



# Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers?



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## ABSTRACT

The consequences of biodiversity loss in the face of environmental change remain difficult to predict, given the complexity of interactions among species and the context-dependency of their functional roles within ecosystems. Predictions may be enhanced by studies testing how the interactive effects of species loss from different functional groups vary with important environmental drivers. On rocky shores, limpets and barnacles are recognised as key grazers and ecosystem engineers, respectively. Despite the large body of research examining the combined effects of limpet and barnacle removal, it is unclear how their relative importance varies according to wave exposure, which is a dominant force structuring intertidal communities. We tested the responses of algal communities to the removal of limpets and barnacles on three sheltered and three wave-exposed rocky shores on the north coast of Ireland. Limpet removal resulted in a relative increase in microalgal biomass on a single sheltered shore only, but led to the enhanced accumulation of ephemeral macroalgae on two sheltered shores and one exposed shore. On average, independently of wave exposure or shore, ephemeral macroalgae increased in response to limpet removal, but only when barnacles were removed. On two sheltered shores and one exposed shore, however, barnacles facilitated the establishment of fucoid macroalgae following limpet removal. Therefore, at the scale of this study, variability among individual shores was more important than wave exposure *per se* in determining the effect of limpet removal and its interaction with that of barnacles. Overall, these findings demonstrate that the interactive effects of losing key species from different functional groups may not vary predictably according to dominant environmental factors.

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## 1. Introduction

The continued decline of global biodiversity is threatening the functioning and provisioning of services by ecosystems (Barnosky et al., 2011; Cardinale et al., 2012). The large body of biodiversity–ecosystem functioning (BEF) research conducted over the past two decades has provided unequivocal evidence that biodiversity loss reduces the efficiency of multiple ecosystem processes (Cardinale et al., 2011) and ranks among multiple global environmental stressors as a major driver of ecological change (Hooper et al., 2012; Tilman et al., 2012). There is still, however, some controversy surrounding the relevance of BEF studies to the conservation and management of real world ecosystems. In particular, studies should extrapolate results to larger scales and assess how the relative importance of biodiversity varies across gradients of environmental disturbance (Srivastava and Vellend, 2005; Stachowicz et al., 2007). Further, the complexity of natural ecosystems makes it

difficult to predict the consequences of biodiversity change. For example, in addition to trophic interactions among species, the effects of species loss may be propagated via non-trophic (direct and indirect) interactions (Kéfi et al., 2012; O'Connor and Donohue, 2012). Our predictions may be enhanced by defining biodiversity in terms of functional traits, rather than focussing on changes in species-level diversity (Crowe et al., 2011; Petchey et al., 2004; Wood et al., 2010).

The strength and direction of interactions among species and the organisation of communities are predicted to vary along gradients of environmental disturbance (Bertness and Callaway, 1994; Bruno et al., 2003; Menge and Sutherland, 1987). Accordingly, the functional role of biodiversity can be strongly context-dependent with regard to spatial and temporal variation in environmental stressors and/or community structure (e.g. Crowe et al., 2011; Fugère et al., 2012). Further, theoretical and empirical work has indicated that the effects of biodiversity change are likely to be more important at larger spatial and temporal scales, and with greater environmental heterogeneity (Cardinale et al., 2000; Stachowicz et al., 2008). Therefore, to assess ecological responses to biodiversity change, studies should be of sufficient extent to capture the levels of heterogeneity that characterise natural systems, and test the role of environmental context explicitly (Bracken et al., 2011; O'Connor and Donohue, 2012). As part of an integrated approach,

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field-based removal experiments provide an effective means of revealing the mechanisms by which losses of species from different functional groups affect ecosystems under variable environmental conditions (Crowe et al., 2012; Díaz et al., 2003).

In addition to contributing significantly to BEF research, temperate rocky shores comprise one of the most extensively studied systems in ecology, following a long history of experimental manipulations of the densities and presence of organisms (Benedetti-Cecchi, 2006; Underwood, 2000). Rocky shores, like other coastal marine ecosystems, are subjected to a range of anthropogenic impacts responsible for widespread habitat modification and dramatic local-scale changes in abundance or extinctions of species (Airoldi and Beck, 2007; Thompson et al., 2002). In communities that comprise high phylogenetic diversity and that are structured by strongly-interacting species, as is postulated for many marine habitats, the effects of species loss are expected to be highly idiosyncratic, i.e., identity-dependent (Allison et al., 1996; Emmerson et al., 2001). Further, there are likely to be interactive effects of losses of organisms from different functional groups, with consequences for the predictability of ecosystem responses (Crowe et al., 2011). On rocky shores, the roles of grazing and habitat engineering organisms such as limpets and barnacles in structuring communities, particularly with regard to the succession and dynamics of algal communities, have received much attention (e.g. Benedetti-Cecchi, 2000; Berlow and Navarrete, 1997; Dungan, 1986; Farrell, 1991; Geller, 1991; Hawkins, 1981a,b; Jernakoff, 1983; Kim, 1997; van Tamelen, 1987).

