Peeling out predation intensity in the fossil record: A test of repair scar frequency as a suitable proxy for predation pressure along a modern predation gradient

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ABSTRACT

Predation represents a major cause of death within marine ecosystems, acting as a major agent of natural selection and evolution. Crushing predation in particular is important, as increasing intensity of durophagy through the Phanerozoic has been argued to influence evolution. Repair frequency (RF) is a common palaeoecological metric used to infer crushing predation pressure within the fossil record, yet whether repair frequency variation accurately represents attack frequency or predator success remains uncertain. To determine if repair frequency variation tracks attack frequency or predator success, repair scar frequency for eight, modern intertidal populations of the gastropod *Chlorostoma funebrale* was calculated along an environmental energy gradient in Barkley Sound, Canada. Attack frequency within intertidal settings is thought to decrease with environmental energy, as crab size, abundance, and intertidal foraging time are greater in sheltered settings than in exposed settings. Spearman's rank correlation of *C. funebrale* repair frequencies along the energy gradient produced a strong inverse correlation ($p \ll 0.0001$) regardless of metric used. These results suggest that repair frequency within crab–gastropod systems serves as a proxy for predator attack frequency. Therefore, the inferences of predation pressure between morphologically similar fossil gastropod populations drawn from repair frequency data are likely accurate.

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1. Introduction

Predation represents an influential process within many ecosystems (Paine, 1966; Kelley et al., 2003). Crushing predation is particularly important as it represents a major cause of mortality in marine ecosystems, and is therefore a major agent of natural selection and evolution (Cadée et al., 1997). Unfortunately, as the prey's skeletal remains are typically destroyed and removed from the fossil record following a successful crushing attack (Stafford and Leighton, 2011), and the predators themselves often have poor preservation potential, identifying and examining predation within the fossil record can be difficult. Thus, repair scars, the healed damage from a failed attack preserved on the prey shell, are often the only remaining evidence of crushing predation, and are measured as repair frequency, i.e., percentage of repairs or repaired individuals within a population (Schoener, 1979; Vermeij et al., 1980, 1981; Schindel et al., 1982; Vermeij, 1982; Geller, 1983;

Vermeij, 1993; Dietl and Alexander, 1998; Alexander and Dietl, 2001; Kowalewski, 2002; Leighton, 2002; Alexander and Dietl, 2003; Dietl and Alexander, 2005, 2009; Dietl et al., 2010; Stafford and Leighton, 2011; Dietl and Kosloski, 2013; Leighton et al., 2013; Nagel-Myers et al., 2013). Variation in repair scar frequency between fossil populations is commonly used to identify differences in predation between populations (Leighton, 2002; Alexander and Dietl, 2003). Studies examining variation in repair frequency between populations of modern gastropods, however, suggest that the interpretation and meaning of trends in repair frequency through space or time may be ambiguous (Geller, 1983; Schmidt, 1989; Schindler et al., 1994; Cadée et al., 1997). This is problematic, as it suggests that repair frequency data cannot be used in the fossil record to accurately infer differences in predation between populations. The present study, therefore, aims to determine if repair frequency accurately tracks crushing attack frequency on intertidal gastropods along a common and well-known modern marine environmental and predation gradient near Bamfield, British Columbia, Canada. If differences in repair frequency between prey populations do accurately reflect differences in predation intensity, then meaningful conclusions may be drawn from repair scar data, both in the modern and the paleontological records.

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Although repair scars record actual attacks, there remain several concerns regarding how repair frequency should be measured, and how to interpret differences in repair frequency between localities, or through time (Dietl and Kosloski, 2013). Studies of modern gastropod populations suggest that repair frequency is quite spatially variable, and so may not be an appropriate measure of attack frequency across space or through time. For example, differences in repair frequency between gastropod populations in rocky intertidal versus sandy modern marine habitats demonstrate that repair frequency can vary, even on small geographic scales (Schmidt, 1989). Furthermore, variation in repair frequency of geographically separated gastropod populations can be so great that it would obscure repair frequency trends through time (Cadée et al., 1997).

In addition to the difficulty of interpreting patterns in repair frequency, it is not clear that repair scars themselves represent an accurate measure of attack frequency (Leighton, 2002). Given that repair scars document unsuccessful (failed) attacks, an increase in repair frequency can arise from two possible end-member scenarios (Vermeij, 1987). The first is when the number of attacks on a population (attack frequency) increases, and the predator's ability to crush and kill prey (predator success rate) remains the same. This results in the number of both successful and unsuccessful attacks rising, increasing both the number of kills and of repair scars. The second scenario occurs when the predator's success rate decreases while the number of attacks remains constant. In this scenario repair frequency increases as a factor of the increased proportion of failed attacks. Although both scenarios result in repair frequency increasing, they involve opposite trends in successful attacks (kills). Therefore, repair frequency variation between population could represent either variation in the number of attacks (attack frequency), or predator success rate. The problem is further exacerbated by the possibility that larger, older, prey specimens have had more opportunities to be attacked (and survive); thus, differences in repair frequency can also be an artefact of differences in prey size among populations (Vermeij, 1987). Without an understanding of what drives repair frequency, interpreting repair scar data remains difficult.

