ($F_{2,109} = 16.4$, $p < 0.001$) and the community that recruited during the blooms ($F_{2,97} = 30.9$, $p < 0.001$; Table

Table 2. Mean barnacle cover (%) and encrusting bryozoan cover (%) for years with and without disturbances and p-values for the Student's t-test or Mann-Whitney U test. For the algal bloom, the p-values are for the ANOVA.

	Barnacle Cover				Encrusting Bryozoan Cover			
	Disturbance		No disturbance		Disturbance		No disturbance	
	Mean ± SD		Mean ± SD	p-value	Mean ± SD		Mean ± SD	p-value
Cold Snap								
Month of Event	45 ± 30		22.2 ± 28.7	0.09	38.8 ± 27.8		31.6 ± 37.5	0.6
3 Months After Event	12 ± 5.7		12.3 ± 20.3	0.2	5 ± 7.1		14.9 ± 23.9	0.6
Algal Bloom	2011	2012			2011	2012		
Middle of Bloom	7 ± 5.4	10.3 ± 2.1	78 ± 23.9	<0.001	26.3 ± 26.3	53.8 ± 13.1	9.2 ± 15.8	<0.001
3 Months After Middle	16.3 ± 4.8	17 ± 6.7	70.6 ± 32.4	<0.001	9.3 ± 4.3	63.8 ± 4.8	8.9 ± 14.1	<0.001
Hurricane								
Month After Event	97.8 ± 1.3		66.3 ± 31.9	<0.01	0		14.1 ± 20.9	<0.01
3 Months After Event	93.5 ± 5.9		60.5 ± 38.3	0.3	0.5 ± 0.6		9.5 ± 12.2	0.2

2), however cover differed between the two blooms. For both time points, encrusting bryozoan cover was not different between the algal bloom in 2011 and years without algal blooms (p > 0.05), but cover was higher during the algal bloom of 2012 (p < 0.001). For example, mean encrusting bryozoan cover was 63.8 ± 4.8% in the community that developed during the algal bloom of 2012, but was 9.3 ± 4.3% and 8.9 ± 14.1% in the community that developed during the algal bloom of 2011 and during the same period in non-algal bloom years, respectively (Table 2). The hurricane in September 2017 impacted the benthic community immediately after the hurricane passed (both p-values < 0.01) but did not impact the community that developed on panels deployed in the month the hurricane occurred (both p-values > 0.1; Table 2). Mean barnacle cover was significantly higher in the year with the tropical cyclone (97.8 ± 1.3% vs 66.3 ± 31.9%), while encrusting bryozoans were absent in the year with a tropical cyclone.

Indicator species analysis was applied to three of the six disturbance-time point combinations: algal blooms and mature communities, algal blooms and developing communities, and the hurricane and mature communities. Barnacles were associated with years with no algal blooms in both mature communities (IndVal.g = 0.91, p = 0.001) and developing communities (IndVal.g = 0.82, p = 0.001). Encrusting bryozoans were associated with the algal bloom of 2012 in the community that recruited during the algal bloom (IndVal.g = 0.89, p = 0.002), but not in the mature communities (p = 0.10). Encrusting bryozoans were also associated with years with no hurricanes (IndVal.g = 0.89, p = 0.01).

Discussion

Seasonal changes in community composition observed from 2008 through 2019 are similar to what has been previously recorded (Mook 1976) for the Indian River Lagoon. Some organisms had their highest coverage at very similar or the same time as reported by Mook (1976). For example, tubeworms and arborescent bryozoans had their highest cover during warmer and cooler months, respectively. Barnacles seemed to peak later, July-August compared to May (Mook 1976), however this can be accounted for by differences in data collection. Panels were submerged for one month previously (Mook 1976) compared to three months in the current study. Barnacles are often numerically dominant in benthic communities within the lagoon (Mook 1976, Mook 1983a, Boudreaux et al. 2006, Barber et al. 2010) with the ivory barnacle, *Amphibalanus eburneus*, being the most numerous (Mook 1976). This barnacle was also observed to be an important component of the benthic community within the present study. Three barnacle species (*Amphibalanus amphitrite*, *A. eburneus* and *Balanus trigonus*), one bryozoan species (*Bugula neritina*), one mollusc species (*Crassostrea virginica*), and one tubeworm genus (*Hydroides* sp.) were observed during the study, which have also all previously been recorded in the lagoon (Mook 1983a).

