


Article

After the Fall: Legacy Effects of Biogenic Structure on Wind-Generated Ecosystem Processes Following Mussel Bed Collapse

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Abstract: Blue mussels (*Mytilus edulis*) are ecosystem engineers with strong effects on species diversity and abundances. Mussel beds appear to be declining in the Gulf of Maine, apparently due to climate change and predation by the invasive green crab, *Carcinus maenas*. As mussels die, they create a legacy of large expanses of shell biogenic structure. In Maine, USA, we used bottom traps to examine effects of four bottom cover types (i.e., live mussels, whole shells, fragmented shells, bare sediment) and wind condition (i.e., days with high, intermediate, and low values) on flow-related ecosystem processes. Significant differences in transport of sediment, meiofauna, and macrofauna were found among cover types and days, with no significant interaction between the two factors. Wind condition had positive effects on transport. Shell hash, especially fragmented shells, had negative effects, possibly because it acted as bed armor to reduce wind-generated erosion and resuspension. Copepods had the greatest mobility and shortest turnover times (0.15 d), followed by nematodes (1.96 d) and the macrofauna dominant, *Tubificoides benedini* (2.35 d). Shell legacy effects may play an important role in soft-bottom system responses to wind-generated ecosystem processes, particularly in collapsed mussel beds, with implications for recolonization, connectivity, and the creation and maintenance of spatial pattern.

Keywords: mussel bed; *Mytilus edulis*; physical ecosystem engineer; shell hash legacy effects; wind condition; biogenic structure; sediment flux; meiofauna and macrofauna transport

1. Introduction

Blue mussels (*Mytilus edulis*) are ecosystem engineers with strong effects on sediment, species composition, and abundances of meiofauna and macrofauna compared to soft-bottoms without mussels [1–10]. Mussel beds can experience dramatic short- and long-term changes in abundance [11–15]. They appear to be declining in the Gulf of Maine, apparently due to climate change [16–21] and predation by the invasive green crab, *Carcinus maenas* [22–25]. When mussels die, they leave behind large expanses of non-living biogenic material in the form of shell hash [3,4,26] (Figure 1A).

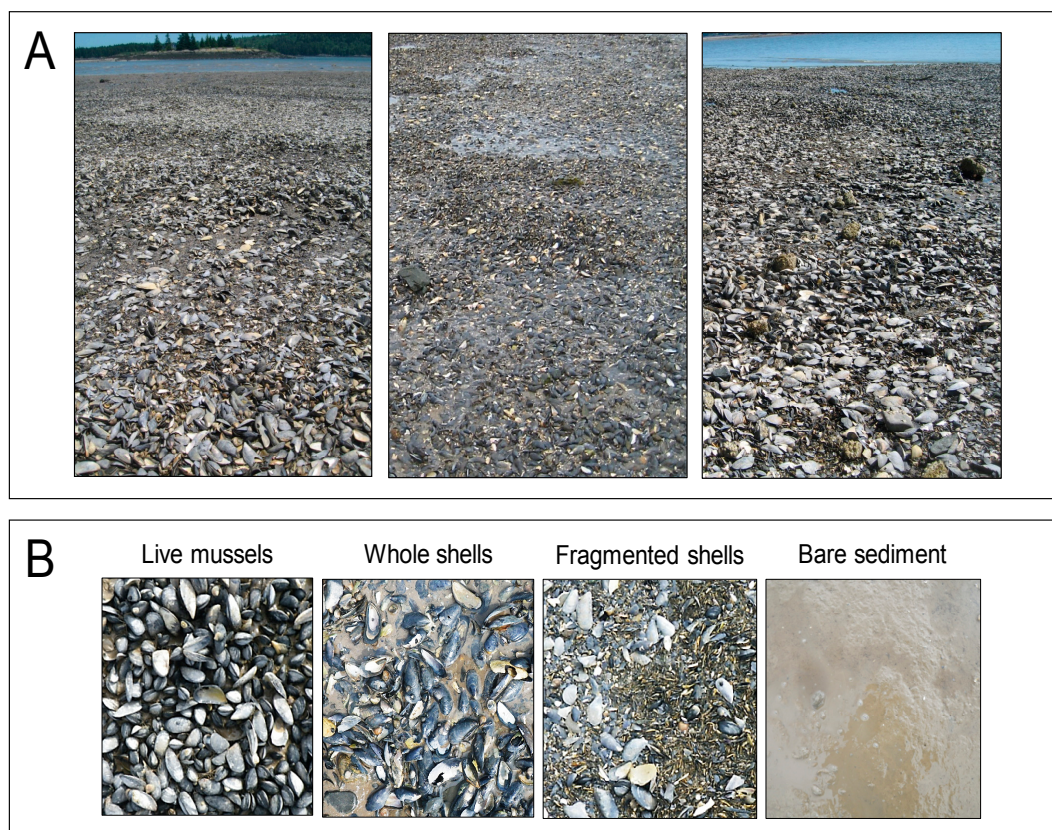


Figure 1. (A) Collapsed mussel beds in eastern Maine, USA. Shell hash is the primary component of the surface of the beds pictured here. (B) The four bottom cover types commonly observed at robust and collapsed mussel beds.

Mussel beds are not a simple matrix of live mussels. At our research sites in Maine, USA, mussel beds have a fractal, hierarchical spatial structure [26–31]. They comprise a complex patchwork of live mussels, bare sediment, and whole (empty) and fragmented shells [3,4,26] (Figure 1B). The influence of these different bottom cover types on flow-related ecosystem processes depends on a variety of patch attributes [4], but remains poorly known. Live mussels and shell hash are roughness elements that project above the sediment surface, creating irregular surface topography that alters water movement over the bottom [4,28]. They convert laminar flow to turbulent flow, where the boundary layer regime affects the transport and resuspension of particles [32–36].

Live mussels and shell hash have significant effects on sediment flux, including the overall mass moved, grain-size proportions, and organic content, as well on univariate and multivariate measures of meiofauna transport, with a smaller influence on macrofauna [2,4]. Rates of sediment flux and animal transport in bedload tend to be positively correlated with wind velocity and the fetch over which the wind blows when water covers the site [37–47]. How does this wind-forcing interact with live mussel, whole shell, fragmented shell, and bare sediment cover types in mussel beds? Does wind-forcing operate independently of bottom cover type, or does a significant interaction occur between wind and cover type?

