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DO HYDROCARBON AND SALINITY DISTURBANCE AFFECT MARINE MEIOFAUNA DIVERSITY AND COMMUNITY STRUCTURE?

By Kyle Edward Anderson B. A. University of Louisville, 2010

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Department of Biology University of Louisville Louisville, Kentucky

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DO HYDROCARBON AND SALINITY DISTURBANCE AFFECT MARINE MEIOFAUNA DIVERSITY AND COMMUNITY STRUCTURE?

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A Thesis Approved on

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ABSTRACT

DO HYDROCARBON AND SALINITY DISTURBANCE AFFECT MARINE MEIOFAUNA DIVERSITY AND COMMUNITY STRUCTURE?

Kyle E. Anderson

April 13, 2015

Coastal areas around the world are subjected to numerous disturbances, both natural and anthropogenic. Coastal meiofauna are an ecologically important group of organisms that may be sensitive to disturbance and especially useful as indicators of habitat status following anthropogenic disturbances. In this research, I compared the effects of five different intensity levels of hydrocarbon contamination, salinity reduction, and random non-disturbance diversity manipulation on communities of marine meiofauna communities in a microcosm experiment. While I did find the expected negative relationship between intensity and morphogroup diversity in the random treatment, the hydrocarbon and salinity disturbance treatments had no effects on overall diversity, dominance, abundance, richness or community composition. I propose three biological explanations for the lack of a relationship: (i) the communities were not at a late enough successional stage when they were exposed to the disturbances; (ii) the disturbances I tested are not important in structuring the meiofaunal community used in my microcosms; or (iii) ecological theories focused of disturbance, in particular the intermediate disturbance hypothesis, may be generally flawed. For the purposes of impact assessment of oil spills and discharge events, meiofauna are probably a relatively poor indicator group.

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INTRODUCTION

Coastal areas around the world are subjected to numerous disturbances, both natural and anthropogenic. Wave action, El Niño/La Niña events, storm surges and rainwater inputs combine to produce a natural disturbance regime, which can be important in maintaining diversity and structuring communities (Bustamante and Branch 1996, Brodeur et al. 2005, Bownes and Perissinotto 2012, Rodriguez-Gallego et al. 2015). Human activities can affect the disturbance regime by modifying natural processes or by introducing new (or naturally rare) types of disturbance. For example, agricultural and urban modifications to the landscape can affect disturbance in coastal areas through rainwater run-off, resulting in larger pulses of freshwater laden with sediment, nutrients, and contaminants (Short and Wyllie-Echeverria 1996). Human activities in and on the water also contribute to the disturbance of our coasts. Most notably, oil spills can disturb large areas of the coast with contaminants not normally found in the environment (Pezeshki et al. 2000). It is important for ecologists and conservation biologists to understand how different disturbances affect a variety of marine communities in order to make predictions about future impacts of human-caused disturbance and effectively manage their impacts.

Coastal meiofauna are an ecologically important group of organisms that provide an important food source for juvenile fishes and macroinvertebrates, while also playing a role in coastal nutrient cycling (Giere 2009). Of the limited research on coastal meiofauna, much has focused on the potential utility of these organisms in environmental impact assessment following disturbance

(Moore and Bett 1989, Millward and Grant 1995, Kennedy and Jacoby 1999, Schratzberger et al. 2000, Grego et al. 2009). Because of their size, abundance and diversity, impact studies based on meiofauna provide fine-scale data with minimal field effort (Giere 2009). It is unclear, however, whether these communities respond in similar ways to different types of disturbance. Some ecological theory such as the intermediate disturbance hypothesis (IDH) (Connell 1978) predicts that highest levels of diversity will be found at intermediate levels of disturbance, independent of the type of disturbance. However, other studies in non-marine systems have shown that the type of disturbance is important in trying to predict community responses. For example, Chambers, et al. (1990) found markedly different effects of disturbance type (particularly nutrient addition, mulching and turf-clearing) on the emergence of herbaceous seedlings on an alpine plateau. Nutrient addition and turf-clearing both increased seedling biomass, while mulching increased survival rates. Nutrient addition increased second-year mortality in certain species, changing the community composition. As conservation biologists attempt to predict ecosystem responses to a wide range of human-induced changes, it becomes important to test whether communities change in predictable ways in response to disturbance in general, or whether the type of disturbance matters.