After the cold snap of 2010, there were no immediate or long-term impacts on the two community metrics (barnacle and encrusting bryozoan cover) indicating that the benthic invertebrate community is robust against short duration, extreme low temperatures. Extreme cold events often restructure ecological communities

(Boucek et al. 2016) and can lead to massive mortality events of tropical benthic invertebrates (Laboy-Nieves et al. 2001, Colella et al. 2012). However, the Indian River Lagoon is in the transition zone between tropical and warm temperate waters (Mook 1976). In the subtropics, communities are composed of both tropical and temperate species, with the temperate species being better adapted for cooler temperatures (Boucek et al. 2016). In the lagoon during the winter, the benthic invertebrate community is comprised of more cosmopolitan species with wider temperature tolerances (Mook 1976), which may explain the apparent resilience to the cold snap in January 2010.

The tropical cyclone, which are acute but extreme disturbances (Mallin et al. 1999), only had an immediate effect on the benthic community. One of the prominent impacts of tropical cyclones on benthic communities is the severe reduction in salinity due to the increase in freshwater inflow from precipitation and runoff (Andrews 1973, Mallin et al. 1999, Munroe et al. 2013). In 2004, the central Indian River Lagoon experienced four tropical cyclones that brought between 72 and 83 cm of rain decreasing the salinity from 30 to less than 15 (Steward et al. 2006). The lowered salinities are often accompanied with large mortality events (Mallin et al. 1999, Munroe et al. 2013) and if severe enough can eradicate entire populations of benthic invertebrates from portions of estuaries (Andrews 1973). However, recovery can be relatively rapid (Mallin et al. 1999). In the IRL, the benthic community recovered three months following the hurricane in 2017. Conversely, barnacle cover was increased in the lagoon in the years with the hurricane, which is likely due to the wide salinity tolerance of the most common barnacle within the lagoon, *Amphibalanus eburneus* (Bacon 1971).

The biggest impact on the benthic community was seen during and after the large-scale algal blooms that occurred in July-November 2011 and June-August 2012. Both blooms had peak cell counts exceeding 1×10^6 cell ml^{-1} in 2011 and 3 $\times 10^6$ ml^{-1} in 2012 (Phlips and Badylak 2012), which can cause severe shading and low oxygen levels as the bloom begins to die off (Gobler et al. 2013). Chlorophyll *a* concentrations were higher than the long term mean (5 µg L^{-1}) during the entire bloom period in both 2011 (48-86 µg L^{-1}) and 2012 (59-196 µg L^{-1}) (Gobler et al. 2013). Following the 2012 bloom low dissolved oxygen levels (<4 mg L^{-1}) were also recorded at several locations in the lagoon (Gobler et al. 2013). These algal blooms severely reduced the barnacle cover on panels during the event and on panels deployed during the blooms. This may be the result of decreased feeding efficiency. Bloom densities of *Aureoumbra lagunensis*, the algal species that causes brown tide, have been shown to reduce the clearance rate of other benthic fauna such as the hard clam *Mercenaria mercenaria* (Galimany et al. 2017). There could also be a lower larval supply, leading to lower recruitment. *Heterosigma akashiwo*, a bloom forming algae, continuously decreased meroplanktonic larvae during an event off Vancouver Island (Almeda et al. 2011). Cover of encrusting bryozoans was low (< 30%) during both the algal bloom of 2011, which was composed of picoplankton and cyanobacteria (Phlips and Badylak 2013), and the years with no algal bloom. However, it was higher during the brown tide of 2012. The differences in composition of the two blooms likely caused the variation in encrusting bryozoan

cover. However, it is unclear whether bryozoans are negatively impacted by picoplankton and cyanobacteria blooms or if they are unaffected by *Aureoumbra lagunensis* thus can grow more under bloom conditions due to a lack of competition.

Barnacles may serve as an effective indicator taxon of the health of the lagoon. Barnacles have historically been and continue to be a dominant part of the benthic invertebrate community. Barnacle coverage was significantly associated with non-algal bloom years and was sensitive to changes in water quality caused by major algal blooms. Barnacles have been shown to be a useful indicator for changes in water quality in Sydney, Australia (Courtenay et al. 2011). Encrusting bryozoans may also be useful in detecting different types of blooms. However, further study is needed to determine if the changes in cover were related more to the changes in water quality or to the changes in barnacle cover. Barnacles may reduce the recruitment of encrusting bryozoans by larval predation (Young and Gotelli 1988) or the large number of barnacles may just limit space for encrusting bryozoan recruitment and growth. Overall, the changing conditions of the Indian River Lagoon does not seem to have had any lasting impact on the benthic invertebrate community. However, an updated species list for the benthic community in the central Indian River Lagoon is needed to identify potential invasive species or to see if species have been lost from the area.

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