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

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Alecia Bellgrove[a*], Prudence F. McKenzie[a], Hayley Cameron[a1], Jacqueline B. Pocklington[b2]

[a]Deakin University, Geelong, Australia. School of Life and Environmental Sciences, Centre for Integrative Ecology, Warrnambool Campus, P.O. Box 423, Warrnambool, Victoria 3280, Australia

[b]Department of Zoology, University of Melbourne, Parkville, Victoria 3010, Australia and Marine Invertebrates, Museum of Victoria, GPO Box 666, Melbourne, Victoria 3001, Australia

[1]Present address: School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia,

[2]Present address: School of Marine Science and Technology, Newcastle University, Dove Marine Laboratory, Cullercoats, Tyne & Wear NE30 4PZ, United Kingdom

*Corresponding author. E-mail: alecia.bellgrove@deakin.edu.au, Fax: +61-3-5563-3462

Co-author E-mails: PF McKenzie: prue.francis@deakin.edu.au, H Cameron: hayley.cameron@monash.edu, JB Pocklington: jacqueline.pocklington@ncl.ac.uk

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.

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 (de-la-Ossa-Carretero et al., 2016; Walker and Kendrick, 1998). Management authorities are actively seeking ways to reduce 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.

Intertidal benthic macroalgae as ecosystem engineers

Before we examine the role of benthic macroalgae as ecosystem engineers, definitions of an ecosystem engineer and a keystone species are given due to both terms often being misused in the literature (e.g. *H. banksii* has been referred to as being both; Keough and Quinn, 1998; Schiel, 2006) and if restoration efforts are to focus on ecosystem engineers, a clear distinction between these terms is required.

Ecosystem engineers and keystone species

It seems intuitively obvious that many species are capable of providing habitat and modifying the environment for other species. As in terrestrial ecosystems, many marine habitats are created by particular species (Altieri and van de Koppel, 2014). Common examples include coral reefs, seagrass meadows, mangroves/mangals, kelp forests and saltmarshes (Bertness and Leonard, 1997; Gilbert and Jannsen, 1998; Gratwicke and Speight, 2005; Hacker and Gaines, 1997; Reed and Foster, 1984). The species that create these habitats change 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). This is referred to as *ecosystem engineering* and the species that cause these types of ecosystem changes are *autogenic ecosystem engineers* (Jones et al., 1994). 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*.

A related concept is that of *keystone species*, whose activities and abundance determine the integrity and persistence of a community (Paine, 1969a). The original keystone species concept was derived from a trophic interaction between a top predator and the associated community (Paine, 1966, 1969b). However, some controversy has arisen over the term subsequently being used for other species that are functionally important to community structure through different trophic interactions or non-trophic interactions (Menge et al., 1994). Importantly, however, Jones *et al.* (1994) suggested that keystone predators (Menge et al., 1994) can also operate as ecosystem engineers, or change the engineering role of other species. For example, sea otters can control sea urchin populations and facilitate extensive kelp forests (Estes and Palmisano, 1974; but see Konar, 2000) that in turn modify the environment for other species (Reed and Foster, 1984).

The key difference between ecosystem engineers and keystone species is that the activity of ecosystem engineers does not rely on trophic or competitive interactions (Jones et al., 1994, 1997); and also that ecosystem engineering is process-focused whilst the keystone species concept is outcome-focused (Wright and Jones, 2006). However, for both ecosystem engineers and keystone species, 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).

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) 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 can constrain the sizes of intertidal

plants and invertebrates (Blanchette, 1997 and references therein). Although

constructed from brittle material, macroalgae are highly extensible and therefore

remarkably resilient to the mechanical forces of waves (Denny et al., 1989). Canopies

of *Fucus vesiculosus* and *A. nodosum* can greatly reduce wave action, which can reduce mechanical stress for understorey species and create a depositional environment for the entrapment of larvae (Leonard, 1999; McCook and Chapman, 1991; Thompson et al., 1996), and presumably algal propagules. Certainly some studies have found initial propagule settlement to be highest under an adult canopy (Johnson and Brawley, 1998).