In marine systems, two important human-induced disturbances are fluctuations in salinity and hydrocarbon contamination (Short and Wyllie-Echeverria 1996, Pezeshki, Hester et al. 2000). Fluctuations in salinity are normal in coastal areas, as rainwater runoff temporarily dilutes sea water after rain events. However, human activities can modify the quantity and quality of runoff, affecting the degree of salinity fluctuation. Impervious surfaces cause pulses of fresh water to be more severe but shorter in duration (Walsh et al. 2005). Some climate change models suggest that rain events might also become more severe but less frequent in the

near future (Trenberth 1999, Trenberth 2011), which would also increase the severity of runoff dilution disturbances.

Alternately, hydrocarbon contamination rarely happens naturally in most areas, (natural oil seeps are observed in some areas (Hornafius et al. 1999)) but can be a chronic pollutant in developed areas, where hydrocarbons associated with motor vehicles are carried to sea by storm sewers after rain events (Short and Wyllie-Echeverria 1996). It can also occur in acute episodes, as the result of large oil spills. Of particular concern are polycyclic (=polynuclear) aromatic hydrocarbons, several of which are considered priority pollutants by the Environmental Protection Agency (Yan et al. 2004). These compounds are found in high concentrations in diesel fuel and other common hydrocarbon mixtures. Oil spills containing these compounds have been shown to drastically alter biodiversity in marine systems, ranging from large fish to planktonic communities (Incardona et al. 2004, Hjorth et al. 2007).

Compared to terrestrial communities, little is known about the response of meiofauna communities to disturbance and most studies consider only a single disturbance. In this research, I compare the effects of hydrocarbon contamination and salinity reduction on communities of marine meiofauna in a microcosm experiment. I also compare these two disturbances with a random non-disturbance treatment. I specifically ask 1) Does disturbance intensity have a predictable effect on meiofaunal community metrics, especially diversity, independent of disturbance type? And 2) Do different types of disturbance affect community composition in different ways? I predicted that, for both disturbance types, I would find a hump-shaped, or negative quadratic relationship, with maximum diversity and richness at moderate levels of disturbance intensity, following IDH predictions. Dominance is often highest when diversity is lowest, so I expected a positive quadratic relationship between dominance and

intensity in these treatments. For the random treatment, I predicted a negative linear relationship of treatment intensity with diversity and richness, but a positive linear relationship with dominance. Given the recovery period incorporated in the experimental time-table, I did not expect the treatments to affect abundance. Given the unique roles of species in communities, I expected that even if diversity responses were similar across treatment intensities, the community composition would shift in response to each disturbance.

MFTHODS

Preparation of the "seed" communities. To create a hyper-diverse initial community for this experiment, I collected and composited sediment samples from seven local established home and commercial reef aquaria (Appendix 1) ranging in size from 75 to 680 liters by siphoning sediment from an area delimited by a short section of 7.5 cm diameter PVC pipe. I mixed these sediment samples to homogenize and distributed the sediments between two large plastic tubs containing 10 cm of "Seaflor Special Grade Reef Sand" aragonite sand (CaribSea) and 30 cm of artificial sea water (Instant Ocean) mixed to 1.025 specific gravity. One small aquarium filter accomplished water movement in each tub. Chemical and mechanical filtration media were used to remove silt for the first three days after the sediment samples were added; otherwise the filters were used for water movement only. I fed the tubs once per week with two grams of pulverized fish flake for six months to allow the seed communities to colonize the sand bed.