Limpets are important in regulating the abundance and distribution of algae on rocky shores in the northeast Atlantic (Coleman et al., 2006; Hawkins et al., 1992; Jenkins et al., 2005). By increasing substratum heterogeneity, barnacles facilitate algae directly by promoting the retention and settlement of propagules, increasing the surface area for attachment and offering protection against desiccation (Farrell, 1991; Hawkins, 1981a; Norton and Fetter, 1981). Further, barnacles may benefit algae indirectly by providing a refuge from grazers (Geller, 1991; Hawkins, 1981a; Lubchenco, 1983). In contrast, barnacles may have negative effects on algae via competition for space (Dungan, 1986), and it has been suggested that their feeding activity may inhibit settlement of algal propagules (Benedetti-Cecchi, 2000; Branch, 1976). Limpets can affect barnacle populations negatively by dislodging or crushing small barnacles (Dayton, 1971; Denley and Underwood, 1979), but they may also enhance barnacle settlement indirectly by removing competitive algae (Dungan, 1986) or depositing pedal mucus trails (Holmes et al., 2005). Conversely, barnacles may reduce the growth, reproductive output and survival of limpets by limiting access to food, disrupting foraging efficiency and decreasing the amount of space available for attachment (Branch, 1976; Geller, 1991; Hawkins and Hartnoll, 1982). Although barnacles may inhibit recruitment of juvenile limpets by occupying settlement space (Choat, 1977), they can also enhance the survival of small limpets by mitigating environmental stress (Branch, 1976; Lewis and Bowman, 1975).

Horizontal variation in wave exposure is a dominant force structuring rocky intertidal communities (Lindegarth and Gamfeldt, 2005; Raffaelli and Hawkins, 1996). Increased wave action is predicted to reduce the importance of grazing relative to competition and physical factors, owing to the limiting effects of hydrodynamic disturbance on the foraging activities of mobile consumers (Menge and Sutherland, 1987). Whereas grazing regulates the initial establishment of algae on rocky shores, the persistence of mature algae is limited by wave action above a certain threshold (Jonsson et al., 2006). Also, variation in wave exposure and water flow regime can influence settlement and recruitment of benthic species, in addition to nutrient concentrations and rates of food supply, thus altering bottom-up processes (Bustamante and Branch, 1996; Leonard et al., 1998). The relative functional roles of species, and therefore the interactive consequences of their loss, are attuned to the balance between top-down and bottom-up regulation, which in turn shifts along gradients of environmental stress or

disturbance (Thompson et al., 2004). To our knowledge, despite the number of studies examining the combined effects of limpet and barnacle removal on rocky shores, there has been no explicit test of their context-dependency by performing simultaneous factorial manipulations at multiple locations differing in wave exposure, which limits our understanding of how interactions among these key organisms vary along a dominant disturbance gradient (O'Connor et al., 2011).

We aimed to determine how the losses of species representing key functional groups (grazers and ecosystem engineers) interact to influence the development and structure of communities, and whether the effects of their removal vary according to a dominant form of physical disturbance on rocky shores. Specifically, we conducted a field experiment involving the singular and combined removal of limpets and barnacles on multiple shores of differing wave exposure to test the following hypotheses: (1) the effect of limpet removal on the development of microalgal and macroalgal assemblages is affected by the presence of barnacles; and (2) increased wave exposure modifies the interactive effects of limpet and barnacle removal on algal assemblages.

## 2. Materials and methods

### 2.1. Study sites

The experiment was carried out at three wave-sheltered and three wave-exposed shores in Co. Donegal, Ireland (Fig. 1). The 'sheltered' shores were at Ballywhoriskey, Downings and Melmore Head and the 'exposed' shores were at Glashagh Bay, Ballywhoriskey Point and Magheranguna Point. These shores are representative of typical exposed and sheltered shores in the region (e.g. O'Connor et al., 2006, 2011) and were selected randomly from a list of potential sites based on suitability and accessibility. Our study was designed to incorporate wave exposure as a categorical variable because this approach is useful for determining the relative importance of factors and for testing interactions among them at particular scales (Lindegarth and Gamfeldt, 2005), which is in agreement with the aim of this study. Treating wave exposure as a continuous variable is more suitable when aiming to maximise explanatory power for making quantitative predictions (Lindegarth and Gamfeldt, 2005). The average wave fetch ( $F$ ), calculated

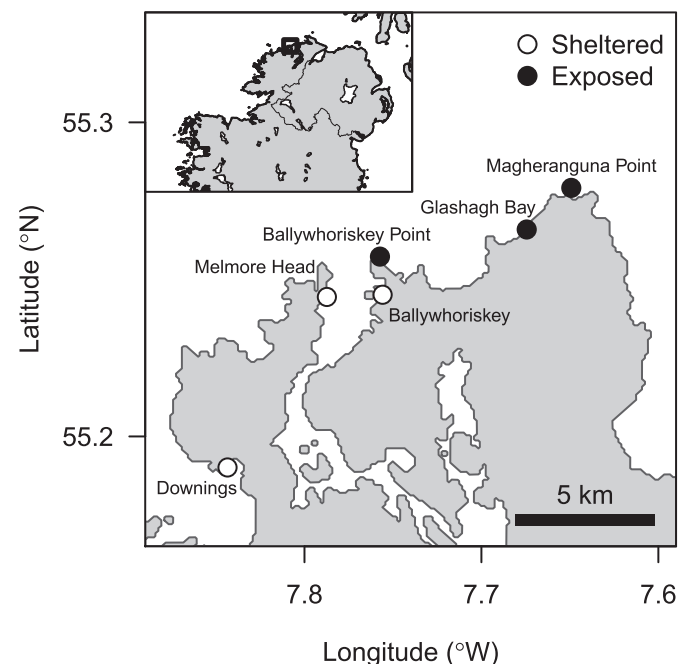


Fig. 1. The northern coast of Co. Donegal, Ireland, showing the locations of sheltered and exposed shores used in the study.

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