

Assessing the relationship between community dispersion and disturbance in a soft-sediment ecosystem

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Abstract

Disturbed ecosystems often exhibit increased community heterogeneity when compared to nondisturbed systems. One way to measure community heterogeneity is statistical dispersion, a measure of how variable individual samples are from the multivariate average of the community condition (species presence/absence and density). In more specific manner, dispersion measures the distance between an individual data point and the centroid, the multivariate average of all data points. Statistical dispersion may be an important parameter to include in environmental assessments, or in studies that attempt to understand the role of disturbances in structuring biological systems. However, disturbances have been observed to increase, decrease, or not impact community dispersion (or community heterogeneity). Therefore, the usefulness of dispersion in studying or identifying disturbances is unclear. We tested if a mechanical disturbance increased community dispersion using the infaunal community of the intertidal mudflats along the north coast of British Columbia, Canada. We observed no statistically significant increase in community dispersion with varying frequency and intensity of a mechanical disturbance. This is likely a result of disturbed and nondisturbed treatments being dominated by the same six taxa, thus minimizing dispersion. Therefore, in ecosystems where differences in community successional stages are subtle (a result of changes in relative abundance rather than species replacement), community dispersion may not be an informative parameter when investigating disturbance. Despite this, we suggest that dispersion can be a useful variable to include in studies attempting to understand or identify disturbances; however, dispersion should only be one parameter amongst many used to understand or identify disturbances.

KEYWORDS

community, dispersion, disturbance, environmental assessment, mudflats, Skeena

1 | INTRODUCTION

Early models attempting to understand the dynamics of biological systems through space and time revolved around the concept of equilibrium. Communities were assumed to be at, or approaching equilibrium states, and the importance of competition was

emphasized in structuring these communities (Connell, 1978; Jackson, 1981; Petraitis, Latham, & Niesenbaum, 1989; Schoener, 1982). However, mounting evidence that some systems may never reach equilibrium, resulted in the development of nonequilibrium models to understand biological systems (Connell, 1978; Paine, 1966; Petraitis et al., 1989; Sousa, 1979, 1980). As these models

developed, the role of disturbances in structuring biological systems was emphasized (Connell, 1978; Connell & Slatyer, 1977; Pearson & Rosenberg, 1978).

A disturbance is a discrete event in space and time that alters resources, substratum or the physical environment, consequently disrupting community or population structure (Petraitis et al., 1989; White & Pickett, 1985). Although debates still exist around the details, there is little doubt that disturbances can have large impacts upon ecosystems (Ayling, 1981; Hobbs & Huenneke, 1992; Paine & Vadas, 1969). Beyond impacting the physical environment (Gerwing, Drolet, Barbeau, Hamilton, & Allen Gerwing, 2015; Thrush, Hewitt, Norkko, Cummings, & Funnell, 2003), disturbances can also impact the physiology (González-Tokman, Martínez-Morales, Farrera, Rosario Ortiz-Zayas, & Lumaret, 2017), behaviour (Sturdivant, Díaz, & Cutter, 2012), biomass (Warwick & Clarke, 1993a), density (Conlan, Lenihan, Kvitek, & Oliver, 1998) and richness (Buckling, Kassen, Bell, & Rainey, 2000; Cox et al., 2017) of species/communities. Understanding the role of disturbances in ecosystems is far from a purely theoretical exercise. In a world undergoing rapid global climate change (Houghton et al., 2001; Stachowicz, Terwin, Whitlatch, & Osman, 2002), and with discrete anthropogenic disturbances often interacting with climate change (Barange et al., 2014; Duinker & Greig, 2006; Halpern, Walbridge, et al., 2008), the practical necessity of understanding and predicting the outcome of disturbances is increasing. By bad luck, the impact(s) of a disturbance may vary so widely that predicting its outcome is challenging.

The response of a community to disturbance varies by habitat type (Schratzberger & Warwick, 1998), type and predictability of disturbance (Austen, Widdicombe, & Villano-Pitacco, 1998; Hobbs & Huenneke, 1992; Reice, Wissmar, & Naiman, 1990), initial population densities (Gerwing, Drolet, et al., 2015), life history stages and strategies of affected individuals (Thistle, 1981), species trophic level (Wootton, 1998), type of resources available (Wootton, 1998), community composition and tolerance of species to disturbance (Hobbs & Huenneke, 1992; Warren, 1996), time of year (Gerwing, Drolet, et al., 2015; Hobbs & Huenneke, 1992), competition within the system (Hughes, Jarrett, Kimbro, & Stachowicz, 2007; Violle, Pu, & Jiang, 2010) and community successional stage (Cadotte, 2007; Sousa, 1979; Zajac, Whitlatch, & Thrush, 1998). Further complicating the situation is the fact that a disturbance is often part of a continuous process, with multiple disturbances interacting and impacting a community in a cumulative manner. Therefore, the cumulative impact of the entire disturbance regime must be understood (Crain, Kroeker, & Halpern, 2008; Hobbs & Huenneke, 1992; Reice et al., 1990). Understanding cumulative impacts is difficult, but doing so is essential to comprehend the role of disturbances in structuring ecosystems (Barange et al., 2014; Crain et al., 2008; Halpern, McLeod, Rosenberg, & Crowder, 2008). In more practical manner, such an understanding is necessary if we are ever to conduct robust environmental assessments that can accurately predict the outcome of disturbances associated with climate change or human development (Duinker & Greig, 2006).

