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Intertidal soft-sediment community does not respond to disturbance as postulated by the intermediate disturbance hypothesis



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ABSTRACT

The Intermediate Disturbance Hypothesis (IDH) predicts that disturbances of an intermediate frequency or intensity will maximize community biodiversity/richness. Once almost universally accepted, controversy now surrounds this hypothesis, and there have even been calls for its abandonment. Therefore, we experimentally evaluated if an infaunal community along the north coast of British Columbia, Canada, would respond to disturbances as predicted by the IDH. The characteristics of this soft-sediment intertidal mudflat (productivity, species pool, population growth rate) maximized our chances of finding evidence to support the IDH. More specifically, we tested if intermediate severities and frequencies of disturbance maximized infaunal community richness by mechanically disturbing sediment, and varying the intensity (0%, 25%, 50%, 75%, and 100% of the surface area of a plot disturbed) and frequency of sediment disturbance (never, once, twice, and every week during a four week period). No effect of frequency or intensity of sediment disturbance on community richness was observed. Further, none of our experimental treatments were statistically different than the controls. This is likely due to the subtle difference between successional stages in this soft-sediment habitat (difference of less than one taxa between treatments). Therefore, in habitats whose productivity, regional species pool, and population growth rates would otherwise suggest a response to disturbances as predicted by the IDH, minor differences between successional stages may result in richness patterns that deviate from those predicted by the IDH.

1. Introduction

There is no doubt that disturbances, discrete events in space and time that alter resources, substratum availability or the physical environment, consequently disrupting community or population structure (Petraitis et al., 1989; White and Pickett, 1985), can have large impacts upon ecosystems (Paine and Vadas, 1969; Vanschoenwinkel et al., 2013). It is therefore not surprising that considerable scientific inquiry has been dedicated to generating theories and hypotheses to explain how disturbances structure natural systems (Crain et al., 2008; Pearson and Rosenberg, 1978; Vanschoenwinkel et al., 2013). One such hypothesis, the Intermediate Disturbance Hypothesis (IDH), was once hailed as one of the best-accepted principles in ecology (Wilkinson, 1999). Recently, however, this hypothesis has seen its near universal support erode to the point of calls for its abandonment (Fox, 2013).

The IDH predicts that disturbances of an intermediate frequency or

intensity will maximize community biodiversity/richness (Connell, 1978; Grime, 1973; Odum, 1963). As reviewed by Fox (2013), peaks in richness under the IDH are thought to occur via four different mechanisms: 1) intermediate disturbances reduce species' densities, weakening competition and precluding competitive exclusion; 2) systems are periodically reset by intermediate disturbances that temporarily lower all species densities, allowing populations to subsequently expand while avoiding competitive exclusion; 3) the identity of the dominant competitor changes due to intermediate disturbances, therefore, no one species has time to exclude others; and 4) the competition-colonization trade-off, in which competitively-inferior, colonizing species are the first to arrive post-disturbance, and are eventually replaced by competitively-superior species. Before this happens, competitively-inferior species reproduce and send out colonizers to other recently disturbed patches. A mosaic of successional stages (patches that are disturbed, in various stages of post-disturbance recovery, and

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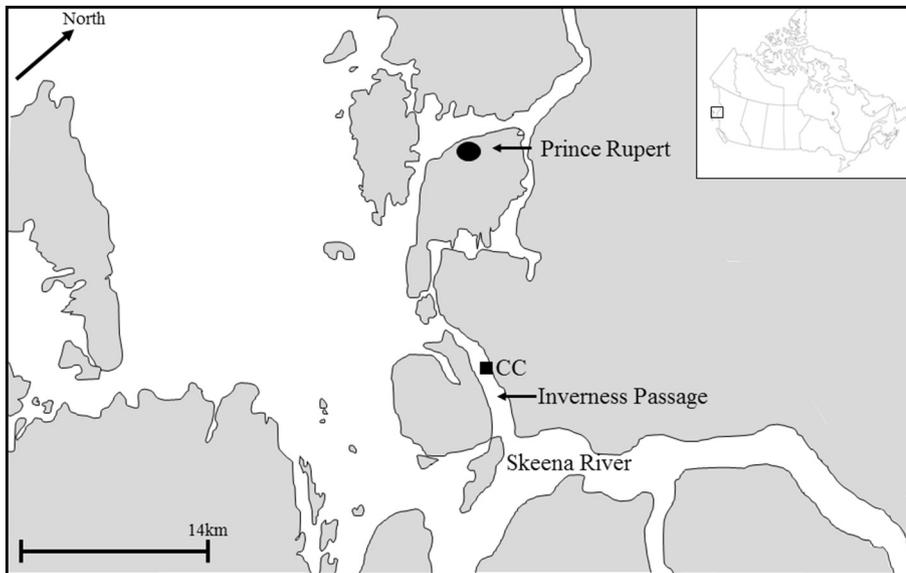