The answers are important because this type of local dispersal plays a major role in regulating population dynamics and persistence in spatially heterogeneous systems like intertidal soft-bottoms [39,48–52]. Wind-generated transport carries sediment and organisms to nearby locations on a steadily recurring basis. It provides a mechanism for juveniles and adults to colonize suitable sites on each tidal cycle rather than only after larvae are produced in a reproductive event. Wind-generated transport may be particularly important for benthic species that do not produce free-swimming larvae, including meiofauna and some macrofauna [2,4,38,39,42,43,53–58].

For this paper we took advantage of an archived data set from a Maine, USA, soft-bottom, intertidal *Mytilus edulis* bed that has undergone a recent decline in live mussel abundance [4]. We partitioned bottom trap data from that study into days with different wind condition values and calculated three measures of animal dispersal. We found that both wind-forcing and biogenic structure had significant effects on sediment flux and bottom fauna dispersal. Somewhat surprisingly, we discovered no significant interaction between wind condition and bottom cover type, suggesting that they acted independently during the short time course of this investigation. The results provide evidence that changes in biogenic structure after mussel bed collapse have significant impacts on transport of sediment and animals in soft-bottom systems in the Gulf of Maine and elsewhere.

2. Materials and Methods

2.1. Study Site

The research was conducted at Carrying Place Cove, Harrington, Maine, USA (44.5451° N, -67.7844° W), a relatively protected embayment with a bottom of muddy sand (Figure 2A). As is typical in this region, the intertidal mussel bed extends across the mouth of the cove near the low tide line. Long-term time series of aerial photographs suitable for mussel cover analysis do not exist for Carrying Place Cove. However, our twice-per-year field observations at the site over the last 30 years indicate a precipitous drop in mussel abundance at Carrying Place Cove. At the time of this investigation in 2011, digital analysis of photo-transects at the site revealed a scattered array of small, isolated patches of live mussels accounting for <4% of the bottom cover within the bed [4]. Whole and fragmented shells combined covered approximately 20%, and the remaining portion was bare sediment [4].

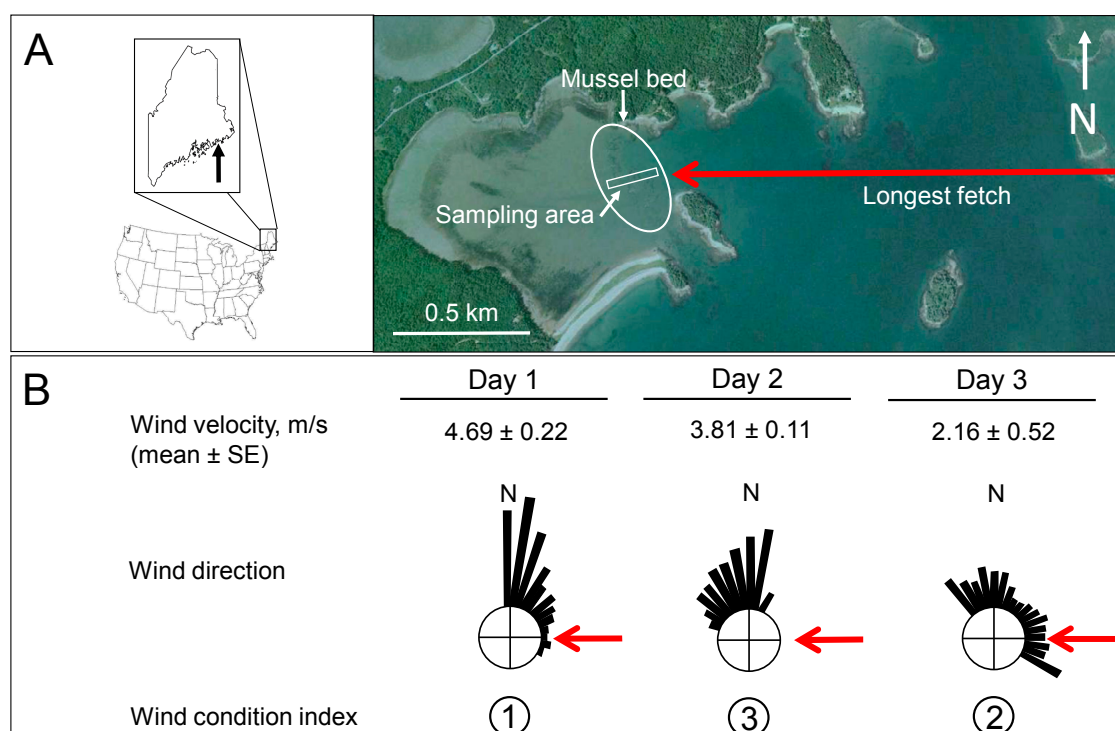


Figure 2. (A) Study site at Carrying Place Cove, Harrington, Maine, USA. Longest fetch is from the east, indicated by red arrow. (B) Wind condition index (Day 1 > Day 3 > Day 2) created by combining wind velocity and fetch values when the bottom was covered with water during the three days of the investigation. Map data copyright 2015 Google.

2.2. Wind Condition

For each of three successive days when the fieldwork was conducted at the site (15–18 May 2011; see below), we created a qualitative wind condition index based on wind velocity and fetch length over which the wind blew. Wind velocity and direction data were obtained from National Ocean Service Station ATGM1-8413320, Bar Harbor, Maine, ≈ 50 km from our study site. For 6-minute intervals when water was covering the bed on each day that traps were deployed (15–18 May 2011), wind velocity was calculated as mean \pm SE and wind direction was plotted on rose diagrams (Figure 2B). For wind velocity, the ranks (highest to lowest velocity) were day 1 > day 2 > day 3. For fetch length, the ranks (longest to shortest length) were day 3 > day 1 > day 2. Assigning equal weight to both factors, the combined wind condition index ranks (strongest to weakest) were day 1 > day 3 > day 2.

2.3. Field and Laboratory Procedures

We used archived data from the study site [4]. Ten patches of each of the four cover types were selected within a 10-m wide band that ran from the upper margin to the lower margin of the center of the bed, using Hurlbert's systematic model [59] to achieve treatment dispersion and reduce the likelihood of segregation, type 1 error, and spurious treatment effects. Large patches of mussels like those used previously [2] could not be found at the site, so patches $\geq 0.5 \text{ m} \times 0.5 \text{ m}$ of all four cover types were utilized.