Disturbances are often studied using a Before-After-Control-Impact (BACI) design (Underwood, 1994), where environmental, population or community conditions are investigated before and after a disturbance, as well as in impacted (or potentially impacted sites) and nonimpacted sites (Gerwing, Hamilton, Barbeau, Haralampides, & Yamazaki, 2017). The BACI design is a powerful method to detect disturbances, but relies upon sampling before and after a disturbance, as well as in disturbed and nondisturbed sites; conditions that are not always available. Further, it is often challenging to select variables to study in situ, given the number of factors (described above) that can modify the outcome of a disturbance. One informative and relatively easy to measure parameter used in investigations of disturbances is community heterogeneity. Disturbed or stressed communities from multiple habitat types are often highly heterogeneous and characterized by high statistical dispersion (Anderson, Gordon, Crawley, & Hassell, 1982; Fraterrigo & Rusak, 2008; Pearson & Rosenberg, 1978; Warwick & Clarke, 1993b; Wootton, 1998). Statistical dispersion is a measure of how variable individual samples are from the multivariate average of the community condition (species presence/absence and density). In more specific manner, dispersion measures the distance between an individual data point and the centroid, the multivariate average of all data points (Fraterrigo & Rusak, 2008; Warwick & Clarke, 1993b). Disturbances occurring heterogeneously through space and time (Cadotte, 2007; Chambers et al., 2013), or influencing individual members of a community in various ways—species-specific decreases, increases, or no impact (Gerwing, Gerwing, et al., 2017; Vaquer-Sunyer & Duarte, 2008)—will result in community patches diverging from each other, as well as the average community condition (Anderson et al., 1982; Fraterrigo & Rusak, 2008; Warwick & Clarke, 1993b). Community dispersion has been used before to assess whether or not an ecosystem was disturbed by discrete human disturbances (Gerwing, Hamilton, et al., 2017). However, although disturbed communities are often characterized by high community heterogeneity and statistical dispersion (Anderson et al., 1982; Fraterrigo & Rusak, 2008; Pearson & Rosenberg, 1978; Warwick & Clarke, 1993b; Wootton, 1998), other disturbed communities are not (Barnes, 1999; Cowie, Widdicombe, & Austen, 2000; Hughes et al., 2007; Mackey & Currie, 2001; Reise, 1984; Sousa, 1980; Thistle, 1981). As such, the usefulness of dispersion in identifying or understanding a disturbance is unclear; however, dispersion could be a powerful tool to study and identify disturbed habitats.

To the best of our knowledge, no other studies have empirically evaluated the relationship between statistical dispersion and disturbance. Therefore, we used the soft-sediment infaunal communities along the north coast of British Columbia (BC), Canada, to determine whether an infaunal (animals living in sediment) community exposed to varying intensities and frequencies of a mechanical disturbance exhibited higher community dispersion than nondisturbed communities. An infaunal invertebrate community was selected as intertidal infaunal often react strongly to disturbance (Cowie et al., 2000; Gómez Gesteira & Dauvin, 2000; Ruiz et al., 2005; Zajac et al., 1998) and has been used as a model to describe community succession

following disturbances (Pearson & Rosenberg, 1978,1976; Pearson & Stanley, 1979). In more specific manner, previous work has shown that the infaunal community along the north coast of BC varies with disturbances (Gerwing, Gerwing, et al., 2017). Therefore, if disturbed communities do in fact exhibit high statistical disturbance, then measurements of community dispersion may be a powerful tool to study and understand the role of disturbances in structuring biological systems, and to identify disturbances in environmental assessments.

2 | MATERIALS AND METHODS

We used the Cassiar Cannery (CC) mudflat along the north coast of BC to investigate whether community dispersion varied with disturbance (Figure 1). This mudflat is strongly estuarine (4–10 PSU during the time of the experiment), as it lies at the mouth of the Skeena River (Gerwing, Cox, et al., 2017; Gerwing, Gerwing, et al., 2017; McLaren, 2016). CC is dominated by fine silts (<63 μm), with small amounts of fine-grained sand (125–250 μm) also present (McLaren, 2016). The top 1–3 mm of surface sediment is usually oxic, with reduced and anoxic sediment below (Gerwing, 2016; Gerwing,

Gerwing, et al., 2017). Within this sediment, the infaunal community is diverse, and 40 infauna taxa have been observed at CC (Gerwing, 2016; Gerwing, Gerwing, et al., 2017). The number of taxa observed within a 1-m² plot is usually 6, but ranges from 4 to 10. The infaunal community is dominated by Cumacea (primarily *Nippoleucon hinumensis* with *Cumella vulgaris* observed less frequency), Polychaetes (Families Phyllodocidae [*Eteone californica*], Capitellidae [*Capitella* Species Complex] and Spionidae [*Pygospio elegans*]), Oligochaetes (*Paranais litoralis*), Nematodes, Copepods (order Harpacticoida), Amphipods (*Americorophium salmonis*) and the bivalve *Macoma balthica* (Gerwing, 2016; Gerwing, Gerwing, et al., 2017).

2.1 | Experimental design

Sediment was mechanically disturbed, using a garden rake with tines 10 cm long, to a depth of ~25 cm (Cowie et al., 2000), simulating ice scour (Gerwing, Drolet, et al., 2015) or dredging (Thomas, 1993). Sediment was scoured homogenously with the rake until the sediment had a soupy consistency. A mechanical disturbance allowed complete control over the frequency, intensity, duration and scale of disturbance (Gerwing, Gerwing, et al., 2017).

To evaluate whether increasing disturbance frequency increased community dispersion, four experimental treatments (Figure 2) were established at CC on June 2, 2016, during the peak of infaunal community richness and density (Gerwing, 2016): control (no disturbance), F_1 (sediment disturbed once at the beginning of a 4-week period), F_2 (disturbed twice; every 2 weeks in a 4-week period) and F_3 (disturbed four times; every week in a 4-week period). In the middle intertidal zone (equidistance from the high and low water lines), 40 1-m² plots were established, 10 plots per treatment. Rebar was used to mark the corners of each plot, and each plot was further subdivided into four 0.25-m² quadrats. Treatments were randomly assigned to individual 1-m² plots and initially disturbed on June 2nd. At the end of 4 weeks, one sediment sample was collected from the centre of each quadrat, to avoid edge effects, on July 23, 2016 (Gerwing, Gerwing, et al., 2017). Samples were collected using a 10-cm-long sediment corer, with a 7 cm diameter (Gerwing, Allen Gerwing, Drolet, Barbeau, & Hamilton, 2015; Gerwing, Drolet, Hamilton, & Barbeau, 2016; Gerwing, Gerwing, et al., 2017). To retain infauna, sediment was later passed through a 250- μm sieve (Crewe, Hamilton, & Diamond, 2001) and preserved in 95% ethanol ($n = 40$ per treatment, 160 total).