Fig. 1. Location of the experimental mudflat, Cassiar Cannery (CC; 54.178092°, -130.176924°), along the north coast of British Columbia, Canada.

not disturbed) are present on the landscape, resulting in peaks of richness due to intermediate disturbances.

In his review Fox (2013) identifies potential logical flaws within mechanisms 1–3, and showed that while mechanism 4 (competition-colonization trade-off) is logically sound, it produces peaks in richness due to intermediate disturbances as often as it does not. As such, studies have observed trends in richness that contradict the IDH (Austen and Widdicombe, 1998; Hall et al., 2012; Mackey and Currie, 2001; Reise, 1984; Violle et al., 2010). Evidence against the IDH not only comes from micro and mesocosm experiments (Cadotte, 2007; Hall et al., 2012; Violle et al., 2010), but also from experiments conducted in a variety of habitats, such as marine soft-sediment systems (Austen and Widdicombe, 1998; Cowie et al., 2000; Thistle, 1981), freshwater systems, grasslands, forests, alpine cushion, heathland, and coral reefs (Hughes et al., 2007; Mackey and Currie, 2000; Mackey and Currie, 2001). When examining the overall support for the IDH, two meta-analyses have concluded that evidentiary support for the IDH is the exception, not the rule (Hughes et al., 2007; Mackey and Currie, 2001). However, the review of Kershaw and Mallik (2013) observed that in terrestrial habitats, 22 of 48 (46%) examined studies supported the IDH. Regardless, Fox (2013) concluded that the IDH should be completely abandoned.

Sheil and Burslem (2013) and Huston (2014) responded to Fox (2013), arguing that criticisms of the IDH are misrepresentations of this theory, and a result of investigators attempting to evaluate the IDH in areas whose productivity, and population growth rates are outside the intermediate range required by the IDH (Connell, 1978; Huston, 2014; Sheil and Burslem, 2013). Further, if the spatiotemporal scale of investigation (in situ sampling, meio- or microcosm design, etc.) does not match that of disturbance or recovery (Mackey and Currie, 2001; Petraitis et al., 1989; Violle et al., 2010), peaks in richness may be missed. It is also intrinsically difficult to elucidate peaks in richness, and the mechanisms driving these trends, in systems with low diversity, productivity, and population/community growth rates (Cowie et al., 2000; Huston, 2014; Mackey and Currie, 2001). Despite these difficulties, and in support of Sheil and Burslem (2013) and Huston (2014), many studies have observed peaks in richness at intermediate intensities and frequencies of disturbance (Austen et al., 1998; Barnes, 1999; Buckling et al., 2000; Grime, 1973; McIntyre et al., 1988). Interested readers can find further studies that both support and contradict the IDH in Cowie et al. (2000), Mackey and Currie (2001), Hughes et al. (2007), Fox (2013), Kershaw and Mallik (2013), and Huston (2014).

