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Review

Restoring rocky intertidal communities: Lessons from a benthic macroalgal ecosystem engineer

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ABSTRACT

As coastal population growth increases globally, effective waste management practices are required to protect biodiversity. Water authorities are under increasing pressure to reduce the impact of sewage effluent discharged into the coastal environment and restore disturbed ecosystems. We review the role of benthic macroalgae as ecosystem engineers and focus particularly on the temperate Australasian fucoid *Hormosira banksii* as a case study for rocky intertidal restoration efforts. Research focussing on the roles of ecosystem engineers is lagging behind restoration research of ecosystem engineers. As such, management decisions are being made without a sound understanding of the ecology of ecosystem engineers. For successful restoration of rocky intertidal shores it is important that we assess the thresholds of engineering traits (discussed herein) and the environmental conditions under which they are important.

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1. Introduction

Coastlines around the world are facing increasing pressure from anthropogenic developments associated with population growth. Disposal of domestic sewage effluent into the marine environment is increasingly becoming a contentious issue as protection of biodiversity comes into the public eye (dela Ossa Carretero et al., 2016; Walker and Kendrick, 1998). Management authorities are actively seeking ways to reduce

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the impact of the wastewater disposal on the nearshore coastal environment (Adams et al., 2008; Molloy et al., 2004; Molloy et al., 2007) and restore biodiversity to disturbed regions. Ecosystem engineers – species that create habitat and modify the environment and resources for other species (Jones et al., 1994, 1997) – may be appropriate species on which to focus restoration efforts because of their direct and indirect interactions with a diverse suite of species (Byers et al., 2006; Crain and Bertness, 2006).

In this review, we examine the role of intertidal benthic macroalgae as ecosystem engineers and focus particularly on the temperate Australasian fucoid *Hormosira banksii* as a case study for rocky intertidal restoration efforts. *H. banksii* provides an excellent system for studying ecosystem engineering and restoration. It is an important habitat-forming brown macroalga that dominates much of the southern Australasian coastline (Osborn, 1948; Schiel, 2004); it contributes tangibly to the biodiversity of rocky intertidal communities, and where this species is lost (or reduced), the biodiversity is also changed (Brown et al., 1990; Lilley and Schiel, 2006). Fucoid algae, including *H. banksii*, have been shown to be very sensitive to anthropogenic disturbances such as human trampling (Araujo et al., 2009; Keough and Quinn, 1998; Schiel and Taylor, 1999), coastal sedimentation (Chapman and Fletcher, 2002; Schiel et al., 2006) and sewage effluent discharge (Bellgrove et al., 1997; Brown et al., 1990; Fairweather, 1990). We focus on the impact of sewage effluent discharge on benthic macroalgae, using *H. banksii* as a case study for intertidal restoration. Based on past restoration efforts of macroalgae (from anthropogenic disturbances), we suggest avenues for study that will lead to an improved understanding of the roles of fucoid algae in community and ecosystem function, with the aim of improving restoration efforts of rocky intertidal shores affected by sewage effluent pollution.

2. Intertidal benthic macroalgae as ecosystem engineers

Autogenic ecosystem engineers are species that create habitats, changing the environment by their physical presence (e.g. increased structural complexity) and by directly or indirectly modifying the abiotic conditions and/or biotic interactions between species, and consequently the availability of resources (Jones et al., 1994, 1997). We note that other authors have used different terminology for the same concept stressing the importance of positive interactions, including *foundation species* (Bruno and Bertness, 2001; Dayton, 1972) and *facilitators* (Altieri and van de Koppel, 2014; Bruno and Bertness, 2001), but we prefer the simplicity and operational definitions (Jones et al., 1994) of *ecosystem engineers*. We contrast ecosystem engineers to *keystone species*, whose activities and abundance determine the integrity and persistence of a community based on trophic and/or competitive interactions (Paine, 1966, 1969a, 1969b). We emphasise that understanding the variation in the strength of the interactions between species (particularly relative to abundance) is integral to assessing their role in community/ecosystem structure and for conservation and management of these systems (Bruno and Bertness, 2001; Crain and Bertness, 2006; Jones et al., 1997; Menge et al., 1994).

2.1. Interactions with habitat-forming intertidal benthic macroalgae

Macroalgae are often dominant space-holders in intertidal and shallow subtidal regions, particularly on temperate coasts. This section focuses on the current literature highlighting intertidal fucoid macroalgae as important ecosystem engineers. Understanding the direct and indirect effects macroalgae can have on the community will provide the necessary insight for restoration ecology practices.