At low tide on 15 May 2011, a 1.3-cm diameter (cross-sectional area = 1.33 cm^2) core sample was taken 5-cm deep in each of the 40 patches. Cores of this size have been used successfully to sample sediment characteristics, meiofauna, and macrofauna at similar sites in Maine and elsewhere. They collect approximately the same numbers of macrofaunal species as larger cores and allowed us to utilize a larger sample size with the same sampling and laboratory processing effort [2,4,54,55,57]. A 15-cm tall bottom trap of the same diameter (aspect ratio = 11.5:1) was filled with seawater and inserted flush with the sediment surface into each of the holes where the cores were extracted. Because trap capture efficiency declines as traps fill with sediment, in the original study each trap was replaced with a new trap in the same hole on each successive day, and the cumulative contents constituted a single sample for the three-day deployment. For this paper, we took advantage of that sampling strategy and utilized each new trap on each day as an individual sample. To achieve sample independence, we randomly selected three traps from each of the four cover types on each of the three days so that no trap location was used more than once.

Core and trap contents were stained with rose bengal and fixed in situ with buffered formalin. In the laboratory, samples were wet sieved (0.5 mm mesh for macrofauna and the coarse sediment fraction; 0.063 mm mesh for meiofauna and the fine sediment fraction), and the material that passed through the sieves (silt-clay sediment fraction) was retained. Meiofauna (to family or higher levels, e.g., Copepoda, Nematoda, Foraminifera) and macrofauna (to species level when possible [60]) were identified and counted in gridded Petri dishes. The three sediment size classes were dried at 85°C for 24 h and weighed. Organic matter was calculated using loss-on-ignition by burning at 500°C for 4 h [61]. Core contents were analyzed and presented elsewhere [4] and used here only to calculate relative dispersal rate (see below).

Trap contents (Table S1) were used to determine rates of sediment and animal movement [2,4,44,57,62]:

- *Sediment flux rate* = g sediment trap⁻¹ d⁻¹
- *Absolute dispersal rate (ADR)* = number of individuals trap⁻¹ d⁻¹
- *Relative dispersal rate (RDR)* = number of individuals trap⁻¹ d⁻¹ ambient individual⁻¹, calculated by dividing the number of individuals collected in a trap by the number of individuals collected in the core from the same location. Relative dispersal rate normalizes for ambient density. It is equivalent to per capita dispersal. For example, RDR > 1 occurs when the number of individuals in a trap is larger than the number of individuals in its corresponding core. Note that in some cases the number of macrofauna individuals in a core = 0, so RDR was undefined due to the 0 in the

denominator. Those samples could not be used, resulting in unequal sample sizes. Our statistical analysis relied on a balanced design, so RDR was not calculated for macrofauna.

- *Bulk dispersal rate (BDR)* = number of individuals $\text{g sediment}^{-1} \text{ trap}^{-1} \text{ d}^{-1}$, calculated by dividing the number of individuals collected in a trap by the sediment mass collected in that trap. It is a measure of dispersal per unit of transported sediment, providing information on how tightly linked animal movement is to passive bedload transport.

2.4. Data Analysis

Analysis of trap sediment included mass for each grain-size, total mass, and percent organic matter. For meiofauna and macrofauna, analysis included taxon richness (for meiofauna) or species richness (for macrofauna), Shannon–Weiner Index (H') using log base e , and the absolute, relative (meiofauna only), and bulk dispersal rates for each dominant taxon or species and the total number of individuals. Because the oligochaete *Tubificoides benedeni* often dominates the macrofauna in mussel beds and exhibits abundance patterns different from other macrofaunal species [2–4], the non-oligochaetes were also analyzed together as one group. Differences were analyzed using a 2-factor ANOVA design with cover types (4 levels: fixed) and days (3 levels: fixed) as orthogonal factors, with 3 replicates. After application of Cochran’s C-test to check for homogeneity of variances, data were transformed if necessary, as indicated in the ANOVA tables. When significant differences were found ($\alpha = 0.05$), a posteriori comparisons were made using Student-Newman-Keuls (SNK) tests. Cases occurred where SNK could not discriminate among alternative hypotheses despite significant ANOVA differences. Because a posteriori multiple comparisons have less power than the original ANOVA F -test, such cases indicated that the 2 groups with the largest and smallest means within the factor were significantly different, and no further resolution among the groups in that factor could be determined [63]. Analyses were performed with the StatSoft 6.1 computer program [64].

The dispersing assemblages were analyzed with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity measures [65,66]. The PERMANOVA used the same design as the ANOVA (see above) and was executed with the “adonis” function in the “vegan” package for R v3.4.2 [67]. The non-metric multidimensional scaling (nMDS) ordination model based on the Bray–Curtis dissimilarity matrix was conducted with the PRIMER v5.2 package [68] and used to plot the differences in meiofauna and macrofauna assemblages among cover types and days.

3. Results

3.1. Sediment

Significant differences in trap sediment variables were found among cover types and days, with no significant interaction between the two factors (Table 1, Figure 3A,B). Among cover types, silt-clay mass was higher in live mussels than in fragmented shells, with no further discrimination possible. Among days, more fine sediment and total sediment was captured on the day with the strongest wind condition rank (day 1) than on the other days, which were not different from each other. The percentage of organic material was highest on the day with the second strongest wind condition rank (day 3), followed in order by day 1 and day 2. Overall, cover types did not matter as much as days, where the highest total sediment flux rate and organic content were on the days with strongest wind condition ranks.

3.2. Meiofauna

The traps collected eight meiofauna taxa and were dominated by copepods (55.6%) and nematodes (39.8%), followed by foraminiferans (3.9%) and much smaller numbers of other taxa (Appendix A). Significant differences in meiofauna variables were found among cover types and days, with no significant interactions between the two factors.

Among cover types (Table 2, Figure 4A,B), H' was higher in bare sediment than in live mussels, with no further discrimination possible. Absolute dispersal rates (ADRs) for copepods and the total assemblage were lower in fragmented shells than in the other cover types, which were not different from each other. The ADR for nematodes was higher in whole shells than in fragmented shells, with no further discrimination possible. The ADR for foraminiferans was higher in bare sediment than in fragmented shells, with no further discrimination possible. Among days, H' and ADR for copepods, nematodes, foraminiferans, and the total assemblage were generally highest on the days with the strongest wind condition ranks (day 1 and day 3, especially day 1) and lowest on day 2 (Table 2, Figure 4A,B). Overall, fragmented shells depressed ADR values, and wind increased them.