With these concerns in mind, we experimentally tested the IDH in a habitat that maximized our chances of observing the predicted peaks in richness. The intertidal mudflats along the north coast of British Columbia, Canada, are an ideal ecosystem to test the IDH. Beyond their ease of access and manipulation, the infaunal (animals living in the sediment) community is both diverse (~40 taxa) and abundant, with densities ranging from 25,000–600,000 individuals/m² (Gerwing, 2016). The productivity and population/community growth rates of these mudflats (mean [$n = 80$] number of infaunal individuals added per week during July/August: Amphipods: 65. Oligochaetes: 500. Cumacea: 5–1400. Sessile Polychaetes: 65–600. Errant Polychaetes: 10. Phylum Nemertea: 15. *Macoma balthica*: 350. Nematodes: 500. Harpacticoida: 450) appears to fall within the intermediate range required by the IDH (Huston, 2014), exhibiting values higher than some mudflats and lower than others (Cowie et al., 2000; Cranford et al., 1985; Gerwing, 2016; Gerwing et al., 2015a; Hargrave et al., 1983; Trites et al., 2005). Furthermore, mudflats often exhibit pronounced community succession following disturbance (Nilsson and Rosenberg, 2000; Pearson and Rosenberg, 1978), and most infaunal species are likely competing with each other for resources (Fauchald and Jumars, 1979; Ferguson et al., 2013; Pagliosa, 2005). Finally, during the peak in infaunal diversity and abundance (June/July), it is relatively easy to design an experiment that accommodates both the spatiotemporal scale of disturbance and recovery.

On the intertidal mudflats of the north coast of BC, we tested the following IDH hypotheses: 1) disturbances of intermediate frequency will result in an observed peak in infaunal community richness; and 2) disturbances of intermediate intensities will result in an observed peak in infaunal community richness. By testing these hypotheses in a setting ideally suited to confirm the IDH, our study will illuminate if this infaunal community responds to disturbances as predicted by the IDH.

2. Methods

2.1. Study site

This experiment was conducted at the Cassiar Cannery (CC) mudflat along the north coast of BC (Fig. 1). This portion of the north coast is strongly estuarine (4–10 PSU during July/August), as it lies between the Nass and Skeena Estuaries (Ages, 1979; McLaren, 2016; Trites, 1956). The sediment at CC is dominated by fine silts (< 63 μm), with small amounts of fine-grained sand (125–250 μm) also present (McLaren, 2016). A thin layer of oxic mud, ~1–3 mm thick is present at

the surface, with reduced and anoxic sediment below (Gerwing, 2016). At the CC mudflat, 40 infauna taxa have been observed (Gerwing, 2016), and the number of taxa observed within a 1 m² plot ranges from 4 to 10, with a mode of 6 (Gerwing, 2016). The infaunal community of this mudflat is dominated by Cumacea (primarily *Nippoleucon hinumensis* with *Cumella vulgaris* observed less frequently), Polychaetes (families Phyllodocidae [*Eteone californica*], Capitellidae [*Capitella* Species Complex], and Spionidae [*Pygospio elegans*]), Oligochaetes (*Paranais litoralis*), Nematodes, Copepods (order Harpacticoida), Amphipods (*Americorophium salomonis*), and the bivalve *Macoma balthica* (Gerwing, 2016).

2.2. Experimental design

In this experiment we used a garden rake, with tines 10 cm long, to mechanically disturb the sediment to a depth of ~25 cm (Cowie et al., 2000), simulating ice scour (Gerwing et al., 2015b) or dredging (Thomas, 1993). A mechanical disturbance was selected as it allowed complete control over the frequency, intensity, duration, and scale of the disturbance. For this experiment we define disturbance frequency as the number of times the sediment was disturbed during the experiment, and disturbance intensity as the proportion of each experimental replicate disturbed.

Hypothesis one (disturbance frequency; Fig. 2) was tested by establishing four treatments at CC on June 2nd 2016, during the peak in infaunal community richness and density (Gerwing, 2016): control (no disturbance), F₁ (sediment disturbed once at the beginning of a four week period), F₂ (disturbed twice; every two weeks in a four week period), and F₃ (disturbed four times; every week in a four week period). Two weeks is enough time for recovery to have begun, but not for competitive exclusion to have occurred (Gerwing, 2016; Gerwing et al., 2015a; Reise, 1984), enabling us to detect peaks in richness. Forty 1 m² plots were established, 10 plots per treatment, in the middle intertidal zone. Rebar, 0.5 m long, was used to mark the corner of each plot by inserting it 0.25 m into the sediment. Treatments were randomly assigned to individual plots, and each plot was subdivided into four 0.25 m² quadrats to increase sample size. Plots were initially disturbed on June 2nd, and one sediment sample was collected from the center of each quadrat (to avoid edge effects) at the end of four weeks (July 23rd 2016). A sediment corer 10 cm long and with a 7 cm diameter was used (Gerwing et al., 2015a; Gerwing et al., 2016). Sediment samples were later passed through a 250 μm sieve (Crewe et al., 2001) to retain infauna, and preserved in 95% ethanol. In total 40 samples were collected from each treatment, for a total sample size of 160 sediment samples.