To determine whether increasing disturbance intensity resulted in an increase of community dispersion, five intensity treatments (Figure 2) were established on June 2, 2016: control (no disturbance), I_1 (plots 25% disturbed), I_2 (plots 50% disturbed), I_3 (plots 75% disturbed) and I_4 (plots 100% disturbed). Plots and quadrats were established as described above, and we collected sediment samples at the end of 2 weeks (July 9, 2016; $n = 40$ per treatment, 200 total). Two weeks is enough time for recovery of this community to have begun, but not to have been completed (Gerwing, 2016; Gerwing, Allen Gerwing, et al., 2015; Gerwing, Gerwing, et al., 2017; Reise, 1984).

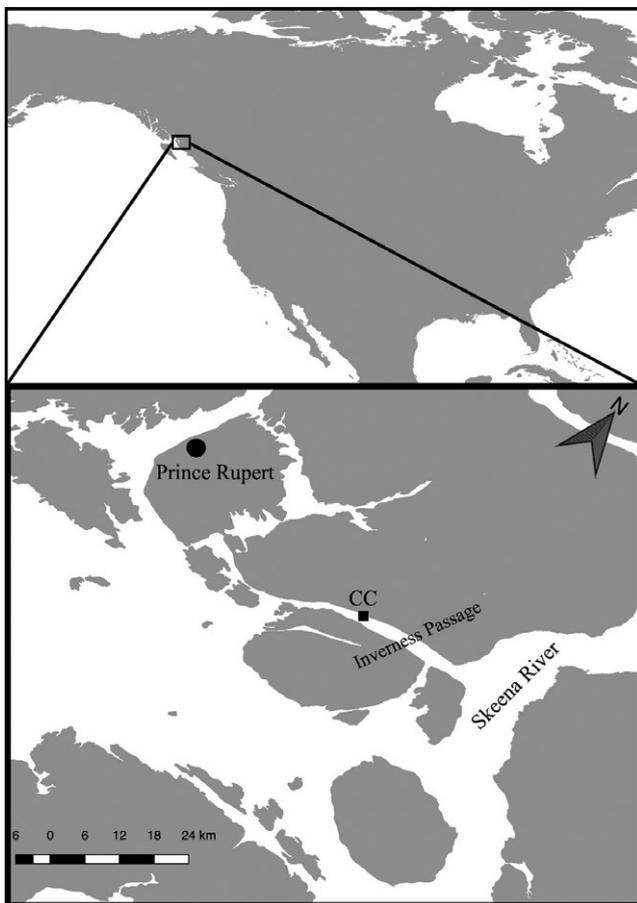


FIGURE 1 Location of the experimental mudflat, Cassiar Cannery (CC; 54.178092°, -130.176924°), along the north coast of British Columbia, Canada

At last, to quantify whether the experimental set-up biased our results, we assessed the appropriateness of control replicates (Underwood, 1997) by also collecting additional experimental control samples (Gerwing, Gerwing, et al., 2017). If control replicates are similar to experimental control replicates, then the rebar set-up did not bias our results, indicating that we can extrapolate our findings to mudflat conditions outside our experimental set-up. On both sides of the experiment, five 3-m transects (10 transects total), separated by 5 m, were established from the top to the bottom of the experiment. The first transect was 5 m away from the experiment to avoid sediment disturbed during experimental set-up. We collected (July 9th) three sediment samples from the top, middle, and bottom of each transect ($n = 30$; collected and processed as described above). Two transects running parallel to, but 5 m from the top and bottom of the experiment were also established. Quadrats were not established, but five sediment samples were collected, as described above, spaced equidistant along each transect ($n = 10$). Overall, we collected 40 additional experimental control samples (Gerwing, Gerwing, et al., 2017).

All sediment samples were later processed under a dissecting microscope, and specimens were identified to the lowest possible taxonomic unit (Gerwing, Gerwing, et al., 2017; Gerwing, Hamilton, et al., 2017; Thrush et al., 2000, 2003). Cumaceans, Amphipods, Polychaetes, Nemertean, and Bivalves were identified to species. Nematodes were identified to phylum, Copepods to order, Ostracods to class, and Chironomids (larvae) to family.

2.2 | Statistical analyses

Community dispersion was calculated using the statistical program PRIMER V.7 with the PERMANOVA (Permutational Multivariate

Analysis of Variance) add-on (McArdle & Anderson, 2001). A resemblance matrix was calculated from infaunal densities using Bray–Curtis coefficients (Clarke, Somerfield, & Chapman, 2006). We fourth-root transformed taxa densities to improve assessment of rare and common taxa on community structure (Clarke & Gorley, 2006). Community data were grouped by treatment and plot (e.g., F_1 treatment, plot 1) to account for multiple measures within a plot, and dispersion, distance of a quadrat from the centroid of grouped data (the four quadrats that make up a plot), was calculated using PERMDISP (Anderson, Gorley, & Clarke, 2008; Fraterrigo & Rusak, 2008; Manly, 2004). In essence, we calculated the statistical distance (in this case unitless) of each quadrat from the multivariate average (centroid) of the four quadrats that made up each 1-m² plot.