Table 1. ANOVA results for sediment in traps: mass values and percent total organic material. Transformations indicated where applied. Significant differences ($P < 0.05$) are in bold and Student-Newman-Keuls (SNK) results are presented. NAH = no alternative hypothesis; the two groups with the largest and smallest means within the factor were significantly different, and no further resolution among the groups in that factor could be determined. L = live mussels, F = fragmented shells. D1 = Day 1, D2 = Day 2, D3 = Day 3.

Sediment							
Source	DF	Coarse (g)		Fine (g)		Silt-Clay (g)	
		F	P	F	P	F	P
Day	2	2.18	0.194	7.13	0.026	2.47	0.165
Cover	3	2.05	0.134	0.70	0.560	5.26	0.006
Day × Cover	6	0.70	0.652	0.92	0.500	1.35	0.275
Residual	24						
Total	35						
Transformation		Ln(x + 1)				Ln(x + 1)	
SNK Day				D1 > D2 = D3			
SNK Cover						NAH (L > F)	

Source	DF	Total (g)		Organic Matter (%)	
		F	P	F	P
Day	2	7.01	0.027	11.34	0.0003
Cover	3	1.21	0.328	0.51	0.680
Day × Cover	6	0.68	0.664	1.02	0.438
Residual	24				
Total	35				
Transformation		Ln(x + 1)		Ln(x + 1)	
SNK Day		D1 > D3 = D2		D3 > D1 > D2	
SNK Cover					

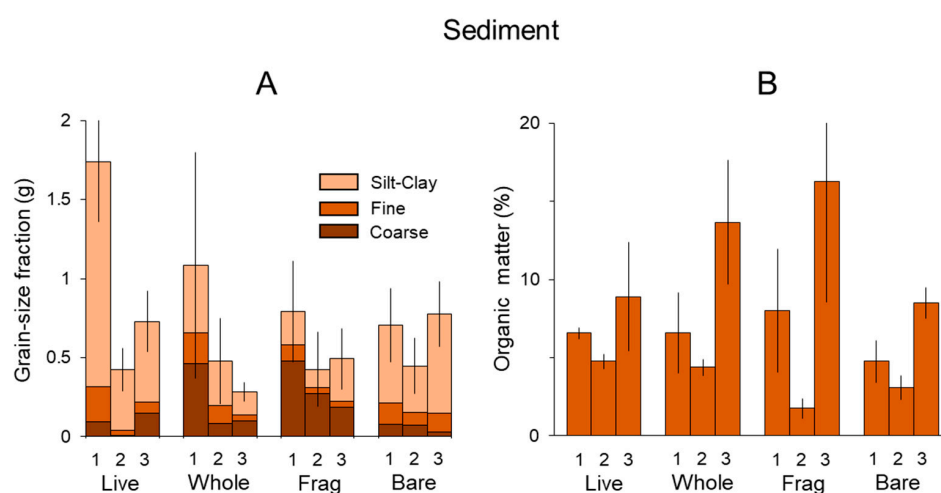


Figure 3. (A) Mass values of silt-clay, fine sand, and coarse material in traps. For clarity, error bars are presented only for total sediment mass. (B) Percent organic matter. Values are mean \pm 1 SE. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. 1 = Day 1, 2 = Day 2, 3 = Day 3.

Table 2. ANOVA results for meiofauna in traps: number of species, H' , and absolute dispersal rates (ADR). Transformations indicated where applied. Significant differences ($P < 0.05$) are in bold and SNK results are presented. NAH = no alternative hypothesis; the two groups with the largest and smallest means within the factor were significantly different, and no further resolution among the groups in that factor could be determined. L = live mussels, W = whole shells, F = fragmented shells, B = bare sediment. D1 = Day 1, D2 = Day 2, D3 = Day 3.

Meiofauna							
Source	DF	No. of Taxa		H'		Total Assemblage	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Day	2	0.72	0.495	4.17	0.028	6.36	0.006
Cover	3	1.20	0.333	5.70	0.004	4.34	0.014
Day × Cover	6	0.54	0.772	2.32	0.066	0.29	0.936
Residual	24						
Total	35						
Transformation						Ln(x + 1)	
SNK Day				D1 > D2 = D3		D1 = D3 > D2	
SNK Cover				NAH (B > L)		W = L = B > F	
Source	DF	Copepods		Nematodes		Foraminiferans	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Day	2	3.72	0.039	10.99	0.0004	3.57	0.044
Cover	3	3.67	0.026	4.04	0.019	4.39	0.013
Day × Cover	6	0.52	0.787	0.38	0.886	1.47	0.229
Residual	24						
Total	35						
Transformation		Ln(x + 1)		Ln(x + 1)		Ln(x + 1)	
SNK Day		D1 = D3 > D2		D1 > D3 = D2		NAH (D1 > D3)	
SNK Cover		W = L = B > F		NAH (W > F)		NAH (B > F)	