To test hypothesis two (intensity of disturbance; Fig. 2) we also established five treatments on June 2nd 2016: control (no disturbance), I₁ (plots 25% disturbed), I₂ (plots 50% disturbed), I₃ (plots 75% disturbed), and I₄ (plots 100% disturbed). Plots and quadrats were established as described above, and sediment samples were collected at the end of two weeks (July 9th 2016; n = 40 per treatment, 200 total).

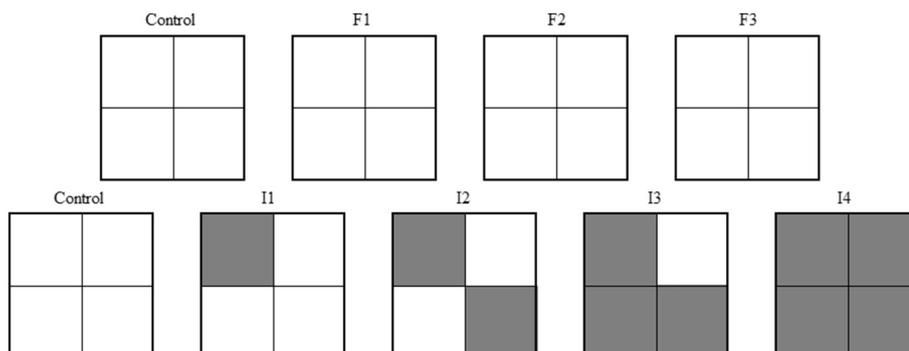


Fig. 2. Schematic of the experimental design to determine if intermediate frequencies or intensities of disturbance resulted in peaks of biodiversity. Each square represent a 1 m² plot. Within each plot are four 0.25 m² quadrats. The frequency experiment (hypothesis one) had four treatments: Control = sediment not disturbed; F₁ = sediment disturbed once at the beginning of a four week period; F₂ = sediment disturbed twice in four weeks, every two weeks; and F₃ = sediment disturbed every week in a four week period. The intensity experiment (hypothesis two) had five treatments: Control = sediment not disturbed; I₁ = 25% of the surface area disturbed (grey squares); I₂ = 50% of the surface area disturbed; I₃ = 75% of the surface area disturbed; and I₄ = 100% of the surface area disturbed. In situ the two experiments were placed next to each other.

Two weeks is enough time for recovery to have begun, but not for competitive exclusion to have occurred (Gerwing, 2016; Gerwing et al., 2015a; Reise, 1984).

To assess the appropriateness of our control replicates, additional experimental control samples were also collected. To the right and left of the experiment, we established five 3 m transects (10 transects total), separated by 5 m, running from the top to the bottom of the experiment. The first transect was 5 m away from the side of the experiment. Along each transect three sediment samples (collected and processed as described above) were taken at the top, middle, and bottom of each transect (n = 30). Further, two transects running parallel to the top and bottom of the experiment, but 5 m from the experiment were established. Five samples were collected, as described above, spaced equidistant along each transect (n = 10). In total 40 additional experimental control samples were collected.

2.3. Statistical analyses

The number of taxa observed in each sample was quantified under a dissecting microscope; however, this does not represent the number of species observed, as we did not identify all organisms to species level. Specimens were identified to the lowest possible taxonomic unit (Gerwing et al., 2017; Thrush et al., 2000; Thrush et al., 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. As such, the richness used in this investigation is not species richness, but taxonomic richness (Gerwing et al., 2015a; Gerwing et al., 2016): the number of taxa observed.

