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Combined impacts of natural and human disturbances on rocky shore communities

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ABSTRACT

Most ecosystems are subject to both natural and human disturbances that can combine to influence populations and assemblages in complex ways. Assessing the relative influences and combined impacts of natural and human disturbance is crucial for managing human uses of ecosystems against the backdrop of their natural variability. We evaluated the separate and combined influences of disturbance from storm waves and disturbance associated with human trampling of rocky shores by conducting an experiment mimicking controlled levels of trampling at sites with different wave exposures, and before and after a major storm event in central California, USA. Results show that trampling and storm waves affected the same taxa and have comparable and additive effects on rocky shore assemblages. Both disturbance types caused significant reduction in percent cover of mussels and erect macroalgae, and resulted in significant re-organization of assemblages associated with these habitat-forming taxa. A single extreme storm event caused similar percent cover losses of mussels and erect macroalgae as did 6–12 months of trampling. Contrary to a predicted synergistic effect of trampling and storm damage, we found that impacts from each disturbance combined additively. Mussel beds in wave-exposed sites are more vulnerable to trampling impacts than algal beds at protected sites. Mussels and erect macroalgae recovered within five years after trampling stopped. These results suggest that impacts from local human use can be reversed in relatively short time frames, and that cumulative impacts can be reduced by setting recreational carrying capacities more conservatively when ecosystems are already exposed to frequent and/or intense natural disturbances.

1. Introduction

Ecosystems may exhibit varying responses to human pressures in part depending on the natural disturbance regimes that shape their structure and dynamics. Ecosystems subject to frequent and/or intense natural disturbance may be less vulnerable to additional human disturbance, as natural disturbance may select for resistant species (Cote and Darling, 2010). However, natural and human disturbances may instead interact synergistically to enhance their individual effects (Breitburg et al., 1998; Folt et al., 1999; Crain et al., 2008). Thus, in contrast with the previous prediction, vulnerability to human impacts may be greater in the presence of intense natural disturbance. Finally, multiple disturbances may add in their impacts on affected ecosystems, resulting in high levels of cumulative impact (Halpern et al., 2008). Understanding how human and

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natural disturbance combine to affect communities and ecosystems is key to devising appropriate management and conservation strategies.

Marine ecosystems are subjected to substantial environmental variation and disturbance over a range of spatial and temporal scales. Among marine ecosystems, intertidal and coastal ecosystems exhibit extreme variation in physical conditions and stressors as they integrate a suite of land and sea-based processes and pressures (Raffaelli and Hawkins, 1996). This is the case for a variety of habitat types, from sandy beaches, to wetlands, macroalgal beds, shallow reefs, tidal flats and rocky shores. Intertidal ecosystems, in particular, are vulnerable to climate change and a variety of anthropogenic disturbances, including pollution, eutrophication, alteration of sedimentation and freshwater input, shoreline modification, introduced species, harvest of organisms, and trampling disturbance (Castilla, 1999, 2000; Crowe et al., 2000; Thompson et al., 2002; Halpern et al., 2007, 2008). These disturbances add to, or combine with natural stressors from exposure to air and high temperatures when the tide is out, and wave disturbance at high tide. Moreover, occasional extreme storms can result in considerable physical disturbance (Denny et al., 2009).

Recreational and educational uses of the shore have been on the rise for the last 50 years due, in part, to improved coastal access and rising coastal populations (Fletcher and Frid, 1996; Thompson et al., 2002) and these can have significant and sometimes lasting effects on populations and communities (e.g. Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Keough and Quinn, 1998; Schiel and Taylor, 1999). On rocky shores, human visitation and trampling affect species directly by dislodging or crushing individuals or weakening their attachment to the substrate, and indirectly by removing important members of interacting species groups (Brosnan and Crumrine, 1994). Schiel and Taylor (1999) showed experimentally along New Zealand rocky shores that the equivalent of ten people walking over an area of the mid-intertidal in a single event could result in reduction of the dominant alga by 25%; at 200 people passes, less than 10% of the alga's cover remained. When foliose algae canopies vulnerable to trampling are lost, understory algae may suffer subsequent declines due to desiccation and heat exposure and more resistant turf algae can develop in their place (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Schiel and Taylor, 1999).