While the reductions in physical stresses of the intertidal environment afforded by fucoid canopies can have direct positive effects, they may also have indirect positive or negative effects on associated species (Fig. 1). Brawley and Johnson (1991) and Johnson and Brawley (1998) noted that despite high settlement and initial survival of zygotes under a canopy, *S. compressa* recruits were rarely found beneath a canopy. They suggested negative indirect effects of increased herbivory under the canopy or whiplash by adult plants might be possible causes. Whiplash was also found to affect germling survival of *F. gardneri*, but the positive canopy effects of reduced heat and desiccation stress were stronger (van Tamelan et al., 1997). Barnacles have been shown to be negatively affected by whiplash from an algal canopy in some studies (Beermann et al., 2013; Grant, 1977; Leonard, 1999) despite positive effects through amelioration of physical stress (Beermann et al., 2013; Leonard, 1999), while other studies have shown no effect of whiplash (Dayton, 1971; Underwood, 1999).

Dense intertidal algal canopies reduce the amount of light reaching the understorey and this can also have direct and indirect, positive and negative effects on understorey species. When a canopy of *Fucus serratus* was removed, encrusting coralline algae bleached and died within one week (Hawkins and Harkin, 1985). Similarly, red algal understorey turfs (primarily *Chondrus crispus*, *Gelidium* spp. and *Corallina officinalis*)

became bleached when an *A. nodosum* canopy was removed, even in winter (Jenkins et al., 1999). In contrast, removals of *Cystoseira* canopies in the Mediterranean resulted in increases in red algal turfs, including articulated corallines, but encrusting corallines were unaffected (Benedetti-Cecchi and Cinelli, 1992; Benedetti-Cecchi et al., 2001; Bulleri et al., 2002); recruitment of *F. vesiculosus* and ephemeral algae were enhanced when *F. vesiculosus* was removed (McCook and Chapman, 1991); and in *A. nodosum* canopy-removal plots, *F. vesiculosus*, *F. serratus* and *A. nodosum* recruitment were enhanced (Jenkins et al., 1999), suggesting that the shade of the canopies suppressed these species' growth.

Additionally, several studies have recorded changes in the species composition of understorey algae and invertebrates in response to canopy removals, which incorporate complex direct and indirect interactions (Fig. 1; Benedetti-Cecchi and Cinelli, 1992; Benedetti-Cecchi et al., 2001; Bertocci et al., 2014; Bulleri et al., 2002; Hawkins and Harkin, 1985; Jenkins et al., 1999; Jenkins et al., 2004; McCook and Chapman, 1991; Migné et al., 2015; Schiel and Lilley, 2011). Fucoid canopies can indirectly affect the abundances of other species by causing changes in consumer pressure (Bertness and Leonard, 1997). For example, the shade provided by a *F. distichus* canopy, while increasing survival of conspecific germlings, also positively affected the densities of the grazing snail *Littorina littorea*, which had an indirect negative effect on growth and survival of *F. distichus* germlings through increased grazing pressure (Bertness and Leonard, 1997). *Fucus evanescens* provides habitat for a diverse taxa of epiphytic algae that facilitate many free-living epifauna (Wikstrom and Kautsky, 2004), which might affect algal recruitment (Buschmann and Bravo, 1990; Buschmann and Vergara, 1993). Green crab (*Carcinus maenus*) predation was higher beneath an *A. nodosum* canopy and

probably limited densities of mussels (*Mytilus edulis*) in the understorey (Bertness et al., 1999). A canopy of *A. nodosum* indirectly affected the grazing range of the limpet *Patella vulgata* by facilitating red algal turf that limited suitable substrata for limpets (Jenkins et al., 1999).

Recent research focussing on metabolic processes of canopy-forming fucoids suggest they are the most productive systems of intertidal habitats (Bordeyne et al., 2015; Crowe et al., 2011a; Golléty et al., 2008; Migné et al., 2015; Tait et al., 2014; Tait and Schiel, 2011) and where canopies are lost (removed), productivity is also lost. For example, photosynthetic rate decreased by 50% after the removal of the fucoid, *H. banksii* (Tait and Schiel, 2011). Furthermore, field experiments have shown canopy removal of *F. serratus* (and other canopy-forming algae) dramatically reduced the community's primary productivity, respiration and biomass levels (Crowe et al., 2011a; Migné et al., 2015). It has also been shown that the fucoids *A. nodosum, F. vesiculosus* and *F. serratus* contribute to most of the carbon fluxes in their zones (Bordeyne et al., 2015; Golléty et al., 2008). Therefore canopy structure appears to influence metabolic processes of algal assemblages, and consequently the removal of fucoid species may also negatively impact ecosystem functions such as coastal primary productivity and nutrient cycling.