Statistical analyses were conducted in Minitab V.17 using one-way ANOVAs. Homogeneity of variance was assessed using Cochran's Test, and normality of residuals was evaluated visually (Underwood, 1997). In all cases, these assumptions were met. To determine the appropriateness of control replicates, separate one-way ANOVAs, with treatment as a fixed factor (2 levels; control and experimental control), were used to compare control and experiment control replicates from both the frequency and intensity experiments. Experimental control samples were compared to the samples collected from control quadrats (n = 40 per treatment, 80 total). The ANOVA evaluating disturbance frequency incorporated treatment (four levels; control, F₁, F₂, and F₃) as a fixed factor. The lowest level of replication for this experiment was the quadrat, n = 40 per treatment, and 160 total. As there were multiple ways to analyze the intensity experiment, we analyzed data from the intensity experiment in two ways, first with the lowest level of replication as the quadrat. This ANOVA was run as described for the frequency experiment, and treatment was once again a fixed factor (five levels: control, I₁, I₂, I₃, and I₄; n = 40 per treatment, 200 total). Secondly, the intensity experiment was analyzed by combining quadrats within a plot, and comparing the overall taxonomic richness of the plot (n = 10 per treatment, 50 total). In all ANOVAs an α = 0.05 was used, and when a statistically significant difference was observed, Tukey's

Table 1

Summary table of ANOVAs assessing if control replicates within the experimental setup were statistically different than control replicates outside the experiment (experimental controls). Significant and interpretable *p* values are in bold.

Experiment	Source	DF	SS	MS	F	<i>p</i>
Frequency	Treatment	1	2.11	2.11	0.75	0.39
	Error	78	219.08	2.81		
	Total	79	221.19			
Intensity	Treatment	1	0.45	0.45	0.23	0.64
	Error	78	154.75	1.98		
	Total	79	155.20			

Tests were used to determine which treatments were significantly different. For Tukey's tests, $\alpha = 0.01$ was used to correct for inflation of the family-wise error rate (Kelaheer et al., 2001). Finally, power analyses, the ability of the ANOVAs to detect a statistical difference of 0.5, one, and two taxa were conducted as prescribed in (Zar, 1999).

3. Results

We observed no statistically significant difference in taxonomic richness between the control (mean taxonomic richness \pm standard error: frequency control: 6.15 ± 0.28 ; intensity control: 6.33 ± 0.19) and experimental control replicates (6.45 ± 0.25 ; Table 1). Given the high power of these ANOVAs to detect a meaningful difference in taxonomic richness (Table 2; one or two taxa), the control replicates within the experimental setup are adequate controls.

A statistically significant difference in taxonomic richness was observed in the frequency experiment (Table 3, Fig. 3a); however, this was due to a difference between the F_1 and F_3 treatments (Table 4). This difference, while not statistically significant after correction to avoid inflation of the family-wise error rate, approached significance. We detected no other statistically significant differences, and none of the experimental treatments were statistically different than the control. The ANOVA assessing the intensity experiment (lowest level of replication: quadrat) also identified a statistically significant difference in taxonomic richness (Table 3; Fig. 3b), however, differences were between the I_1 and I_2 , as well as the I_1 and I_3 treatments. As above, these differences, while not statistically significant after correction to avoid inflation of the family-wise error rate, approached significance. None of the experimental treatments were statistically different from the control (Table 4). No statistically significant difference was observed between treatments in the ANOVA assessing intensity data with the plot as the lowest level of replication (Table 3, Fig. 3c). All ANOVAs had sufficient statistical power (Table 2) to detect meaningful differences (one or two taxa) in taxonomic richness between treatments. Treatments with observed taxonomic richness higher than all other treatments (Fig. 3a–c) are non-significant and represent differences of less than one taxa.

Table 2

Power (%) of one-way ANOVAs to detect a statistically difference between treatments of 0.5, one, and two taxa.

Comparison	Difference in richness		
	0.5	1	
Frequency: control and experimental control	97	78	40
Intensity: control and experimental control	> 99	98	82
Frequency	95	65	35
Intensity (quadrat as the base unit of replication)	97	72	40
Intensity (plot as the base unit of replication)	82	50	25

Table 3

Summary table of ANOVAs assessing if disturbances with an intermediate frequency and intensity resulted in a peak of infaunal taxonomic richness along the north coast of BC. Significant and interpretable *p* values are in bold.