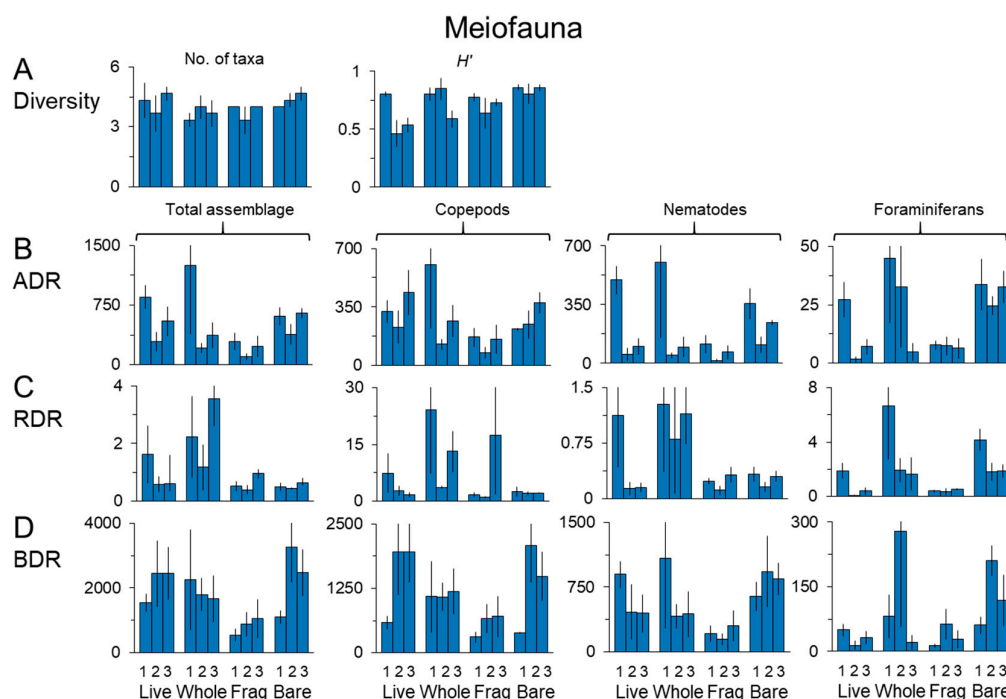


Figure 4. (A) Meiofauna values for number of taxa and H' in traps. (B) Meiofauna absolute dispersal rates (ADR). (C) Meiofauna relative dispersal rates (RDR). (D) Meiofauna bulk dispersal rates (BDR). Values are mean \pm 1 SE. Live = Live mussels, Whole = Whole shells, Frag = Fragmented shells, Bare = Bare sediment. 1 = Day 1, 2 = Day 2, 3 = Day 3.

At the multivariate level, PERMANOVA revealed significant differences in the structure of the dispersing meiofauna assemblage among cover types and days, with no significant interactions between the 2 factors (Table 3). The nMDS plot showed separation among cover types and days (Figure 5A), highlighting the PERMANOVA results. Dissimilarity values were large for fragmented shells compared to the other cover types, as well as for the weakest wind condition day (day 2) compared to day 1 and day 3 with stronger wind condition ranks, consistent with the univariate ANOVA results for ADR.

Table 3. PERMANOVA results for meiofauna and macrofauna in traps. Significant differences ($P < 0.05$) are in bold. For parameters with significant differences among Days or Cover Types, the mean Bray-Curtis dissimilarity values (%) within and among Days and Cover Types are presented. L = Live mussels, W = Whole shells, F = Fragmented shells, B = Bare sediment. D1 = Day 1, D2 = Day 2, D3 = Day 3.

		Meiofauna		Macrofauna	
Source	DF	F	P	F	P
Day	2	3.69	0.006	1.34	0.179
Cover	3	3.03	0.011	1.35	0.153
Day × Cover	6	0.56	0.934	1.41	0.076
Residual	24				
Total	35				
Within Days:					
	D1		40.41		
	D2		48.92		
	D3		41.65		
Among Days:					
	D1 vs. D2		53.39		
	D1 vs. D3		43.87		
	D2 vs. D3		47.84		
Within Cover Types:					
	L		45.32		
	W		47.15		
	F		49.51		
	B		30.04		
Among Cover Types:					
	B vs. L		38.69		
	B vs. W		43.06		
	B vs. F		52.83		
	L vs. W		48.8		
	L vs. F		56.21		
	W vs. F		48.66		

Relative dispersal rates (RDR) were > 1 , indicating high mobility relative to ambient densities, particularly for copepods (Table 4, Figure 4C). RDR among cover types for copepods and the total assemblage were higher in whole shells than in the other cover types, which were not different from each other. RDR was higher for foraminiferans in whole shells than in fragmented shells, with no further discrimination possible, and higher on the day with the strongest wind condition rank (day 1) than on the other 2 days, which were not different from each other. These foraminiferan results should be interpreted with caution because the RDR data for foraminiferans were heterogeneous despite several types of transformation. They are presented because ANOVA is robust to deviations from the assumption of homogeneity of variance when sample sizes are equal [69]. Overall, whole shells and days with high wind condition ranks had the strongest effects on meiofauna RDR. Both increased RDR values.

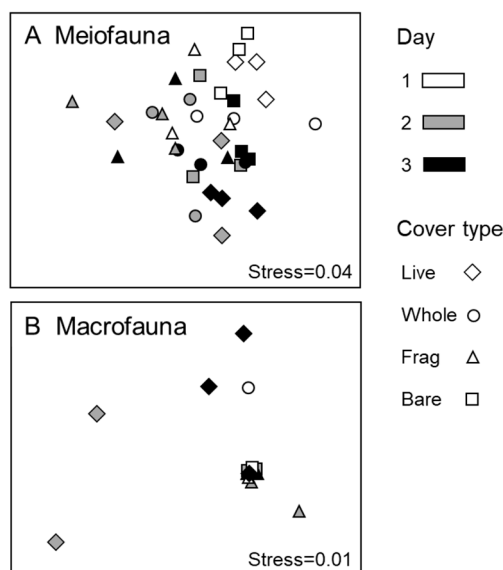


Figure 5. Nonmetric multidimensional scaling (nMDS) plots for traps: (A) meiofauna, (B) macrofauna.

Table 4. ANOVA results for meiofauna in traps: relative dispersal rates (RDR). Transformations indicated where applied. Significant differences ($P < 0.05$) are in bold and SNK results are presented. NAH = no alternative hypothesis; the 2 groups with the largest and smallest means within the factor were significantly different, and no further resolution among the groups in that factor could be determined. L = Live mussels, W = Whole shells, F = Fragmented shells, B = Bare sediment. D1 = Day 1, D2 = Day 2, D3 = Day 3.

Meiofauna					
Source	DF	Total Assemblage		Copepods	
		F	P	F	P
Day	2	2.32	0.120	1.40	0.267
Cover	3	5.21	0.007	3.29	0.038
Day × Cover	6	1.02	0.437	0.96	0.474
Residual	24				
Total	35				
Transformation		Ln(x + 1)		Ln(x + 1)	
SNK Day					
SNK Cover		W > L = F = B		W > F = L = B	
Source	DF	Nematodes		Foraminiferans	
		F	P	F	P
Day	2	1.75	0.196	4.06	0.030
Cover	3	3.00	0.051	3.87	0.022
Day × Cover	6	0.57	0.752	0.89	0.521
Residual	24				
Total	35				
Transformation					
SNK Day				D1 > D3 = D2	
SNK Cover				NAH (W > F)	

Bulk dispersal rate (BDR) among cover types for nematodes was higher in bare sediment than in fragmented shells, with no further discrimination possible (Table 5, Figure 4D). Among days, BDR for copepods was lower on the day with the strongest wind condition rank (day 1) than on the other days, which were not different from each other. Overall, cover types and days had weak effects on BDR compared to their effects on ADR and RDR. Each unit of moving sediment was transported with similar numbers of animals, regardless of cover type or day.