Effects of treated sewage effluent on benthic macroalgae

Discharge of treated sewage effluent (wastewater) into the nearshore marine environment has been shown to have detrimental effects on rocky intertidal and shallow subtidal communities around the world (Brown et al., 1990; Bustamante et al., 2012; Coleman et al., 2008; Cormaci and Furnari, 1999; Díez et al., 2013; Fairweather, 1990;

Hirose, 1978; Littler and Murray, 1975; May, 1985). Our understanding of these effects in the intertidal zone is summarised in Fig. 2. The dominant brown algae (predominately fucoids or laminarians) that are often important ecosystem engineers, generally decline in abundance or are absent altogether from polluted sites, and are replaced by an increase in the abundance of opportunistic and turf-forming species such as *Ulva* (including *Enteromorpha* Borowitzka, 1972; Brown et al., 1990; Fairweather, 1990; Golubic, 1970; Hirose, 1978; Klavestad, 1978; Littler and Murray, 1975; May, 1985; Tewari and Joshi, 1988), *Ceramium* (Brown et al., 1990; Klavestad, 1978), *Gelidium* (Littler and Murray, 1975, 1978) and *Capreolia implexa* (Brown et al., 1990; as *Gelidium pusillum* May, 1985; Womersley, 1994). These ephemeral and turf-forming species may benefit from high nutrient loads because of their high surface-area:volume ratios and rapid nutrient uptake (Rosenberg and Ramus, 1984), facilitating the high levels of recruitment of ephemeral species observed at polluted sites (Bellgrove et al., 1997).

In some studies the articulated coralline alga, *Corallina officinalis,* has been abundant in the immediate vicinity of a sewage outfall (Littler and Murray, 1975; May, 1985), but in others this species was absent from outfall sites, but formed extensive turfs at intermediately polluted sites (Bellgrove et al., 1997; Bellgrove et al., 2010; Borowitzka, 1972; Brown et al., 1990). Bellgrove *et al.* (1997) suggested that high phosphate concentrations near the outfall may inhibit calcification of the cell walls (following from Brown et al., 1977). Clearly mat-forming algae are more tolerant or actively benefit from anthropogenic stressors such as sewage effluent discharge (Strain et al., 2014).

Sites that are affected by sewage effluent discharge typically show a decrease in species richness (Borowitzka, 1972; Brown et al., 1990; Fairweather, 1990; Littler and Murray, 1975). The reduction in diversity is possibly a consequence of both direct effects of the sewage effluent on species and indirect effects of the loss of a brown algal canopy. The loss of the important habitat-forming species such as the low-shore laminarian *Eisenia arborea*, resulted in decreased habitat stratification and complexity and probably contributed to the loss of diversity of understorey flora and fauna (Littler and Murray, 1975). In fringing areas where the canopy of *E. arborea* was maintained, the changes to the community were minimised. Changes in species richness at effluent-affected sites may also be driven by high nutrient loads favouring certain species that will then out-compete a variety of space-holders, lowering diversity. Recruitment of some fucoid algae in nutrient-enriched conditions has been reduced by competition for space by ulvoid and filamentous opportunistic algae (Korpinen and Jormalainen, 2008; Steen, 2004). However, other studies (Bokn et al., 2003) have shown that opportunistic algae are unable to displace established dominant fucoid algae under enriched conditions unless space is made available.

Although many studies have recorded similar patterns of community change in response to sewage effluent discharge (Fig. 2), we still have relatively little understanding of the mechanisms that are causing these changes. For example, Bellgrove *et al.*(1997) did not find any negative effect of sewage effluent on the recruitment of macroalgae. However, no perennial species, including the pre-discharge dominant *H. banksii* (Manning, 1979), recruited during their study (even at unpolluted shores), which may have been an artefact of the type of artificial substrata used in their experiments (Bellgrove et al., 2004). While field evidence confirming that effluent exposure can

limit fucoid recruitment is scarce, laboratory-based toxicity assays have demonstrated that the early developmental stages (fertilization, germination, cell wall formation and cell division) of fucoids can be negatively affected by sewage effluent. In particular, ammonium concentrations (EC_{50} values of 0.08 mg – 3.19 NL^{-1} for *H. banksii*) and salinity appear to be the most harmful effluent constituents to early life-stages, but effects are variable amongst developmental stages and amongst studies (Kevekordes, 2001), Myers et al., 2006; (Stauber et al., 2003)).