ANOVAs using community dispersion as the response variable were conducted in Minitab V.17. Homogeneity of variance was assessed using Cochran's test, and normality of residuals was evaluated visually (Underwood, 1997). In all cases, variances were homogenous, but dispersion data were log transformed to correct for skewed residuals. The appropriateness of control replicates was assessed using ANOVAs, with treatment as a fixed factor (2 levels; control and experimental control). We compared experimental control samples to the samples collected from control quadrats ($n = 40$ per treatment, 80 total). The ANOVA evaluating the relationship between disturbance frequency and community dispersion incorporated treatment as a fixed factor (four levels; control, F_1 , F_2 and F_3 ; $n = 40$ per treatment, 160 total), and plot, nested within treatment as a random factor. The ANOVA investigating the relationship between community dispersion and disturbance intensity was run as described for the frequency experiment (five treatment levels: control, I_1 , I_2 , I_3 and I_4 ; $n = 40$ per treatment, 200 total). In all cases,

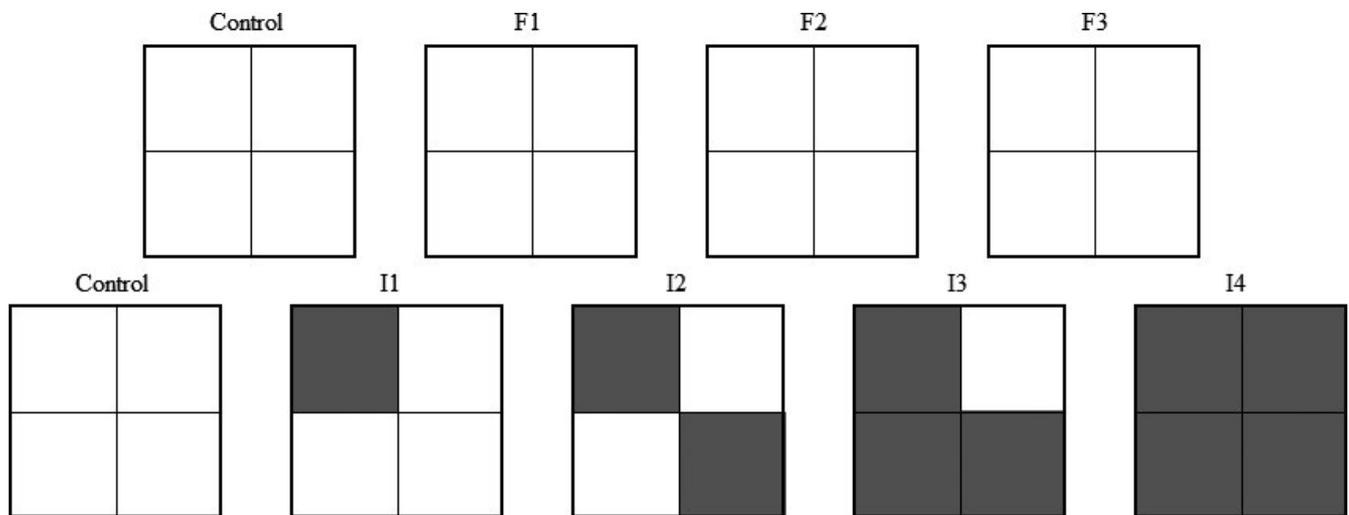


FIGURE 2 Schematic of the experimental design to determine whether community dispersion increased with frequency or intensity of disturbance. Each square represents a 1-m² plot. Within each plot are four 0.25 m² quadrats. The frequency experiment had four treatments: Control = sediment not disturbed; F_1 = sediment disturbed once at the beginning of a 4-week period; F_2 = sediment disturbed twice in 4 weeks, every 2 weeks; and F_3 = sediment disturbed every week in a 4-week period. The intensity experiment had five treatments: Control = sediment not disturbed; I_1 = 25% of the surface area disturbed (grey squares); I_2 = 50% of the surface area disturbed; I_3 = 75% of the surface area disturbed; and I_4 = 100% of the surface area disturbed. In situ, the two experiments were placed next to each other

TABLE 1 Summary table of ANOVAs assessing if community dispersion of experimental controls (replicates outside the experimental set-up) was statistically different than control replicates within the experimental set-up. Significant and interpretable *p* values are in bold

Experiment	Source	df	SS	MS	F	<i>p</i>
Frequency	Treatment	1	0.11	0.11	11.37	0.001
	Error	78	0.75	0.01		
	Total	79	0.86			
Intensity	Treatment	1	0.03	0.03	0.64	0.43
	Error	78	3.13	0.04		
	Total	79	3.15			

$\alpha = 0.05$ was used. In conclusion, post hoc power analyses, the ability of ANOVAs to detect a statistical difference, were conducted as described in Zar (1999). Based upon community dispersion values from similar soft-sediment systems (Gerwing, Allen Gerwing, et al., 2015; Gerwing, Hamilton, et al., 2017), we assumed that a biologically significant difference in community dispersion was a difference of 50%–100% of the average observed community dispersion (17.76).

3 | RESULTS

A statistically significant difference in dispersion was observed between the frequency controls (mean \pm SE: 22.58 ± 1.53) and the experimental controls (16.81 ± 1.31); however, no difference was observed between the experimental control and the intensity control replicates (14.83 ± 0.95 ; Table 1). Given the small observed difference (~5) between experimental and frequency controls, and the high power of the ANOVA (Table 2), we concluded that this difference is not biologically significant. As such, control replicates are considered to be adequate for this investigation.

We did not observe a statistically significant difference in community dispersion between disturbances of varying frequency and intensity (Figure 3; Tables 2 and 3). Not only was there no statistically significant difference between experimental treatments, but none of the treatments were different from the controls. Therefore, disturbance did not increase infaunal community dispersion.