Table 5. ANOVA results for meiofauna in traps: bulk dispersal rates (BDRs). Transformations indicated where applied. Significant differences ($P < 0.05$) are in bold. For parameters with significant differences, the SNK results are presented. NAH = no alternative hypothesis; the two groups with the largest and smallest means within the factor were significantly different, and no further resolution among the groups in that factor could be determined. F = fragmented shells, B = bare sediment. D1 = Day 1, D2 = Day 2, D3 = Day 3.

Meiofauna					
Source	DF	Total Assemblage		Copepods	
		F	P	F	P
Day	2	0.98	0.389	3.77	0.038
Cover	3	2.22	0.112	2.20	0.114
Day \times Cover	6	0.59	0.734	0.81	0.571
Residual	24				
Total	35				
Transformation					
SNK Day				D2 = D3 > D1	
SNK Cover					

Source	DF	Nematodes		Foraminiferans	
		F	P	F	P
Day	2	0.62	0.544	0.92	0.412
Cover	3	3.61	0.028	1.40	0.268
Day \times Cover	6	0.29	0.938	1.02	0.438
Residual	24				
Total	35				
Transformation		Ln(x + 1)		Ln(x + 1)	
SNK Day					
SNK Cover		NAH (B > F)			

3.3. Macrofauna

The traps collected 19 macrofauna species and were dominated by the oligochaete *Tubificoides benedeni* (42.3%), with smaller numbers of polychaetes, an isopod, and other species (Appendix A). None of the macrofaunal variables showed significant differences among cover types or days except for BDR, where non-oligochaetes and the total assemblage had highest values on the weakest wind condition day (day 2), and the other days were not different from each other (Tables 6 and 7, Figure 6A–C).

Table 6. ANOVA results for macrofauna in traps: number of species, H' , and absolute dispersal rates (ADRs). Transformations indicated where applied.

Macrofauna							
Source	DF	No. of Species		H'		Total Assemblage	
		F	P	F	P	F	P
Day	2	1.61	0.221	0.98	0.391	1.57	0.229
Cover	3	0.81	0.502	0.30	0.825	1.34	0.284
Day \times Cover	6	0.34	0.910	0.24	0.958	0.49	0.809
Residual	24						
Total	35						
Transformation						Ln(x + 1)	

Source	DF	Oligochaetes		Non-Oligochaetes	
		F	P	F	P
Day	2	1.96	0.163	1.88	0.175
Cover	3	1.29	0.302	0.48	0.698
Day \times Cover	6	0.76	0.605	0.24	0.959
Residual	24				
Total	35				
Transformation		Ln(x + 1)			

Table 7. ANOVA results for macrofauna in traps: bulk dispersal rates (BDRs). Transformation indicated where applied. Significant differences ($P < 0.05$) are in bold and SNK results are presented. D1 = Day 1, D2 = Day 2, D3 = Day 3.

Source	DF	F	N	P	Macrofauna Parameter			
					Oligochaetes		Non-Oligochaetes	
Day	2	4.65		0.020	F	P	F	P
Cover	3	2.09		0.128	0.94	0.405	4.91	0.016
Day × Cover	6	1.08		0.403	1.68	0.197	0.62	0.612
Residual	24				0.91	0.502	0.64	0.699
Total	35							
Transformation					Ln(x + 1)			
SNK Day				D2 > D3 = D1			D2 > D3 = D1	

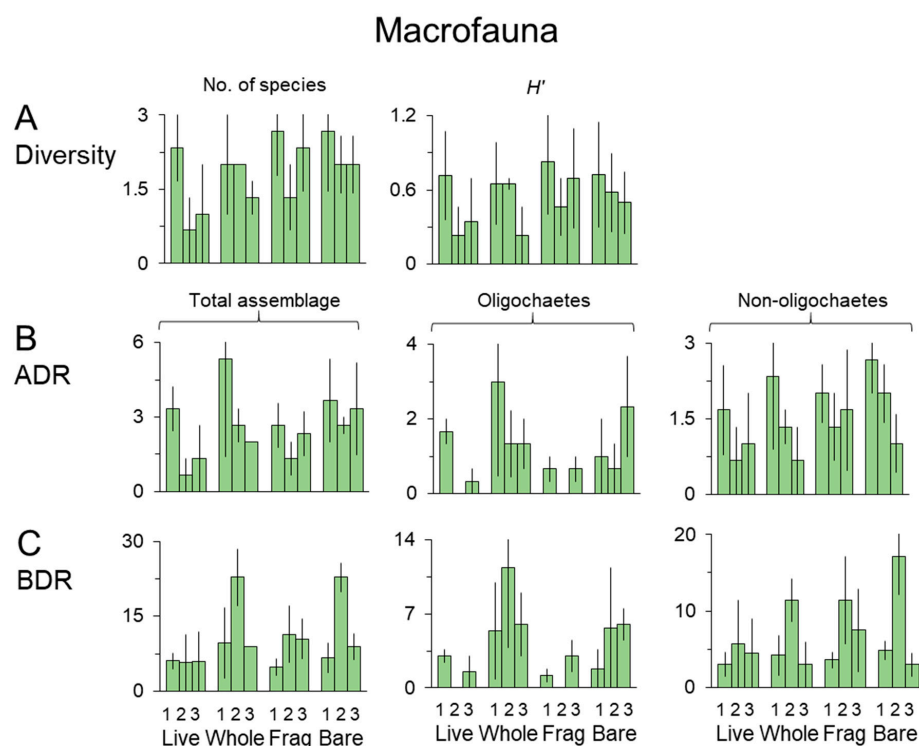


Figure 6. (A) Macrofauna values for number of taxa and H' in traps. (B) Macrofauna absolute dispersal rates (ADRs). (C) Meiobenthos bulk dispersal rates (BDRs). Values are mean \pm 1 SE. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. 1 = Day 1, 2 = Day 2, 3 = Day 3.

At the multivariate level, PERMANOVA revealed no significant differences in the structure of the dispersing macrofaunal assemblage among cover types or days (Table 3B). The nMDS plot showed no separation among cover types and days (Figure 5B). The multivariate and univariate results were consistent in showing little effect of cover types or days on the dispersing macrofaunal assemblage.

4. Discussion

4.1. Cover Types

Fragmented shells were the cover type with the largest impact on sediment flux and animal dispersal. Of the 10 univariate cases with significant ANOVA differences among cover types, fragmented shells were responsible for the lowest value in seven of them (silt-clay; ADR of total meiobenthos, copepods, nematodes, foraminiferans; RDR of foraminiferans; BDR of nematodes).