Discrepancies in reported EC_{50} values for the fucoid *H. banksii* may be due at least in part to different concentrations of ammonium and ammonia (and associated differences in toxicity of the two compounds), with tests run at different temperatures and pH amongst studies (Kevekordes, 2001; Myers et al., 2006; Stauber et al., 2003). The concentrations of ammonia and ammonium are in dynamic equilibrium in solution and are affected moderately by temperature, but dramatically by changes in pH. Thus, to ensure comparable EC_{50} values between different toxicity tests for individual species, it is essential that the protocols used for bioassays are identical and that the pH and temperatures of test solutions are the same. However, if laboratory toxicity tests are to be meaningful for the environmental conditions surrounding the sewage outfalls, then it would be sensible to repeat these bioassays under a range of temperatures and pH conditions that reflect seasonal fluctuations of the coastal receiving waters. Moreover, effluent volumes, total ammonia concentrations and salinity can vary over fine and coarse temporal scales (Batley and Simpson, 2009; Molloy et al., 2004). Thus to be able to set realistic water quality targets for restoration of coastal ecosystems, it is imperative that we also understand the effects of pulses of toxic constituents on the fucoid algae.

Reducing the toxicity of sewage effluent discharged into the marine environment alone may not be sufficient to restore fucoid populations. There are multiple factors that might limit the recovery of fucoids and other lost seaweed species into remediated areas (Bellgrove et al., 2010; Díez et al., 2013), highlighting the need to compliment laboratory studies with manipulative field experiments to appropriately predict outcomes of management decisions aimed at restoring communities affected by sewage effluent discharge. Furthermore, the recruitment potential of early-life stages and long-term survival of adults on remediated shores should be investigated in the field to evaluate the effectiveness of wastewater upgrades in achieving a water quality that permits re-establishment and self-perpetuation of fucoid populations.

Ecosystem engineers and restoration

Ecosystem engineers may have positive effects on some species and negative effects on others (Bertness et al., 1999; Bruno and Bertness, 2001; Jones et al., 1997). This may increase or decrease species richness and abundances on local scales (Bellgrove et al., 2004; Thompson et al., 1996), but at larger spatial scales that incorporate both engineered and non-engineered environments the net effect on biodiversity is likely to be positive (Bertness and Leonard, 1997; Halpern et al., 2007; Jones et al., 1997); with a mosaic of habitats and associated species and potentially a transfer of energy between them (Bustamante et al., 1995; Estes and Palmisano, 1974; Griffiths et al., 1983; Halpern et al., 2007; Robertson and Lenanton, 1984; Thomsen et al., 2013).

The importance or role of a species as an ecosystem engineer depends on 1) patch size, 2) density/cover, 3) architectural complexity, 4) spatial arrangement/connectivity, and 5) the stability or residence of traits 1 – 4 (Bruno and Bertness, 2001). Furthermore,

there are likely to be thresholds between these five traits and environmental stress (Bruno and Bertness, 2001). In reviewing the current literature, the role, and sometimes the importance, of ecosystem engineers varies along environmental gradients (Crain and Bertness, 2006; but see Viejo et al., 2008) and with environmental context (Crowe et al., 2011b). The example given about the interaction between canopy cover of *H. banksii*, whelk predation and barnacle densities (Underwood, 1999; see *H. banksii* section of review) illustrates the potential for such thresholds.

In addition to the traits of ecosystem engineers defined by Bruno and Bertness (2001), Jones *et al.* (1994, 1997) suggested that 6) the amount of engineered habitat created by an individual in its lifetime, 7) the type and durability of the constructed habitat and impacts once the original engineer has died (or left), and 8) the number of resource flows that are modulated by the engineer and the number of species dependent on these flows will also be important for scaling the impact of an ecosystem engineer. To maximise the effectiveness of restoration efforts, it would thus be ideal to understand the thresholds for each of these traits and the environmental conditions under which they operate. Indeed, there are yet few notable attempts to examine this for intertidal fucoid macroalgae (e.g. Pocklington et al., in review; Schiel and Lilley, 2007)