Experiment	Lowest level of replication	Source	DF	SS	MS	F	<i>p</i>
Frequency	Quadrat	Treatment	3	24.05	8.017	3.14	0.03
		Error	156	397.85	2.55		
		Total	159	421.9			
Intensity	Quadrat	Treatment	4	13.43	3.358	2.9	0.02
		Error	195	225.73	1.158		
		Total	199	239.16			
Intensity	Plot	Treatment	4	13.88	3.47	1.70	0.17
		Error	45	91.80	2.04		
		Total	49	105.68			

4. Discussion

Using intertidal mudflats along the north coast of BC, we tested if intermediate frequencies or intensities of a mechanical disturbance resulted in a peak of infaunal community taxonomic richness. While Fig. 3a–c does exhibit a humped pattern of taxonomic richness, all experimental treatments were not significantly different than controls, and observed differences were less than one taxa. All analyses had high statistical power (Table 2) to detect biologically significant (1–2 taxa) differences in taxonomic richness. Further, it is unlikely that the observed peaks, representing disturbances occurring once in the experimental period (F_1), or disturbances affecting 75% of a plot (I_3) could be considered intermediate. Therefore, we conclude that the intertidal communities along the north coast of BC did not respond to this mechanical disturbance as predicted by the IDH. However, while the mechanical disturbance used in this study may not have impacted taxonomic richness, it did result in differences in community composition and densities between treatments (Supplemental Table S1). Therefore, scouring of the sediment was an effective disturbance agent in this system, even if it did not have a strong impact upon taxonomic richness between treatments.

As discussed above, these intertidal mudflats appear to represent optimal conditions to test for the IDH, avoiding most of the methodological limitations proposed to obscure evidence in support of the IDH (e.g. scale of disturbance not matching the scale of investigation, low community diversity, productivity and growth rates) (Hall et al., 2012; Huston, 2014; Violle et al., 2010). However, one of the critical assumptions of the IDH is that the productivity and population growth rates in question must fall within an intermediate range (Huston, 2014). Currently, the boundaries of this range are far from clear, and direct comparisons between habitat types are difficult due to variation in methods and response variables. As such, it is possible that our mudflat did not fall within this intermediate range, with productivity and population growth rates exceeding the required intermediate range. While possible, we doubt this is the case, as the productivity and population growth rates of the CC mudflat is intermediate with regards to other mudflats (Cowie et al., 2000; Cranford et al., 1985; Gerwing, 2016; Gerwing et al., 2015a; Hargrave et al., 1983; Trites et al., 2005). While more work is required to determine the boundaries of the intermediate range of productivity and population growth rates required for the IDH, given that the CC mudflat is intermediate to other mudflats, our results are likely not a result of the productivity and population growth rates of this habitat falling outside the intermediate range required by the IDH. Instead, this infaunal community not responding as predicted by the IDH is likely a result of the dominant infaunal taxa. In this area, 40 infaunal taxa have been observed, and nearly all 40 were observed in experimental plots; nevertheless, plots (control and experimental) were primarily dominated by six taxa: the Cumacean *Nippoleucon hinumensis*, the Polychaete *Capitella* Species Complex, the Oligochaete *Paranais littoralis*, Nematodes, Copepods from the order Harpacticoida, and the