Establishment of the microcosms. Beginning in January, 2014, I added material from the tubs to 45 microcosm aquaria. These microcosms were 3.8L plastic containers with 5 cm of aragonite sand and 12 cm of artificial sea water. Each was lidded, with an airstone and vent to provide water movement and gas exchange. To inoculate microcosms, I siphoned sediments from the seed community using a 4 x 4 cm square acrylic form. I fed the microcosms weekly with 12.5 mg of fish flake in the form of a slurry for six weeks before the disturbance treatments (described below) were applied. Each of the three disturbance types had five levels of intensity, and each treatment was replicated three times.

Random Treatment (R). This treatment simulated a hypothetical (but probably unrealistic) disturbance which affects an equal probability of mortality for all organisms. This "random" manipulation regime was produced by varying the size of the core taken from the seed tanks to inoculate the microcosms. Instead of using a 4 x 4 cm square to inoculate microcosms, I used 6-, 5-, 4-, 3-, or 2-cm square forms when sample the seed community, corresponding to R0 through R4, respectively. This disturbance was expected to result in loss of rare species as the intensity of disturbance increased, only as a demographic consequence of sampling a smaller area, rather than as a consequence of any biological species responses to disturbance.

Hydrocarbon Disturbance (H). Exposure to diesel fuel-contaminated sand at different concentrations defined my hydrocarbon disturbance. To prepare contaminated sand, I mixed 7.6 liters of diesel fuel with 6.8 kg of aragonite sand in a sealed container, which was agitated weekly for six months. After this period, I drained off the diesel and rinsed the sand three times with 7.6 liters of fresh water. I mixed clean sand with contaminated sand to create 5 levels of disturbance, and added 100 g of a given sand mixture to each microcosm. The most severe hydrocarbon treatment was 50% contaminated sand, with subsequent levels containing 37.5%, 25% 12.5% and 0% contaminated sand. After one week, the hydrocarbon treatment was reversed by adding 15 g of activated carbon to each microcosm to adsorb the polycyclic aromatic hydrocarbons and other organic compounds (Woo and Moon 2006).

Salinity Disturbance (S). I reduced salinity in microcosms for this disturbance. I removed water from each microcosm assigned to a salinity treatment and replaced it with de-ionized water to achieve specific gravity of 1.020, 1.015, 1.010, and 1.005 (26.6 to 6.6 ppt) in levels one through four. Salinity control (level zero) replicates were maintained at 1.025 SG (33.2 ppt).

After one week of exposure, the specific gravity was returned to 1.025 by replacing water from the microcosms with hypersaline solution.

disturbance treatments were halted. 90 ml samples were obtained by scooping sediment from the center of the sand bed. I deposited this sediment into beakers and slowly added 100 ml of isotonic magnesium chloride solution to narcotize and relax the fauna. I then stained the samples with aqueous rose bengal and fixed them with formalin (Reid 2000). I separated animals from the sediment by centrifugation in concentrated sucrose solution, sieved through 710 and 38 micron mesh and preserved them in ethyl alcohol. I sorted samples under a dissecting microscope at 10-30x magnification and mounted individuals on slides as necessary for further identification using a compound microscope. I assigned all individuals to one of 19 morphogroups, described below.

Data Analyses. Because early analyses showed no difference between the four-week and nine-week samples, I summed the abundances in these samples to give one larger sample per microcosm. I then calculated richness, abundance, Shannon diversity (H') and Simpson's dominance (D) for each microcosm. I tested for hump-shaped relationships between these univariate community measures and disturbance intensity (levels 0-4) for each type of disturbance using general linear models in SYSTAT 12 (Systat Software 2007). I also initially included experiment start date for each microcosm as a fixed covariate, but removed this term after initial analyses showed it to be non-significant.