Modern systems, particularly crab–gastropod interactions, are in many ways ideal for determining which factors drive repair frequency in crushing predation scenarios. Many species of crabs are voracious predators capable of great crushing strengths (>50 N of force for larger individuals) that prey upon a wide variety of mollusks (Boulding, 1984). Gastropods grow their shells by accretion, and their visible growth lines make identifying and collecting repair scar data from them relatively straightforward. Both crabs and gastropods are abundant in many marine settings, making the study of their interactions over large scales possible in both the modern and fossil records.

Attack frequency within intertidal settings is thought to vary with wave energy, as crab size, abundance, and intertidal foraging time differ between sheltered and exposed settings (Menge and Lubchenco, 1981; Robles, 1987; Boulding et al., 1999; Robles et al., 2001). Large adult cancrid crabs are most abundant in quieter (lower energy), more sheltered settings, moving in and out of the intertidal area with the tides to feed (Robles et al., 1989). Smaller, younger crabs are found within both exposed and sheltered settings, however they are less restricted and proportionally more abundant in exposed higher energy settings due to a lack of competition and predation from their larger conspecifics. Furthermore, sheltered, quieter water settings provide longer foraging times as their narrower swash zones and reduced currents do not cover large portions of the intertidal area during a change in tide. As crabs have difficulty navigating turbulent conditions, like those of the swash zone, more exposed, high energy settings typically have fewer crabs as the large swash zones limit crab foraging (Menge and Lubchenco, 1981; Robles, 1987). Generally, quieter, sheltered settings tend to have larger crabs on average and more dense crab populations than do more exposed settings (Robles, 1987; Robles, et al., 1989).

Given the difference in average crab size and population density between quieter and more exposed intertidal settings, crushing predation pressure experienced by prey (gastropods) within these settings will also vary. Greater crab densities, larger crab size, and longer foraging times generate higher attack frequencies (larger crabs eat more, longer foraging time) and attack success rate (larger crabs are stronger). Likewise, less dense crab populations, smaller crabs, and less foraging time reduces predation pressure, lowering attack frequency (smaller crabs eat less, shorter foraging time) and attack success rate (smaller crabs are weaker). These factors ultimately generate an environmentally controlled predation gradient, where crab population size and density differences between quieter and higher energy settings result in different predation pressures (Robles, 1987; Robles et al., 1989; Boulding et al., 1999).

To determine whether attack frequency or predator success rate drive repair frequency, we examined repair frequency across an increasing energy gradient. If repair frequency is driven by attack frequency, then repair frequency should increase with decreasing wave-energy, as a result of environmentally driven changes in foraging time, crab size, and population density. Essentially, larger, more abundant crabs with more time to forage will produce more attacks. In contrast, if repair frequency is driven by predator success and failure, then repair frequency should decrease with decreasing wave-energy, as the larger, stronger crabs that live in quieter settings will be more successful, more likely to destroy the prey shell, and thus will leave fewer opportunities for repair. If repair frequency does not vary predictably with this known predation gradient, then repair frequency may not be a valid measure of predation intensity.

2. Materials and methods

2.1. Study location

The southern coast of Barkley Sound and northern portion of Bamfield inlet, located along the western shores of Vancouver Island, British Columbia (Fig. 1), provides an environmentally controlled predation gradient in which to test whether attack frequency or predator success rate drives repair frequency. Eight sites varying in wave energy and predation pressure were chosen based on their proximity to the Sounds' opening to the Pacific Ocean (Fig. 1). The sites closest to the Pacific Ocean were characterised by higher environmental energy and larger waves. Sites located further northeast and inland towards the northern portion of Bamfield inlet were characterised by lower environmental energy and smaller waves. Localities were ranked in order based on their proximity to the open ocean (Table 1 with Whittlestone Point, the closest locality to the open ocean, ranked the highest (8) and Grappler Island, the farthest locality from the open ocean, ranked the lowest (1)).

Although the ranking of sites in accordance to their proximity to the open ocean is relative, this ranking is consistent with previous studies documenting relative differences in environmental energy at these sites. Wave energy along the southern coast of Barkley Sound decreases from the mouth of the sound inland (Rawlings, 1994; Gosselin and Rehak, 2007). Mean maximum wave velocities decrease dramatically from Nudibranch Point (0.97 ± 0.5 m/s^{-1}) to Scott's Bay (0.52 ± 0.33 m/s^{-1}) (Robles et al., 1989.). The northern portion of Bamfield inlet possesses wave energies much less than those outside the inlet, and mean wave energy at Grappler Inlet (a point between our sites at Strawberry Point and Grappler Island) is 0.05 m/s^{-1} (Marchinko and Palmer, 2003; Neufeld and Palmer, 2008). The ranking of sites along the southern coast of Barkley Sound and northern Bamfield inlet used in this study, therefore, is a reasonable approximation of the observed differences in environmental energy experienced by each site.

More exposed sites (Whittlestone Point, Nudibranch Point, and Prasiola Point) have steeper intertidal areas, with sparse, large rocks and kelp beds towards the subtidal–intertidal boundary. Exposed sites