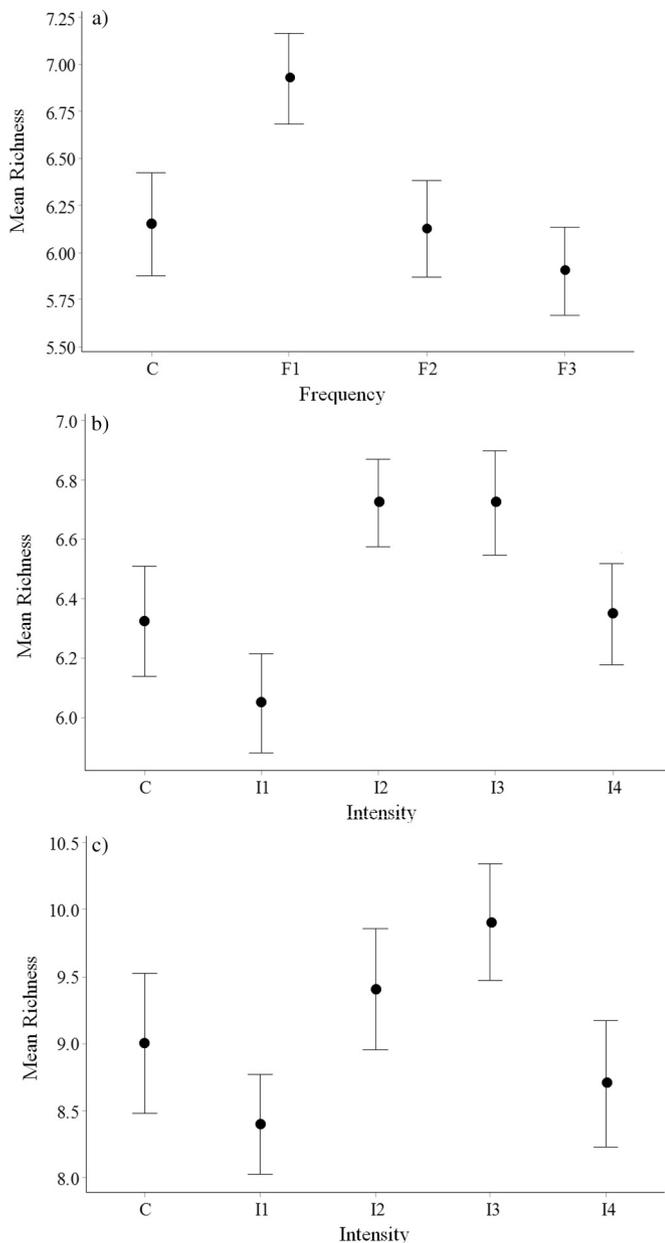


Fig. 3. Mean taxonomic richness (number of observed taxa) \pm the standard error ($n = 40$) for experiments assessing if intermediate frequencies (panel a) or intensities (panels b and c) of disturbance resulted in peak richness. Intensity of disturbances are presented two ways, b) depicts average richness quantified from the experimental quadrats ($n = 40$ per treatment); c) depicts average richness quantified from experimental plots ($n = 10$; see Fig. 2). C = control, sediment not disturbed; F₁ = sediment disturbed once at the beginning of a four week period; F₂ = sediment disturbed twice in four weeks, every two weeks; and F₃ = sediment disturbed every week in a four week period; I₁ = 25% of the surface area disturbed; I₂ = 50% of the surface area disturbed; I₃ = 75% of the surface area disturbed; and I₄ = 100% of the surface area disturbed.

bivalve *Macoma balthica*. The Cassiar Cannery mudflat was dominated by opportunistic species that often characterize disturbed habitats (Fauchald and Jumars, 1979; Pearson and Rosenberg, 1978; Wilson, 1991). Intertidal mudflats are often dominated by such species (Ambrose, 1984; Gerwing et al., 2015a; 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 et al., 2011). However, not all intertidal mudflats exhibit the subtle differences between successional stages observed on the CC mudflat (Gerwing et al., 2015a; Gerwing et al., 2015b; Gerwing et al., 2017; Nilsson and Rosenberg, 2000; Pearson and Rosenberg, 1978). The

subtle differences between successional stages in this system, differences of < 1 taxa between treatments (Fig. 3), may explain why taxonomic richness of this infaunal community did not peak at intermediate severities or intensities of disturbance.

The results of our study are similar to those of Cowie et al. (2000), who evaluated the IDH on estuary mudflats in southwest England, by also scouring the sediment; however, Cowie et al. (2000) only investigated disturbance frequency, not intensity. Using both in situ examinations and mesocosms ($2.96 \text{ m} \times 1.05 \text{ m}$), Cowie et al. (2000) found no evidence that their intertidal communities responded to changing disturbance frequencies as predicted by the IDH (Cowie et al., 2000). As explained by Cowie et al. (2000), this is likely a product of the limited and isolated species pool in these habitats, and the absence of new species to act as colonizers when dominant competitors are removed via a disturbance. This is in contrast with the intertidal environment along the north coast of BC, which has a large species pool (~ 40 taxa), and many species that can act as colonizers. Cowie et al. (2000) conclude that while the IDH may be important in other habitats, it does not explain the processes that control community structure in intertidal habitats. Our work supports this postulate, and builds upon it. Whether due to a limited species pool (Cowie et al., 2000), or subtle differences between successional stages (this study), intertidal soft-sediment communities do not appear to respond to disturbances as predicted by the IDH.