Mobile invertebrates tend to be more resistant to trampling effects, but shifts in abundance are often observed in experimental trampling treatments as some species decline while others, like grazing molluscs, increase in number as they invade new patches of unoccupied space (Povey and Keough, 1991; Keough and Quinn, 1998). Effects of trampling can be detected a year after the disturbance event (Schiel and Taylor, 1999) and recovery has been shown to vary with location, timing and intensity of impact, as well as habitat and species (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Keough and Quinn, 1998; Schiel and Taylor, 1999; Araujo et al., 2012).

Though important insights emerge from prior work, there are many remaining open questions on how impacts from human recreational use of the shore compare, combine and interact with natural disturbances. Moreover, the questions of how natural and human disturbances interact, and how to manage human disturbance under varying regimes of natural disturbance apply to a suite of marine and terrestrial ecosystems.

In this study, we experimentally evaluated the separate and combined influences of physical disturbance from waves and storms, and human disturbance associated with trampling in intertidal temperate rocky reef ecosystems. First, we examine what, if any, are the human-visitation trampling effects on benthic community structure and taxonomic richness. Second, we examine the interaction between wave-related and trampling disturbance, and investigate whether co-occurring disturbances impact intertidal communities additively or multiplicatively – where combined impacts are lower or greater than the sum of individual effects (Breitburg et al., 1998; Folt et al., 1999; Crain et al., 2008; Cote and Darling, 2010). Rocky shore species have many adaptations to withstand natural stresses and disturbance, including an ability to reduce physical dislodgement and injury, which may also provide some inherent resistance to physical disturbances associated with trampling. We hypothesized that trampling effects would be less severe at wave-exposed sites experiencing greater and more frequent physical disturbance from waves than at sheltered sites. Furthermore, we examined whether occasional extreme storm events act independently or synergistically with trampling effects. We hypothesize an interactive effect due to weakening of sessile species' attachment to the rock by trampling, making trampled sites more vulnerable to extreme waves from storms. Finally, to examine management implications of trampling related to human visitation, we examined whether communities in wave-exposed or wave-protected areas recover more quickly from human-visitation trampling effects and asked what are sustainable human visitation levels in rocky intertidal habitats. Thus, we addressed the following questions: 1) Are trampling effects less severe at wave-exposed sites than at wave-protected sites? 2) Do the impacts of extreme waves from storms act independently or synergistically with any trampling impact? 3) What are the timeframes for recovery from trampling disturbance, and do these vary with physical exposure of the shore?

2. Materials and methods

2.1. Study site

The experiment was conducted at Soberanes Point in central California (36° 27′ N 121° 55.7′ W) (Appendix 1 in *Supplementary Materials*) between January 2002 to January 2008. Soberanes Point is open for public access. However, intertidal visitation is difficult due to steep cliffs that protect the area, allowing us to control experimental trampling levels to prescribed amounts. Two wave-exposed headlands and two wave-protected shores were randomly selected along the coastline, 300–500 m apart, with one experimental site (each approx. a 50-m stretch of the coastline) established on each of the exposed headlands and one on each of the protected shores ($N = 2$ sites per exposure level). Exposed and protected sites were alternated along the coastline (from north to south: protected – exposed – protected - exposed), and separated by 50–100 m stretches of rocky shore. Wave-exposed and wave-protected sites exhibited clear differences in their physical settings and associated benthic communities. Wave-protected shores had offshore rocks that attenuated incoming waves, whereas waves were unobstructed in wave-exposed headlands. Wave-exposed sites were dominated by mussels (the California mussel, *Mytilus californianus*) and articulated and encrusting coralline algae, whereas wave-protected sites were dominated by mixtures of macroalgae – typically the red algae, *Mastocarpus papillatus*, *Endocladia muricata,* and *Mazzaella* spp. Within each site, we haphazardly placed 16 1.0 m^2 permanent plots in the mid-high intertidal zone (1.5–1.8 m above MLLW), for a total of 64 permanent plots across the four sites. Each plot was marked with two screws drilled in the rocky substrate at opposite corners and numbered metal tags.

2.2. Trampling treatments

Plots within study sites were randomly assigned to one of four