To compare effects of the different types of disturbance on community composition, I used PERMANOVA (Anderson et al. 2008), followed by non-metric multidimensional scaling (NMS) ordination of the morphogroup data in PC-ORD (McCune and Mefford 1999) to visualize

any differences. Because rare species can have disproportionate effects on these methods, I eliminated rare morphogroups (< 0.5% of total abundance) from the multivariate analyses. Only six controls (level 0) and the most extreme disturbance intensity treatments (levels 3 and 4) were used for the ordination to maximize differences among treatment types while maintaining even group size. PERMANOVA and NMS were conducted on similarity matrices based on Bray-Curtis distance measures. Initially, I used 250 NMS runs with the real data and performed a Monte Carlo test for significance with 250 runs of randomly shuffled data. After determining the best result from this initial NMS output, I used the best result as the starting position for one final run, which is presented here.

To test whether the my disturbance and dominance data were modeled better as linear or quadratic relationships, I used a model selection approach based on the Corrected Akaike's Information Criterion AIC(cor) from SYSTAT 12 general linear models. The AIC(cor) provides a way of accounting for the tendency of more complex models (the quadratic model, in this case) to fit data better purely by chance and increased flexibility (Akaike 1987). I calculated the probability that the model with the lowest AIC(cor) value was the best model following Posada and Buckley (2004).

RESULTS

Morphogroup descriptions. I identified a total of 19 morphogroups of meiofaunal animals in the sediment samples. Five of these were rare (<0.5% total abundance) and were eliminated from consideration in our multivariate analyses. These morphogroups are described in appendix 2. Copepods dominated the communities in general, with five morphogroups accounting for 74% of the 2200 animals included in the analysis. The most abundant copepod comprised 47% of the total abundance. Because copepods exhibit sexual dimorphisms and indirect development, I was careful to count only adult animals, and avoid defining morphogroups based on traits like antenna and fifth leg shape, which commonly vary between males and females of the same species. For the three most common copepod morphogroups, I was able to identify males and females within the group. See appendix 2 for data on the individual morphogroups, and appendix 3 for micrographs of the copepod morphogroups.

Diversity-Disturbance relationships. Most measures of diversity and abundance were not significantly related to disturbance intensity at all. However, a significant quadratic relationship was found between disturbance intensity and Shannon diversity (H') and Simpson dominance (D) in the random disturbance (R) only (Table 1, Fig. 1).

Disturbance effects on composition. The PERMANOVA showed no significant effects of disturbance type on community composition (Pseudo F= 0.82175; p=0.629). This is clear in the NMS, which shows overlap in community composition among all three disturbance types (Figure

2). A Monte Carlo test on the penultimate NMS result indicates a probability of 0.39 that equal or lesser stress could have been achieved in random data.

Model selection. My analysis showed that the linear relationship model was more likely than the quadratic model to be optimal in five of the six relationships I tested. The only exception was the relationship between the random treatment and dominance, for which there was approximately a 60% chance that it is modeled better by a quadratic relationship. See table 2 for complete results.

DISCUSSION

Results from this study showed no clear relationships between disturbance and community composition in this system. While I did find the expected negative relationship between disturbance intensity and diversity in the random disturbance treatment, the more realistic hydrocarbon and salinity disturbances had no effects on overall diversity or community composition. I can propose three biological explanations for the lack of a relationship: (i) the communities were not at a late enough successional stage when they were exposed to the disturbances; (ii) the disturbances I tested are not important in structuring the meiofaunal community used in our microcosms; or (iii) ecological theories focused of disturbance, in particular the intermediate disturbance hypothesis, may be generally flawed.

The communities used in this study were early in their successional history when we applied the disturbance regimes, as evidenced by the dominance of copepods and scarcity of nematodes. Initial analysis of the source materials harvested from reef aquaria, which had been established two to ten years, showed that nematodes accounted for 86.6% of the total abundance. In the microcosms (established a few months), nematodes account for less than 1% of the total abundance. Contrarily, copepods, which comprised 7.7% of the source community abundance, increased in the microcosms in both absolute and relative terms, more than doubling in density and increasing their share of the total abundance to 73.7%. Copepods mature quickly, with generation times on the order of weeks, bear their eggs externally, and can produce dozens of eggs in a clutch, while meiofaunal nematodes typically mature later, and bear fewer eggs per clutch (Giere 2009). Disturbance can be conceptualized as a force that sets back succession, as in the flipping of marine boulders during storms, which exposes fresh substrate

for colonization and destroys developed communities (Sousa 1979). Because our communities never achieved a late-successional stage, slower-growing competitors never approached equilibrium abundances, so the expected replacement of competitors with tolerators upon disturbance never occurred.