4 | DISCUSSION

We found no evidence to support the postulate that disturbed infaunal communities would exhibit higher community dispersion (heterogeneity) than nondisturbed communities on intertidal mudflats along the north coast of BC. Many studies have reported increased dispersion or community heterogeneity in disturbed communities when compared to nondisturbed areas (Anderson et al., 1982; Fraterrigo & Rusak, 2008; Pearson & Rosenberg, 1978; Warwick & Clarke, 1993b; Wootton, 1998); however, other studies report findings similar to ours, no increase in community dispersion, or even decreased variability with disturbance (Barnes, 1999; Cowie et al., 2000; Hughes et al., 2007; Mackey & Currie, 2001; Reise, 1984; Sousa, 1980; Thistle, 1981). Decreasing variability with disturbance

TABLE 2 Power (%) of ANOVAs to identify a statistically significant difference in community dispersion. Investigated differences were as follows: 100% (17.76), 50% (8.88) and 25% (4.44) of the average observed community dispersion (17.76)

Comparison	Difference in dispersion		
	100%	50%	25%
Frequency: Control and experimental control	97	72	45
Intensity: Control and experimental control	97	78	48
Frequency	88	60	30
Intensity	92	65	35

is often the case when disturbances are very severe or occur homogeneously across a landscape (Conlan et al., 1998; Miller, Roxburgh, & Shea, 2011; Petraitis et al., 1989; Sousa, 1979). Although dispersion did not vary between control replicates and the experimental treatments in our study, there were statistical differences between them. These differences are due to the location of the centroid (multivariate average of community composition and densities) of each treatment, not the spread of individual data points around the centroid (dispersion) (Gerwing, Gerwing, et al., 2017). In short, mechanically disturbing the sediment did impact this infaunal community; however, disturbed plots were not characterized by higher dispersion than nondisturbed plots.

The lack of increased community dispersion in disturbed treatments is likely a result of the dominant infaunal taxa. Overall, 40 infaunal taxa were observed; however, control and experimental plots were primarily dominated by six taxa: the Cumacean *Nippoleucon hinumensis*, the Polychaete *Capitella* Species Complex, the Oligochaete *Paranais litoralis*, Nematodes, Copepods from the order Harpacticoida and the bivalve *Macoma balthica* (Gerwing, Gerwing, et al., 2017). Such uniformity resulted in low community dispersion in experimental and control treatments. This ecosystem, even when not disturbed by ecologists, is dominated by opportunistic species that often characterize disturbed habitats (Fauchald & Jumars, 1979; Pearson & Rosenberg, 1978; Wilson, 1991). Other intertidal mudflats are dominated by similar species (Ambrose, 1984; Gerwing, Allen Gerwing, et al., 2015; Thrush et al., 2003), likely a product of the highly stressful nature (frequent sediment scouring, daily hypoxia at low tide, etc.) of intertidal habitats in general (Altieri, 2006; Valdivia, Scrosati, Molis, & Knox, 2011). Although the mechanical

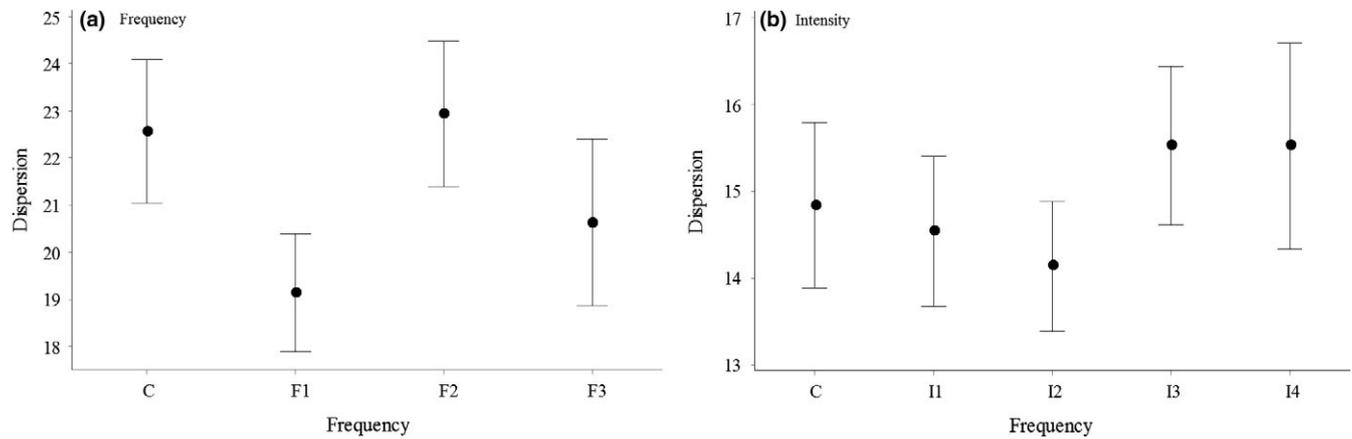


FIGURE 3 Mean and standard error ($n = 40$) of experimental treatments determining if infaunal community dispersion varied with intensity or severity of a mechanical disturbance. C = control, sediment not disturbed; F_1 = sediment disturbed once at the beginning of a 4-week period; F_2 = sediment disturbed twice in 4 weeks, every 2 weeks; and F_3 = sediment disturbed every week in a 4-week period; I_1 = 25% of the surface area disturbed; I_2 = 50% of the surface area disturbed; I_3 = 75% of the surface area disturbed; and I_4 = 100% of the surface area disturbed

Experiment	Source	df	SS	MS	F	p
Frequency	Treatment	3	375.77	125.26	0.92	0.44
	Plot (Treatment)	36	4,920.51	136.68	1.66	0.02
	Error	120	9,881.79	82.35		
	Total	159	15,178.08			
Intensity	Treatment	4	59.59	14.90	0.36	0.83
	Plot (Treatment)	45	1846.81	41.04	1.21	0.20
	Error	150	5,097.53	33.98		
	Total	199	7,003.93			

TABLE 3 Summary table of ANOVAs assessing if infaunal community dispersion varied with intensity or severity of a mechanical disturbance. Significant p values are in bold

disturbance used in this study did impact community composition and densities (Gerwing, Gerwing, et al., 2017), dispersion did not increase with disturbance due to the uniform dominance of the six taxa mentioned above. Therefore, in ecosystems where the differences between successional stages are subtle (a result of changes in relative abundance rather than species replacement), statistical dispersion may not be an effective tool to study or identify disturbance. Further study is required to better understand how other factors, such as diversity, community successional stage, species life history strategies and mobility will influence community dispersion in response to disturbances.