Lessons from the recovery of intertidal benthic macroalgae

The recovery rates of canopy-forming fucoid algae have been shown to vary both between (e.g. Hawkins and Harkin, 1985; Jenkins et al., 2004) and within (Keough and Quinn, 1998; Lilley and Schiel, 2006; Schiel, 2006) species. Following experimental removals of canopies of *Fucus serratus* from the intertidal, recruitment and recovery of all canopy species was rapid (6 mth to 1 y) (Hawkins and Harkin, 1985). However,

while the habitat had been restored, the associated algal assemblages remained different from controls after 1 y (Hawkins and Harkin, 1985). In contrast however, removal of a canopy of *Durvillaea antarctica* from the lower intertidal zone of an exposed shore resulted in an altered assemblage, where turfing articulated coralline algae (*Corallina officinalis, Jania* spp., *Haliptilon roseum*) had increased cover with little recovery of *D. antarctica* (Taylor and Schiel, 2005).

Experimental removal of *Ascophyllum nodosum* on the Isle of Man, UK, resulted in a mixed canopy of *Fucus vesiculosus* and *F. serratus* that provided similar shade to turfing species as the original canopy (Jenkins et al., 1999). However, despite successful recruitment (Jenkins et al., 1999), *A. nodosum* had not regained the canopy even 12 y post initial removals, apparently due to very slow growth (Jenkins et al., 2004). Changes to the community from the initial loss of the *A. nodosum* canopy were still present after 12 y (Jenkins et al., 1999; Jenkins et al., 2004). In the Gulf of Maine (Bertness et al., 1999), recruitment of *A. nodosum* was comparably high (Jenkins et al., 1999), but was restricted to shaded and canopy plots from which grazers were excluded high on the shore. Bertness *et al.* (1999) suggested that the amelioration of abiotic conditions by the canopy could facilitate recruitment of conspecifics providing positive feedbacks (Jones et al., 1997) once a canopy was established (Fig. 1).

In the Mediterranean, removals of canopies of *Cystoseira* spp. have resulted in rapid changes to assemblages dominated by coralline turfs (Benedetti-Cecchi and Cinelli, 1992; Benedetti-Cecchi et al., 2001; Bulleri et al., 2002). Once established the turfs appear to prevent the recruitment of the canopy algae such that the changes to the assemblages are long-lasting (Benedetti-Cecchi and Cinelli, 1992; Bulleri et al., 2002).

The above examples illustrate that the effects of removing ecosystem engineers can be long-lasting, even in cases where there is an ample supply of propagules and good recruitment. For many of these species there is no functional replacement after canopy loss (Schiel, 2006). For anthropogenic disturbances, the negative effects on ecosystem engineers are usually over much larger spatial scales than those adopted for many canopy-removal experiments (Benedetti-Cecchi et al., 2001; Brown et al., 1990; Chapman et al., 1995). For example, recovery of *Fucus gardneri* following broad-scale decimation of populations due to the Exxon Valdez oil spill and subsequent clean up, was initially slow because of low densities of reproductive plants and poor dispersal (van Tamelen et al., 1997). Additionally, habitat characteristics such as substratum rugosity and provision of a canopy (and associated reduction in heat and desiccation), improved recruitment for restoration efforts (van Tamelen et al., 1997).

Recovery of fucoid assemblages following wastewater remediation appears to be limited in many parts of the world; with efforts focusing on seeding (Bellgrove et al., 2010; Hernandez-Carmona et al., 2000; Stekoll and Deysher, 1996; Yoon et al., 2014; Yu et al., 2012) and/or transplantation of juvenile or adult thalli (Campbell et al., 2014; Hernandez-Carmona et al., 2000; Whitaker et al., 2010) to sites where the populations were lost, or by artificially increasing the substratum complexity (Deysher et al., 2002; Terawaki et al., 2001; Yu et al., 2012). For example, Soltan et al. (2001) noted that even 8 years following upgrades to industrial and domestic effluent treatment in Marsielle, France, populations of the fucoid *Cystoseria amantacea* were yet to recolonize; even at sites most distant from the point of discharge. Similarly, improvements to the effluent discharged into the Nerviòn River in northern Spain has allowed some recovery of macroalgal communities along the Basque coast, with these

communities progressing towards a state similar to a reference site (Diez et al., 2009; acknowledging the limitations of sampling only one reference site). However, complete restoration has not been achieved within the low intertidal for any of these sites, which is largely driven by the continued absence of the fucoids *Bifurcaria bifurcaria* and *Cystoseria tamariscifolia*. In Sydney, Australia the subtidal fucoid *Phyllospora comosa* was lost along a 70 km stretch of coastline following discharge of primary-treated sewage effluent and has not recovered naturally since sewage treatment was improved in the 1990's (Coleman et al., 2008). Preliminary transplants of fertile adult plants back into this region is looking promising for restoration even after 18 months post-transplantation (Marzinelli et al., 2014; Marzinelli et al., 2016). Results indicate limited dispersal may have prevented re-establishment following remediation (Campbell et al., 2014).