While somewhat surprising, it is possible that hydrocarbon disturbances and salinity shifts may not matter for these communities. The interstitial niche of many meiobenthos can also to buffer the organisms against rapid environmental changes, such as the salinity manipulations we performed (Giere 2009). These communities are not immune to all disturbances, however. Other studies have found effects of metal pollution, hydrological and predation disturbances on meiofauna (Webb and Parsons 1991, Coull and Chandler 1992, Schratzberger and M Warwick 1999, Semprucci et al. 2011). These types of disturbance may be more important than hydrocarbon pollution and salinity reduction in most meiofaunal communities.

It is also important to consider the source of the fauna used in this experiment, and the possibility that the community I started with may have been pre-conditioned to be composed primarily of stress tolerators. I sourced sediments from marine reef aquaria; most of the fauna present in these sediments would have been transported unintentionally with ornamental specimens or "live rock." The harvesting and transportation is stressful, and induces significant mortality (up to 80% for some methods) in the ornamental species (Cato and Brown 2008), so it would be reasonable to expect that stress-sensitive meiofauna would also experience high mortality. Thus, the remaining species of meiobenthos would be those that are pre-evolved to tolerate a range of stressors.

Despite decades of research by ecologists, it may be time to accept the fact that a simple relationship between disturbance and community diversity is not realistic. Although the intermediate disturbance hypothesis continues to be frequently cited, recent reviews find that non-significant relationships between diversity and disturbance are most common (even in published literature), and that the expected, peaked relationship is identified in less than 20% of studies (Mackey and Currie 2001, Randall Hughes et al. 2007). Fox (2013) details the empirical and theoretical critiques of the intermediate disturbance hypothesis, and suggests that it should be wholly abandoned. Mackey and Currie (2001) suggest that it be used only in a narrow set of circumstances.

It is likely that all three of the explanations above contributed to the lack of significant relationships between diversity and disturbance in our experiment. Both meiofauna in general and the communities used in this study may be relatively tolerant to the disturbances we tested, in part due to micro-habitat heterogeneity (Giere 2009), and in part because of species' natural tolerances to disturbance. For the purposes of impact assessment of oil spills and discharge events, meiofauna are probably a relatively poor indicator group. They may be much better indicators of other types of pollution, especially heavy metal contamination. This leads to the final point: this research clearly adds to a large and growing body of evidence showing that the intermediate disturbance hypothesis is not a valid predictor of the relationship between diversity and disturbance for many types of communities and disturbances. The theoretical explanation behind IDH may be a useful interpretation of the "peaked" relationship when it is found, but in most cases alternative models should be developed.

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Table 1. General Linear Model Results. Linear and quadratic effects of disturbance intensity on Shannon diversity, Simpson's dominance, abundance and morphogroup richness. Bold text indicates results significant at α =0.05.

Diversity (H')						
Treatment	Term	Coefficient	Coefficient	Model		
			р	р		
R	LVL	0.194	0.368	0.041		
	LVL*LVL	-0.085	0.117			
Н	LVL	-0.084	0.738	0.886		
	LVL*LVL	0.011	0.88			
S	LVL	0.15	0.227	0.388		
	LVL*LVL	-0.04	0.186			
		Dominance (S)			
Treatment	Term	Coefficient	Coefficient	Model		
			р	р		
R	LVL	-0.087	0.208	0.026		
	LVL*LVL	0.034	0.057			
Н	LVL	0.024	0.857	0.797		
	LVL*LVL	0	0.992			
S	LVL	-0.057	0.231	0.466		
	LVL*LVL	0.013	0.267			
		Abundance				
Treatment	Term	Coefficient	Coefficient	Model		
			р	р		
R	LVL	1.252	0.952	0.85		
	LVL*LVL	-1.103	0.826			
Н	LVL	-3.138	0.887	0.952		
	LVL*LVL	0.31	0.953			
S	LVL	11.197	0.611	0.844		
	LVL*LVL	-2.966	0.576			
Morphogroup Richness						
Treatment	Term	Coefficient	Coefficient	Model		
			р	р		
R	LVL	0.171	0.915	0.127		
	LVL*LVL	-0.284	0.47			
Н	LVL	-0.886	0.525	0.758		
	LVL*LVL	0.238	0.477			
S	LVL	0.464	0.649	0.542		
	LVL*LVL	0.174	0.48			