Another potential source of error is our inclusion of multiple species of copepods, ostracods and nematodes into bulk taxonomic categories (Harpacticoida, Ostracods and Nematoda) that were analysed with specimen identified to the species level. Binning was a taxonomic necessity, as copepod and ostracod taxonomy is unresolved along the north coast of BC, and nematodes would require a scanning electron microscope to identify to species (Gerwing, Gerwing, et al., 2017; Light, 2007). However, it is possible that this introduces enough taxonomic noise into the dataset that important trends could be obscured. This is not the case here, as reanalysis with these bulk taxonomic categories

removed did not alter the results already presented here. As discussed above, this likely has to do with relatively uniform densities of these taxa between treatments (Gerwing, Gerwing, et al., 2017). Future studies investigating the relationship between dispersion and disturbance will also need to account for taxonomic noise.

5 | CONCLUSIONS

Despite failing to observe an increase in community dispersion with disturbance in our experiment, we still suggest that statistical dispersion can be an informative parameter to use when studying or attempting to identify disturbances. On the Atlantic coast of Canada, Gerwing, Hamilton, et al., 2017 examined whether the opening of the spillway gates of a river causeway had negative impacts upon downstream intertidal ecosystems. Although Gerwing, Hamilton, et al., 2017 did investigate community dispersion, they also measured community composition and population densities, sediment conditions and resource availability. Dispersion was only one piece of evidence, amongst many, used to holistically study the potential impacts of this disturbance. Although more study is required to better

understand the relationship between dispersion and disturbance, disturbance can increase community dispersion (Anderson et al., 1982; Fraterrigo & Rusak, 2008; Wootton, 1998). Therefore, dispersion is an important parameter to include when studying, or identifying disturbances (Duinker & Greig, 2006). However, as disturbances do not always result in increasing community dispersion (Hughes et al., 2007; Mackey & Currie, 2001), statistical dispersion should only be one parameter amongst many used in any attempt to understand or detect a disturbance.

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REFERENCES

- Altieri, A. H. (2006). Inducible variation in hypoxia tolerance across the intertidal-subtidal distribution of the blue mussel *Mytilus edulis*. *Marine Ecology Progress Series*, 325, 295–300. <https://doi.org/10.3354/meps325295>
- Ambrose, W. G., Jr. (1984). Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. *Journal of Experimental Marine Biology and Ecology*, 81(2), 115–145. [https://doi.org/10.1016/0022-0981\(84\)90002-9](https://doi.org/10.1016/0022-0981(84)90002-9)
- Anderson, R., Gordon, D., Crawley, M., & Hassell, M. (1982). Variability in the abundance of animal and plant species. *Nature*, 296, 245–248. <https://doi.org/10.1038/296245a0>
- Anderson, M., Gorley, R. N., & Clarke, R. K. (2008). *Permanova+ for Primer: Guide to software and statistical methods*. Plymouth, UK: Primer-E Ltd.
- Austen, M. C., Widdicombe, S., & Villano-Pitacco, N. (1998). Effects of biological disturbance on diversity and structure of meiobenthic nematode communities. *Marine Ecology Progress Series*, 174, 233–246. <https://doi.org/10.3354/meps174233>
- Ayling, A. (1981). The role of biological disturbance in temperate subtidal encrusting communities. *Ecology*, 830–847. <https://doi.org/10.2307/1937749>
- Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., ... Jennings, S. (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change*, 4, 211–216. <https://doi.org/10.1038/nclimate2119>
- Barnes, D. K. (1999). The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the UK*, 79(3), 401–407. <https://doi.org/10.1017/S0025315498000514>
- Buckling, A., Kassen, R., Bell, G., & Rainey, P. B. (2000). Disturbance and diversity in experimental microcosms. *Nature*, 408(6815), 961–964.
- Cadotte, M. W. (2007). Competition-colonization trade-offs and disturbance at multiple scales. *Ecology*, 88(4), 823–829.
- Chambers, J. Q., Negron-Juarez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., ... Higuchi, N. (2013). The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proceedings of the National Academy of Sciences USA*, 110(10), 3949–3954. <https://doi.org/10.1073/pnas.1202894110>
- Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User manual/tutorial*. Plymouth, UK: Primer-E Ltd.
- Clarke, K. R., Somerfield, P. J., & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330(1), 55–80.
- Conlan, K., Lenihan, H., Kvitek, R., & Oliver, J. (1998). Ice scour disturbance to benthic communities in the Canadian High Arctic. *Marine Ecology Progress Series*, 166(1), 1–16. <https://doi.org/10.3354/meps166001>
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302–1310.
- Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111(992), 1119–1144. <https://doi.org/10.1086/283241>
- Cowie, P. R., Widdicombe, S., & Austen, M. C. (2000). Effects of physical disturbance on an estuarine intertidal community: Field and mesocosm results compared. *Marine Biology*, 136(3), 485–495. <https://doi.org/10.1007/s002270050708>
- Cox, K., Black, M., Filip, N., Miller, M., Mohs, K., Mortimer, J., ... Dudas, S. (2017). Comparison of community assessment techniques and implications for diversity indices and species accumulation curves. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.3580>
- Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11(12), 1304–1315. <https://doi.org/10.1111/j.1461-0248.2008.01253.x>
- Crewe, T. L., Hamilton, D. J., & Diamond, A. W. (2001). Effects of mesh size on sieved samples of *Corophium volutator*. *Estuarine, Coastal and Shelf Science*, 53(2), 151–154. <https://doi.org/10.1006/ecss.2001.0795>
- Duinker, P. N., & Greig, L. A. (2006). The impotence of cumulative effects assessment in Canada: Ailments and ideas for redeployment. *Environmental Management*, 37(2), 153–161. <https://doi.org/10.1007/s00267-004-0240-5>
- Fauchald, K., & Jumars, P. A. (1979). The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review*, 17, 193–284.
- Fraterrigo, J. M., & Rusak, J. A. (2008). Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters*, 11(7), 756–770. <https://doi.org/10.1111/j.1461-0248.2008.01191.x>
- Gerwing, T. G., Allen Gerwing, A. M., Drolet, D., Barbeau, M. A., & Hamilton, D. J. (2015). Spatiotemporal variation in biotic and abiotic features of eight intertidal mudflats in the Upper Bay of Fundy, Canada. *Northeastern Naturalist*, 22(12), 1–44.
- Gerwing, T. G., Cox, K., Gerwing, A. M. A., Carr-Harris, C. N., Dudas, S. E., & Juanes, F. (2017). Depth to the apparent redox potential discontinuity (aRPD) as a parameter of interest in marine benthic habitat quality models. *International Journal of Sediment Research*, 32(4), 472–480.
- Gerwing, T. G., Drolet, D., Barbeau, M. A., Hamilton, D. J., & Allen Gerwing, A. M. (2015). Resilience of an intertidal infaunal community to winter stressors. *Journal of Sea Research*, 97, 40–49.
- Gerwing, T. G., Drolet, D., Hamilton, D. J., & Barbeau, M. A. (2016). Relative importance of biotic and abiotic forces on the composition