Intertidal rocky shores are physically stressful environments, with gradients in wave action, heat and desiccation stress. We may expect that in such environments, ecosystem engineers that can ameliorate these physical stresses might be particularly important, especially at lower latitudes (Bertness and Leonard, 1997; Bertness et al., 1999; Crain and Bertness, 2006). Macroalgae can have both direct (providers of habitat and shelter) and indirect (e.g. habitat facilitation, altered species interactions) effects on intertidal community structure, and either may be equally important (Menge, 1995). Moreover, changes in the intertidal abiotic conditions by ecosystem engineers may have both positive and negative effects on associated species.

While many species of foliose algae are often abundant in the rocky intertidal, creating and modifying habitats and resource availability for associated species (Gosselin and Chia, 1995; Jernakoff, 1986; Kelaher et al., 2001; Sanchez-Moyano et al., 2001; Worm and Chapman, 1998), fucoid algae are often the dominant habitat-forming algae on intertidal rocky shores (Schiel, 2004) and there is much evidence of their importance as ecosystem engineers (Fig. 1). The complex three dimensional structure of fucoid canopies provides more microhabitats than less complex abiotic habitats, and have been shown to be important for biodiversity (Bertness et al., 1999; Bishop et al., 2012; Bishop et al., 2013; Fredriksen et al., 2005; Hily and Jean, 1997; Jenkins et al., 2004; Schiel and Lilley, 2011). Additionally, fucoid canopies can ameliorate the physical stresses associated with temperature, desiccation and wave action. For example, a canopy of *Fucus gardneri* reduced rock surface temperatures and desiccation rates, and increased survival of conspecific germlings (van Tamelen et al., 1997). Similarly a canopy of *Silvetia compressa* prevented dehydration of agarose beads after 4.1 h emersion in summer, and this correlated with 100% survival of zygotes of *S. compressa* (c.f. 0% survival on bare rock and in canopy removal plots; Brawley and Johnson, 1991, 1993). For *Ascophyllum nodosum* and *Fucus distichus* on Rhode Island, survivorship of conspecifics high on the shore was greater under natural canopies than under experimentally thinned canopies due to reduced heat and desiccation stress (Bertness and Leonard, 1997). A canopy of *F. distichus* also increased barnacle recruitment on a northwestern Pacific shore where desiccation was high, suggesting that the canopy moderated the desiccation stress (Dayton, 1971). Similarly, on a sheltered shore in the Gulf of Maine, rock temperatures and evaporative water loss were greatly reduced below a canopy of *A. nodosum* compared to canopy removal plots, positively affecting recruitment, growth and survival of understorey species in the high intertidal (Bertness et al., 1999). As well as reducing heat stress, fucoid canopies can provide insulation and reduce thermal stress to understorey species caused by freezing temperatures (McCook and Chapman, 1991; Thompson et al., 1996).

Hydrodynamic forces created by wave action can place severe mechanical stress on organisms living in wave-swept environments and

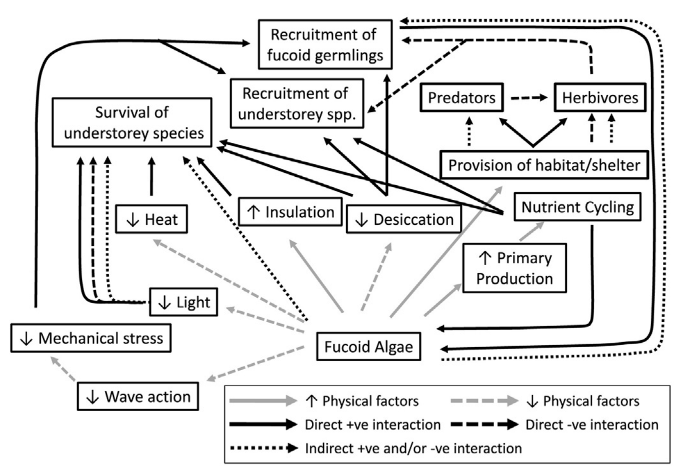

Fig. 1. Schematic diagram expressing the current understanding of the autogenic ecosystem engineering roles of intertidal fucoid algae (see text for further explanation and citations). Grey arrows indicate an increase (solid) or decrease (dashed) in physical factors due to the presence of a fucoid canopy. Consequent positive (solid) and negative (coarse dashed) direct and indirect (fine dashed) interactions with other organisms and ecological processes are indicated by black arrows. Other indirect interactions are implied by the series of arrows.