Table 2. AIC Values for Linear and Quadratic Models. Corrected Akaike's Information Criterion and probability of best modeling (%) for linear and quadratic models of treatment intensity effects on Shannon diversity and Simpson's dominance.

Divorsity	AIC	AIC (cor)		0//Quad)	
Diversity	Quadratic	Linear	%(Lin)	%(Quad)	
R	17.58	16.96	57.69	42.31	
Н	28.02	24.23	86.93	13.07	
S	-0.18	-1.90	70.27	29.73	
	AIC	AIC (cor)		0//Ouad)	
Dominance	Quadratic	Linear	%(Lin) %(Qu	%(Quad)	
R	-16.88	-16.00	39.17	60.83	
Н	3.49	0.33	82.92	17.08	
S	-27.99	-29.50	68.03	31.97	

Figure 1. Quadratic best-fit lines showing relationships between disturbance level and A) Shannon diversity and B) Simpson Dominance for each type of disturbance (R: random, H: hydrocarbon, S: salinity). Only the random treatment relationship is significant.

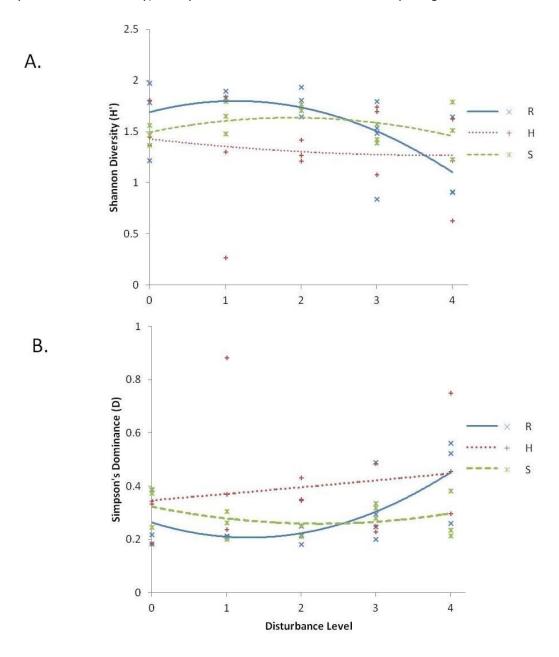
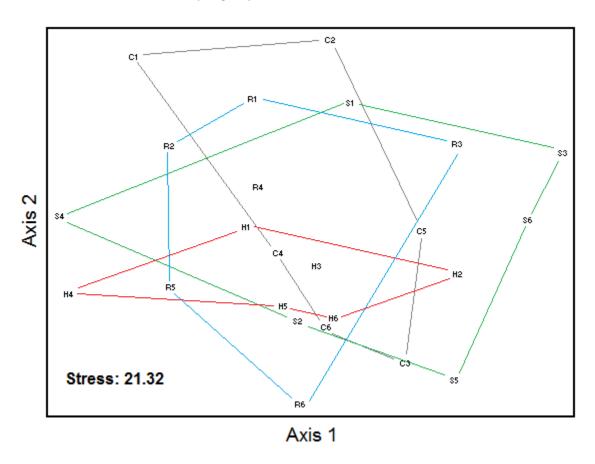


Figure 2. *NMS Plot.* Non-metric multidimensional scaling ordination of community composition associated with randomly-selected control treatments (C1-C6) and the most extreme disturbance treatments (R-random disturbance; H-Hydrocarbon disturbance; S- Salinity disturbance). The first axis of this NMS plot explains 52.6% of the variance in the distance matrix (based on Sorensen distance), and is strongly correlated with the dominant copepod morphogroup. The second axis explains 27.3% of the variance, and is strongly correlated with the second-most abundant morphogroup.