More broadly, our results contribute to the controversy that still engulfs the IDH (Fox, 2013; Huston, 2014; Sheil and Burslem, 2013). Many studies have reported experimental evidence that appears to refute the IDH (Cadotte, 2007; Mackey and Currie, 2001; Violle et al., 2010; Warren, 1996; Wootton, 1998). Evidence that comes not only from micro and mesocosm experiments (Cadotte, 2007; Hall et al., 2012; Violle et al., 2010), but also from a variety of habitats, such as marine soft-sediment systems (Austen and Widdicombe, 1998; Cowie et al., 2000; Thistle, 1981), freshwater systems, grasslands, forests, alpine cushion, heathland, and coral reefs (Hughes et al., 2007; Mackey and Currie, 2000; Mackey and Currie, 2001). As argued by Fox (2013), this is not surprising given the logical failings that underlie the IDH. However, Sheil and Burslem (2013) and Huston (2014) contend that criticisms of the IDH arise from misrepresentations of the hypothesis, as well as by investigators attempting to evaluate the IDH in situations outside of the intermediate productivity and population growth rates required by the IDH (Connell, 1978). In support of this, many investigations have observed peaks in richness at intermediate severities and intensities of disturbance (Buckling et al., 2000; Grime, 1973; McIntyre et al., 1988; Paine, 1966; Widdicombe and Austen, 1998).

Our study does not resolve the question of if the IDH should be abandoned entirely (Fox, 2013), or if it is still a useful theory within specific productivity and population growth rate parameters (Huston, 2014; Sheil and Burslem, 2013). It does, however, contribute to the debate by further specifying conditions in which communities do not respond to disturbances as predicted by the IDH. On the intertidal mudflats along the north coast of BC, we failed to observe peaks in taxonomic richness at intermediate intensity or frequencies of disturbance. An observation likely due to the subtle difference in successional stages in this soft-sediment habitat. Therefore, in habitats whose productivity, regional species pool, and population growth rates would otherwise suggest a response to disturbances as predicted by the IDH, minor differences between successional stages may result in richness patterns not supporting those predicted by the IDH.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2017.09.001>.

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Table 4

Results of Tukey's Tests, contrasting experimental treatments of ANOVAs (see Table 3) that identified statistical differences between treatments. A corrected α of 0.01 was used. Significant and interpretable p values are in bold. p values approaching significance are denoted in italics.

Experiment	Lowest level of replication	Groups	Difference between means	SE of difference	95% CI	T	p
Frequency	Quadrat	C - F ₁	0.78	0.36	−0.15 to 1.70	2.17	0.14
		C - F ₂	−0.03	0.36	−0.95 to 0.90	−0.07	1
		C - F ₃	−0.25	0.36	−1.18 to 0.68	−0.7	0.90
		F ₁ - F ₂	−0.80	0.36	−1.73 to 0.13	−2.24	0.12
		F ₁ - F ₃	−1.03	0.36	−1.95 to −0.10	−2.87	0.02
		F ₂ - F ₃	−0.23	0.36	−1.15 to 0.70	−0.63	0.92
Intensity	Quadrat	C - I ₁	−0.28	0.24	−0.94 to 0.39	−1.14	0.78
		C - I ₂	0.40	0.24	−0.26 to 1.06	1.66	0.46
		C - I ₃	0.40	0.24	−0.26 to 1.06	1.66	0.46
		C - I ₄	0.03	0.24	−0.64 to 0.69	0.10	1
		I ₁ - I ₂	0.68	0.24	0.01 to 1.34	2.81	0.04
		I ₁ - I ₃	0.68	0.24	0.01 to 1.34	2.81	0.04
		I ₁ - I ₄	0.30	0.24	−0.36 to 0.96	1.25	0.72
		I ₂ - I ₃	0	0.24	−0.66 to 0.66	0	1
		I ₂ - I ₄	−0.38	0.24	−1.04 to 0.29	−1.56	0.53
		I ₃ - I ₄	−0.38	0.24	−1.04 to 0.29	−1.56	0.53

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