Fragmented shells also had the largest Bray–Curtis dissimilarity values among cover types revealed by the multivariate PERMANOVA.

Why were fragmented shells so important? Some investigations have shown that mollusk shell material can increase abundance and diversity in benthic systems [36,70–78]. Other studies found mixed, weak, or no effects [40,79–83]. But the effects on flow-related ecosystem processes have not been well-studied. What is it about fragmented shells in particular that caused its flow-related effects at our site? Shell fragments are often observed with their edges projecting upward from the bed [28]. Rough surface elements like these would be expected to increase erosion and resuspension of sediment and animals due to higher turbulent energy and bed shear stress [35,84,85], with reduced flow velocity leading to higher rates of sediment and animal deposition [36].

But fragmented shells had lower rates, not higher. A possible reason is that shell fragments, like terrestrially-derived pebbles and gravel [86], can form a dense layer that acts as bed armor to protect the sediment beneath it from erosion and transport [4]. Because fragments vary in size and shape, they can pack together tightly, with small pieces fitting into the interstices between larger pieces, as predicted by packing theory [87]. This configuration is not possible with whole shells. Whole shells do not exist in as wide a range of sizes, and they are curved, with gaps between shells even when in contact with each other [28]. Compared to shell fragments, whole shells form a more porous, loosely packed layer with exposed sediment between the biogenic elements. In addition, whole shells tend to lie flat on the bed, with a tendency for the convex side to face upward, thus presenting a relatively smooth surface over which water may flow [28].

This argument is not meant to downplay the effects of whole shells. Of the other three significant ANOVA cases, whole shells had the lowest value in two of them (total meiofauna and copepods). In addition, PERMANOVA showed that whole shells had Bray–Curtis dissimilarity values second only to those for fragmented shells. So, both forms of shell hash had significant depressing effects on flow-related ecosystem processes.

Live mussels have been shown in some other studies to affect ambient sediment and community structure [1–4,88]. So, it might make sense that they would have effects on flow-related ecosystem processes. Yet live mussels were responsible for only two significant ANOVA differences among cover types, the highest silt-clay mass and lowest value of H' . Mussels produce copious feces and pseudofeces and project up above the bed surface as roughness elements [28], both of which factors may explain the significant silt-clay result. Increased rates of sediment deposition have been observed in beds of *Mytilus edulis* [2,88–90], other mussel species [91,92], and pinnid bivalves [93,94]. Live mussel cover also represents a pool of species different from the other cover types [1–4,88], which may explain the H' result. The small overall impact of live mussels may have been due to wind conditions that produced turbulent mixing sufficient to lift sediment and animals away from the bottom and export them elsewhere [95]. That kind of interplay might be expected to produce significant interactions between cover types and days, which we never observed.

Bare sediment was responsible for three significant ANOVA difference among cover types (the highest values of H' , ADR of foraminiferans, and BDR of nematodes). As explained above, these results reflect the depressing effect of other cover types on these three variables compared to bare sediment, the dominant cover type at our study site [4].

4.2. Days and Wind Condition

Our results revealed rapid sediment flux and animal dispersal responses to changes in wind condition. Wind condition was strongest on day 1, weakest on day 2, and intermediate on day 3. Had it increased (or decreased) monotonically during the 3-day period, any daily wind condition effects could have been smoothed or obscured by the sustained addition to (or removal from) the water column of resuspended sediment and animals. But wind condition changed non-monotonically over the 3-day period. Concomitant with these changing daily wind conditions, we were able to observe significant daily changes in sediment flux and animal transport. Of the 12 univariate cases with significant

ANOVA differences among days, day 1 (strongest wind condition) was responsible for the highest value in seven of them (fine sediment; total sediment; meiofauna H' ; ADR of nematodes, foraminiferans; RDR of foraminiferans; BDR of copepods). Day 2 (weakest wind condition) was responsible for the lowest value in four of them (percentage of organic material; ADR of total meiofauna, copepods, foraminiferans) and the highest value in two of them, the latter two being the only significant effects observed for macrofauna (BDR of total macrofauna and non-oligochaetes). Day 2 had the largest Bray–Curtis dissimilarity values among cover types revealed by the multivariate PERMANOVA, followed by day 1. Day 3 (intermediate wind condition) had intermediate dissimilarity values, and it never produced any highest or lowest significantly different univariate responses.

Sediment flux and animal transport tend to be positively correlated with wind condition [37,38,40–47,62]. So, our results are consistent with this general pattern. However, bottom hydrodynamics in mussel beds are complex, with laminar flow being converted to turbulent flow over the roughness elements, especially as flow velocity increases [32,35]. Thus, it seemed likely that significant interactions would occur between cover types and days due to varying wind-driven water velocities over the different kinds of roughness elements. Yet neither the ANOVA nor the PERMANOVA results revealed such interactions.

4.3. Modes of Dispersal, Mobility, and Turnover Times

Copepods and nematodes were by far the two most abundant meiofauna taxa in cores and traps at our site, with foraminiferans a distant third. Copepods engage in active emergent behavior and subsequent transport, whereas nematodes are eroded from the bed and transported passively in bedload [53,57]. Relative dispersal rates (RDRs) were >1 individual trap⁻¹ d⁻¹ ambient individual⁻¹ for copepods, indicating that more individuals were caught in a trap in a single day than were located in a core of the same diameter in the same location. Their high per capita mobility contrasts with that of nematodes, which had $RDR < 1$ individual trap⁻¹ d⁻¹ ambient individual⁻¹. In addition, BDR values were higher for copepods than for nematodes, consistent with the RDR results.

In this study, the overall copepod/nematode RDR ratio = $(6.64 \text{ individuals trap}^{-1} \text{ d}^{-1} \text{ ambient individual}^{-1}) / (0.51 \text{ individuals trap}^{-1} \text{ d}^{-1} \text{ ambient individual}^{-1}) = 13.0$. For comparison, we calculated RDR values for copepods and nematodes from data available in other studies. Whether RDR values were larger or smaller than those in this study, their ratios all indicated higher per capita mobility for copepods than for nematodes: intertidal mudflats in Maine [57] ($10.09/0.11 = 91.7$) and Louisiana, USA [96] ($0.97/0.07 = 14.0$) and a high energy intertidal sandflat in North Carolina, USA [54] at high tide ($0.066/0.013 = 5.14$) and flood tide ($0.256/0.126 = 2.03$).