Appendix 1: Sediment sources for seed material.

			General	
	Size		Location in	
Label	(L)	Purpose	Louisville, KY	Notes
F1	190	Home Display	Barbourmeade	Heavily Fed
K1	75	Home Display	Prestonia	At Primary Author's Home
			Mt.	Well Lit, Ca and Carbonate
W1	290	Home Display	Washington	Dosing
S1	280	Coral Stock Tank	Audubon Park	Frequent Stock Rotation
S2	280	Coral Stock Tank	Audubon Park	Frequent Stock Rotation
S3	280	Coral Stock Tank	Audubon Park	Infrequent Stock Rotation
S4	680	Commercial Display	Audubon Park	Soft Corals Only

Appendix 2. Morphogroups.

Morpho- group	General Taxon	Putative Taxon / Identifier	Abundance	% Total Abundance	# Samples	Prop. Samples
1	Harpacticoid copepod	Harpacticoides	1037	46.46	44	100.00
2	Harpacticoid copepod	Arenosetella	195	8.74	34	77.27
3	Harpacticoid copepod	no rostrum, long setae on A1	369	16.53	39	88.64
4	Harpacticoid copepod	Tachidius	30	1.34	11	25.00
5	Halicarid mite		2	0.09	2	4.55
6	Gastrotrich		144	6.45	28	63.64
7	Nematode	predatory	1	0.04	1	2.27
8	Nematode	deposit feeder	20	0.90	11	25.00
9	Oligochaete annelid	Tubificidae	16	0.72	13	29.55
10	Polychaete annelid	"typical"	9	0.40	8	18.18
11	Testate Amoeba		53	2.37	17	38.64
12	Foram	Trochammina	59	2.64	30	68.18
13	Foram	Texularia	35	1.57	22	50.00
14	Foram	Quinqueloculina	193	8.65	41	93.18
15	Ostracod		45	2.02	25	56.82
16	Cnidarian		3	0.13	3	6.82
17	Polychaete annelid	Terrebellidae	2	0.09	1	2.27
18	Oligochaete annelid	non-tubificid	4	0.18	2	4.55
19	Harpacticoid copepod	Tisbe	15	0.67	9	20.45

Appendix 3. *Micrographs of copepod morphogroups.*

Morphogroup 1. 100x magnification.



Morphogroup 2. 200x magnification.



Morphogroup 3. 200x magnification.



Morphogroup 4. 200x magnification.



Morphogroup 19. 200x magnification.



CURRICULUM VITAE

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Diversity and Community Structure?

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RESEARCH INTERESTS:

Generally, I am interested in ecosystem functions, especially invasion resistance, and interspecies biotic interactions. I also have interests in a broad variety of ectothermic taxa including arthropods, corals and fishes. My current research is about the relationship between diversity and invasibility in marine meiofauna -- diverse, abundant animals between about 38 and 500 microns in size. I am using three stress treatments to manipulate diversity, and observing the results of an invasion after recovery. I am interested in furthering my knowledge of advanced quantitative methods including dynamic modeling and multivariate statistics.

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2011: International Public Aquarium Husbandry Series; Husbandry, Management and Conservation of Syngnathids. Shedd Aquarium. (symposium participant)

2010: Marine Ornamental Fish Health Symposium. University of New England. (symposium participant)

TEACHING:

2013-2014: Tutor and Supplemental Instructor, REACH Department, University of Louisville.

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2013: Student Guest Instructor, Advanced Invertebrate Zoology. "Nematodes and other

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PRESENTATIONS:

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ACT - Comprehensive: 31

SAT - Total: 1480

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