- and dynamics of a soft-sediment intertidal community. *PLoS One*, 11(1), 11, e0147098. <https://doi.org/10.1371/journal.pone.0147098>
- Gerwing, T. G., Gerwing, A. M. A., Macdonald, T., Cox, K., Juanes, F., & Dudas, S. E. (2017). Intertidal soft-sediment community does not respond to disturbance as postulated by the intermediate disturbance hypothesis. *Journal of Sea Research*, 129, 22–28.
- Gerwing, T. G., Hamilton, D. J., Barbeau, M. A., Haralampides, K. A., & Yamazaki, G. (2017). Short-term response of a downstream marine system to the partial opening of a tidal-river causeway. *Estuaries and Coasts*, 40(3), 717–725.
- Gerwing, T. G. (2016). Preliminary report of intertidal research along the north coast of British Columbia: Summer 2016. Report to the Kitsumkalum First Nations. 34 p.
- Gómez Gesteira, J. L., & Dauvin, J.-C. (2000). Amphipods are good bio-indicators of the impact of oil spills on soft-bottom macrobenthic communities. *Marine Pollution Bulletin*, 40(11), 1017–1027. [https://doi.org/10.1016/S0025-326X\(00\)00046-1](https://doi.org/10.1016/S0025-326X(00)00046-1)
- González-Tokman, D., Martínez-Morales, I., Farrera, A., del Rosario Ortiz-Zayas, M., & Lumaret, J. P. (2017). Effects of an herbicide on physiology, morphology, and fitness of the dung beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Environmental Toxicology and Chemistry*, 36(1), 96–102.
- Halpern, B. S., McLeod, K. L., Rosenberg, A. A., & Crowder, L. B. (2008). Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean & Coastal Management*, 51(3), 203–211.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., ... Fox, H. E. (2008). A global map of human impact on marine ecosystems. *Science*, 319(5865), 948–952.
- Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology*, 6(3), 324–337. <https://doi.org/10.1046/j.1523-1739.1992.06030324.x>
- Houghton, J. T., Ding, Y. D. J. G., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., ... Johnson, C. A. (2001). *Climate change 2001: The scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change* (p. 881). Cambridge, UK: Cambridge University Press.
- Hughes, H. A., Jarrett, B. E., Kimbro, D. L., & Stachowicz, J. J. (2007). Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters*, 10(9), 849–864. <https://doi.org/10.1111/j.1461-0248.2007.01075.x>
- Jackson, J. B. C. (1981). Interspecific competition and species' distributions: The ghosts of theories and data past. *American Zoologist*, 21(4), 889–901. <https://doi.org/10.1093/icb/21.4.889>
- Light, S. F. (2007). *The Light and Smith manual: Intertidal invertebrates from central California to Oregon*. Berkeley, CA: University of California Press.
- Mackey, R. L., & Currie, D. J. (2001). The diversity–disturbance relationship: Is it generally strong and peaked? *Ecology*, 82(12), 3479–3492. <https://doi.org/10.2307/2680166>
- Manly, B. F. J. (2004). *Multivariate statistical methods: A primer*. Boca Raton, FL: Chapman and Hall.
- McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, 82(1), 290–297. [https://doi.org/10.1890/0012-9658\(2001\)082\[0290:FMMTC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTC]2.0.CO;2)
- McLaren, P. (2016). The environmental implications of sediment transport in the waters of Prince Rupert, British Columbia, Canada: A comparison between kinematic and dynamic approaches. *Journal of Coastal Research*, 32(3), 465–482. <https://doi.org/10.2112/JCOASTRES-D-15-00134.1>
- Miller, A. D., Roxburgh, S. H., & Shea, K. (2011). How frequency and intensity shape diversity–disturbance relationships. *Proceedings of the National Academy of Sciences USA*, 108(14), 5643–5648. <https://doi.org/10.1073/pnas.1018594108>
- Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100(910), 65–75. <https://doi.org/10.1086/282400>
- Paine, R. T., & Vadas, R. L. (1969). The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography*, 14(5), 710–719.
- Pearson, T. H., & Rosenberg, R. (1976). A comparative study of the effects on the marine environment of wastes from cellulose industries in Scotland and Sweden. *Ambio*, 5, 77–79.
- Pearson, T. H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review*, 16, 229–331.
- Pearson, T., & Stanley, S. (1979). Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. *Marine Biology*, 53(4), 371–379. <https://doi.org/10.1007/BF00391620>
- Petraitis, P. S., Latham, R. E., & Niesenbaum, R. A. (1989). The maintenance of species diversity by disturbance. *Quarterly Review of Biology*, 64, 393–418. <https://doi.org/10.1086/416457>
- Reice, S. R., Wissmar, R. C., & Naiman, R. J. (1990). Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management*, 14(5), 647–659. <https://doi.org/10.1007/BF02394715>
- Reise, K. (1984). Experimental sediment disturbances on a tidal flat: Responses of free-living Platyhelminthes and small Polychaeta. *Hydrobiologia*, 118(1), 73–81. <https://doi.org/10.1007/BF00031790>
- Ruiz, F., Abad, M., Bodergat, A. M., Carbonel, P., Rodríguez-Lázaro, J., & Yasuhara, M. (2005). Marine and brackish-water ostracods as sentinels of anthropogenic impacts. *Earth-Science Reviews*, 72(1), 89–111. <https://doi.org/10.1016/j.earscirev.2005.04.003>
- Schoener, T. W. (1982). The controversy over interspecific competition: Despite spirited criticism, competition continues to occupy a major domain in ecological thought. *American Scientist*, 70(6), 586–595.
- Schratzberger, M., & Warwick, R. M. (1998). Effects of physical disturbance on nematode communities in sand and mud: A microcosm experiment. *Marine Biology*, 130(4), 643–650. <https://doi.org/10.1007/s002270050286>
- Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. *Ecology*, 60(6), 1225–1239. <https://doi.org/10.2307/1936969>
- Sousa, W. P. (1980). The responses of a community to disturbance: The importance of successional age and species' life histories. *Oecologia*, 45(1), 72–81. <https://doi.org/10.1007/BF00346709>
- Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences USA*, 99(24), 15497–15500.
- Sturdivant, S. K., Díaz, R. J., & Cutter, G. R. (2012). Bioturbation in a declining oxygen environment, in situ observations from wormcam. *PLoS One*, 7(4), e34539. <https://doi.org/10.1371/journal.pone.0034539>
- Thistle, D. (1981). Natural physical disturbances and communities of marine soft bottoms. *Marine Ecology Progress Series*, 6(2), 223–228. <https://doi.org/10.3354/meps006223>
- Thomas, J. D. (1993). Biological monitoring and tropical biodiversity in marine environments: A critique with recommendations, and comments on the use of amphipods as bioindicators. *Journal of Natural History*, 27(4), 795–806. <https://doi.org/10.1080/00222939300770481>
- Thrush, S. F., Hewitt, J. E., Cummings, V. J., Green, M. O., Funnell, G. A., & Wilkinson, M. R. (2000). The generality of field experiments: Interactions between local and broad-scale processes. *Ecology*, 81(2), 399–415. [https://doi.org/10.1890/0012-9658\(2000\)081\[0399:TGOFE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0399:TGOFE]2.0.CO;2)
- Thrush, S. F., Hewitt, J. E., Norkko, A., Cummings, V. J., & Funnell, G. A. (2003). Macrobenthic recovery processes following catastrophic