Macrofauna RDR values were not calculated using individual trap and core values for cover types and days in this study, as explained above. However, rough estimates of RDR based on summed values of traps and cores for combined cover types and days were $0.21 \text{ individuals trap}^{-1} \text{ d}^{-1} \text{ ambient individual}^{-1}$ for the oligochaete *Tubificoides benedeni* (by far the dominant macrofauna species) and $0.87 \text{ individuals trap}^{-1} \text{ d}^{-1} \text{ ambient individual}^{-1}$ for the non-oligochaetes as a group. These estimates are in agreement with RDR values < 1 individual trap⁻¹ d⁻¹ ambient individual⁻¹ for *T. benedeni* and a variety of macrofauna elsewhere [2,44,45,62]. These values demonstrate on a per capita basis that macrofauna were somewhat less mobile than passively dispersing nematodes and much less mobile than actively emerging copepods. Macrofauna probably have lower rates of erosion and transport than meiofauna because of their larger size and deeper life position within the sediment. Oligochaetes in particular burrow downwards in response to flow-induced sediment erosion [97].

Turnover time is the number of days it would take for the individuals in an ambient community core to be replaced by new individuals arriving by post-larval transport and settling to the bottom. It is mathematically equivalent to the inverse of the RDR. The RDR, hence turnover time, varied among cover types and days at our research site, but turnover times based on overall mean RDR values were 0.15 d for copepods, 1.96 d for nematodes, 0.55 d for foraminiferans, and 2.35 d for *T. benedeni*. These turnover times point out the highly dynamic nature of our intertidal, soft-bottom research site, despite its location in a low-energy, muddy-sand cove. Meiofauna and macrofauna are on the move

with sediment every day, with implications for recolonization, connectivity, and the creation and maintenance of spatial pattern across scales [47,52].

4.4. Space and Time in Collapsed Mussel Beds

Some of the largest, densest mussel beds where we have conducted research since the mid-1970s, including Carrying Place Cove, contained virtually no live mussels at the time of this study in 2011, and we have observed no rebound since then. The Gulf of Maine sea surface temperature has risen faster in the past decade than in 99% of the world ocean [98]. The region has the world's fastest sea level rise, approximately 3–4 times faster than the world average [99], drowning saltmarshes [100] and posing a serious threat to the very existence of intertidal mudflats [101]. As mussel beds collapse in the Gulf of Maine and elsewhere due to climate change [16–21] and predation by the invasive green crab, *Carcinus maenas* [22–25], at what density and spatial arrangement of individuals will we decide they have ceased to exist as ecosystem engineers? Is it possible that the formerly robust mussel bed at Carrying Place Cove has been depleted of mussels to such a degree that it can no longer even be called a mussel bed? Will there be a time in the future when the different cover types will be so homogenized that biogenic structure ceases to matter?

These existential questions about this important ecosystem engineer have no firm answers. Maine mussel beds could return to their previous levels in response to long-term oscillating oceanographic conditions in the northwest Atlantic region [102–104]. Mussel beds have been observed elsewhere to bounce back relatively quickly after population declines [11–15]. Or mussel beds may shift to a new configuration. In northern Europe where Pacific oysters, *Magallana* (formerly *Crassostrea*) *gigas*, have invaded *M. edulis* beds, both bivalve species can coexist because the oysters provide mussels with a physically complex spatial refuge from predators [105].

In Maine, where invasive oysters have not been observed, a different path is likely. It appears that mussels are producing high cover values of whole or fragmented shells [4], depending on the mode of death, e.g., one or both valves broken by crushing predators, neither valve broken by physiological senescence or thermal stress [106–108]. Over time, shells are exported, buried, or broken down into smaller and smaller pieces, similar in size to terrestrially-derived sand and mud, resulting in bare sediment [106–108]. During this taphonomic time course, we predict a commensurate shift in ecosystem processes affected by flow over the bottom, including sediment flux and animal transport. We predict an initial period with lowered rates of these ecosystem processes because of high bottom cover values of shell hash, particularly fragmented shells, and then a rebound to the rates observed over bare sediment. Because mussels can cover extensive areas in soft-bottom systems [14,29], even subtle changes in these ecosystem processes may assume great importance when integrated over the large spatial extent of potentially collapsing mussel beds worldwide.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/11/1/11/s1>, Table S1: Sediment, meiofauna, and macrofauna data for bottom traps from Carrying Place Cove, Maine, USA.

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Appendix A

Table A1. Macrofauna and meiofauna captured in traps (overall mean + SE individuals per trap) by rank order. For macrofauna: A = Arthropoda, M = Mollusca, N = Nemertea, O = Oligochaeta, P = Polychaeta.

Taxon		Rank	Mean	SE
Meiofauna				
Copepoda		1	268.94	39.57
Nematoda		2	192.06	45.47
Foraminifera		3	19.22	3.76
Ostracoda		4	1.53	0.36
Kinorhyncha		5	0.42	0.13
Halacaridae		6	0.28	0.18
Cumacea		7	0.08	0.06
Acarina		8	0.03	0.03
Macrofauna				
<i>Tubificoides benedini</i>	O	1	1.08	0.27
<i>Lepidonotus squamatus</i>	P	2	0.42	0.14
Polychaeta errant juvenile juvenile	P	3	0.22	0.08
Isopoda sp. A	A	4	0.17	0.07
Ampharetidae sp. A	P	5	0.11	0.05
<i>Capitella capitata</i>	P	6	0.06	0.04
Polychaeta sp. A juvenile	P	6	0.06	0.04
<i>Mya arenaria</i>	M	6	0.06	0.04
<i>Ampelisca abdita</i>	A	6	0.06	0.04
<i>Carcinus maenas</i>	A	6	0.06	0.04
Gammaridae sp. A	A	6	0.06	0.04
<i>Littorina littorea</i>	M	6	0.06	0.04
Phyllodocidae sp. A	P	6	0.06	0.04
<i>Lineus viridis</i>	N	14	0.03	0.03
<i>Hetermastus filiformis</i>	P	14	0.03	0.03
<i>Gammarus finmarchicus</i>	A	14	0.03	0.03
Polychaeta sp. B juvenile	P	14	0.03	0.03
<i>Gammarus oceanicus</i>	A	14	0.03	0.03
Polychaeta sp. C juvenile	P	14	0.03	0.03

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