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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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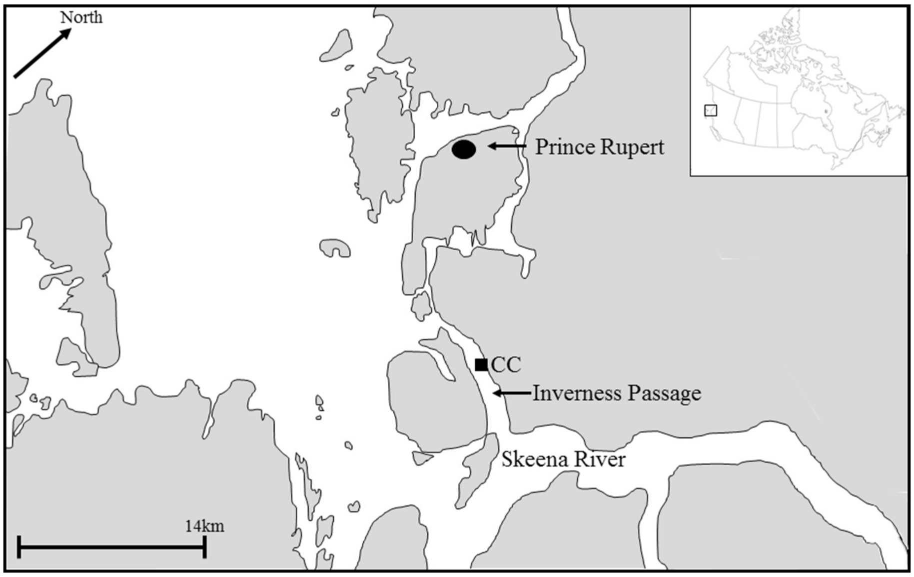

Fig. 1. Location of the experimental mudflat, Cassiar Cannery (CC; 54.178092°, − 130.176924°), along the north coast of British Columbia, Canada.

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/m^2 (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