Most studies investigating recovery of algal assemblages following wastewater remediation (such as the examples above) focus on changes in community composition and abundances of adult plants. While it is informative to track changes in algal communities in response to wastewater remediation, such studies cannot distinguish mechanisms contributing to recovery failure that may need to be regulated for successful restoration to be achieved. Consequently, there is an urgent need for future manipulative studies to untangle potential limitations to recolonization in order for implementation of appropriate restoration initiatives. It is also clear that we must have a thorough understanding of the factors that lead to the initial demise of ecosystem engineers, to ensure that initial drivers of loss are reversed.

An understanding of connectivity between populations is essential for understanding the patterns of gene flow between populations and how they may recover from disturbances (Schiel, 2004). Understanding gene flow is also essential if restoration involves re-establishing ecosystem engineers by augmentation of populations from remnant sites, in order to maintain genetic diversity and avoid genetic pollution (McKay et al., 2005). While populations of marine organisms with a pelagic dispersal stage have traditionally been considered to be 'open', with local reproduction and recruitment de-coupled (Underwood and Fairweather, 1989) there is a lot of evidence from both oceanographic modelling (Cowen et al., 2000), field and laboratory experimentation (Santelices, 1990) and genetic studies (Coleman et al., 2011; Kinlan and Gaines, 2003; Williams and Di Fiori, 1996) that suggest for most macroalgae and many invertebrates, dispersal may be limited. In particular, for fucoid algae, with large non-motile and negatively-buoyant eggs, dispersal is often thought to be limited to within metres or 10s m from the parent (Bellgrove et al., 2004; reviewed in Santelices, 1990; Schiel, 2004). However, while the potential for long-distance dispersal of macroalgae by floating fertile fragments has been discussed (Santelices, 1990; van den Hoek, 1987) the importance of this mode of dispersal has had little investigation (Gagnon et al., 2015; Hernández-Carmona et al., 2006; Macaya et al., 2005; McKenzie and Bellgrove, 2008, 2009; Rothausler et al., 2015). For coastal areas affected by anthropogenic disturbances where the habitat-forming fucoid algae often disappear from large stretches of coast (e.g. Benedetti-Cecchi et al., 2001; Brown et al., 1990), an understanding of the dispersal capabilities of the ecosystem engineers is an essential precursor to understanding whether populations can re-establish from distant undisturbed populations, if inhibitory conditions are removed.

Hormosira banksii: a case study

Hormosira banksii *as an ecosystem engineer*

In southern Australasia, the only fucoid species that forms extensive canopies in the intertidal zone is the endemic *Hormosira banksii* (Osborn, 1948; Schiel and Taylor, 1999; Womersley, 1987). However, despite its abundance on both wave-exposed and sheltered shores throughout southern Australasia (Bellgrove et al., 2004; Keough and Quinn, 1998; Schiel and Taylor, 1999; Underwood, 1998; Womersley, 1987), we know relatively little about the role *H. banksii* plays in intertidal community structure, with only a handful of studies, but all suggest an important autogenic engineering role (Fig. 1).

Like other perennial fucoids, *H. banksii* is long-lived (>5 y; Kain (Jones), 2015; Keough and Quinn, 1998), and can form extensive mats often with 70 – 100 % cover (Bellgrove et al., 2004; Keough and Quinn, 1998; Schiel and Taylor, 1999; Underwood, 1998). Recruitment of *H. banksii* was higher under the adult canopy than in an adjacent low-relief mixed algal assemblage (Bellgrove et al., 2004), suggesting either very limited dispersal or amelioration of physical stresses beneath the canopy. For example, reduced wave action might improve 'stickability' of zygotes (Taylor and Schiel, 2003) and the moisture maintained beneath the canopy on emersion (Davenport et al., 1999, A. Bellgrove personal observations; Keough and Quinn, 1998) may facilitate post-settlement survival. The absence of an adult canopy and increased susceptibility to heat and desiccation stress of settlers, may explain slow recovery of *H. banksii* in canopy removal experiments (Schiel, 2006). Thus, there may be positive feedbacks to *H. banksii* through the provision of an extensive canopy (Jones et al., 1997). Vegetative

regeneration of senesced fronds from the basal holdfast (Schiel and Taylor, 1999) may

also ensure the relative stability of the canopy in undisturbed conditions (Keough and

Quinn, 1998; Schiel and Taylor, 1999).