- sedimentation on estuarine sandflats. *Ecological Applications*, 13(5), 1433–1455. <https://doi.org/10.1890/02-5198>
- Underwood, A. J. (1994). On beyond BACI: Sampling designs that might reliably detect environmental disturbances. *Ecological Applications*, 4(1), 4–15. <https://doi.org/10.2307/1942110>
- Underwood, A. J. (1997). *Experiments in ecology: Their logical design and interpretation using analysis of variance*. New York, NY: Cambridge University Press.
- Valdivia, N., Scrosati, R. A., Molis, M., & Knox, A. S. (2011). Variation in community structure across vertical intertidal stress gradients: How does it compare with horizontal variation at different scales? *PLOS One*, 6(8), e24062. <https://doi.org/10.1371/journal.pone.0024062>
- Vaquier-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences USA*, 105(40), 15452–15457. <https://doi.org/10.1073/pnas.0803833105>
- Violle, C., Pu, Z., & Jiang, L. (2010). Experimental demonstration of the importance of competition under disturbance. *Proceedings of the National Academy of Sciences USA*, 107(29), 12925–12929. <https://doi.org/10.1073/pnas.1000699107>
- Warren, P. H. (1996). Dispersal and destruction in a multiple habitat system: An experimental approach using protist communities. *Oikos*, 77, 317–325. <https://doi.org/10.2307/3546071>
- Warwick, R. M., & Clarke, K. R. (1993a). Comparing the severity of disturbance: A metaanalysis of marine macrobenthic community data. *Marine Ecology Progress Series*, 92, 221–231.
- Warwick, R. M., & Clarke, K. R. (1993b). Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology*, 172(1), 215–226.
- White, P. S., & Pickett, S. T. A. (1985). *Natural disturbance and patch dynamics: An introduction*. Orlando, FL: Academic Press.
- Wilson, W. H. Jr. (1991). The importance of epibenthic predation and ice disturbance in a Bay of Fundy mudflat. *Ophelia*, 507, 507–514.
- Wootton, J. T. (1998). Effects of disturbance on species diversity: A multitrophic perspective. *The American Naturalist*, 152(6), 803–825. <https://doi.org/10.1086/286210>
- Zajac, R. N., Whitlatch, R. B., & Thrush, S. F. (1998). Recolonization and succession in soft-sediment infaunal communities: The spatial scale of controlling factors. *Hydrobiologia*, 375(376), 227–240.
- Zar, J. H. (1999). *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice Hall.

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