The thallus of *H. banksii* consists of chains of hollow vesicles that contain internal

reserves of water for replenishing dehydrated tissues on emersion (Osborn, 1948). The

thallus is thus resistant to desiccation at low tide and also appears to moderate the water

loss and heat stress in the understorey (Davenport et al., 1999; Keough and Quinn,

1998; but see Pocklington, 2003). Temperature increases of 4 – 9.5 ºC have been

recorded in canopy removal plots compared to controls (Lilley and Schiel, 2006). The

cell walls of *H. banksii* contain phenolic compounds (Schoenwaelder and Clayton,

1999) that have been shown to protect the inner photosynthetic tissues from UV

radiation (Schoenwaelder, 2002). The canopy of *H. banksii* is thus also able to provide

shade and UV protection for understorey species during summer low tides. However,

some canopy loss of *H. banksii* occurs in most summers (Keough and Quinn, 1998) due

to 'thallus sunburn' (Schoenwaelder, 2002) associated with daytime summer low tides

exacerbated by barometric influences; and a single, very hot (> 28 ºC) spring day

caused ~ 30 % reduction in percentage cover of the canopy (Keough and Quinn, 1998).

H. banksii supports a relatively diverse, and in some cases unique, assemblage of

understorey algae (Bellgrove, 1998; Bellgrove et al., 2004; Lilley and Schiel, 2006;

Schiel, 2006), epifauna (Davenport et al., 1999; Schiel, 2006; Schreider et al., 2003) and

macroinvertebrates (Bishop et al., 2009; Keough and Quinn, 1998; King, 1992; Schiel,

2006) and can also provide important shelter for the fish *Enneapterygius rufopileus*

(Silberschneider and Booth, 2001). Similarly, as for some northern hemisphere fucoids,

several studies have shown that articulated and encrusting corallines are rapidly bleached and fragmented when a canopy of *H. banksii* is removed (Keough and Quinn, 1998; Schiel and Taylor, 1999; Underwood, 1999). However, experimental canopy removals of *H. banksii* in southern New Zealand resulted in initial bleaching of articulated coralline algae, followed by recovery to become the primary benthic cover . Further, removals had positive effects on the abundance of ephemeral algae but an overall negative effect on floral and faunal diversity with a 37 % decline relative to controls, primarily because of strong non-trophic interactions between *H. banksii* and understorey species (Lilley and Schiel, 2006). Another long-term canopy removal experiment in New Zealand, showed that removal of *H. banksii* only resulted in death and removal of articulated coralline turf in the higher mid-intertidal region (0.8 m) at one site (Schiel, 2006). In this case, there was up to 42 % decline in taxon richness in canopy removals compared to controls across sites (Schiel, 2006).

Unlike abiotic habitats (*e.g.* cracks and crevices in rocks), biotic habitats are dynamic and can vary in space and time (Underwood, 1999), where such fluctuations could modify the roles of autogenic engineers (Jones et al., 1997). There is evidence that the amount of cover provided by the canopy of *H. banksii* directly or indirectly affects associated species. Abundances of the grazing snail *Austrocochlea constricta* and percentage cover of articulated and encrusting corallines increased with canopy cover (Keough and Quinn, 1998). *H. banksii* provided shelter for whelks, which increased their effectiveness as predators of barnacles, indirectly affecting the abundance of barnacles (Underwood, 1999). However, this interaction was modified by the size and extent of the *H. banksii* canopy, which is in turn modified by unpredictable processes, such as storm events (Underwood, 1999), extreme thallus sunburn (Keough and Quinn,

1998) or fluctuations in recruitment (Bellgrove et al., 2004). Additionally, no significant differences in desiccation or temperature in mixed species (including *H. banksii)* canopy and canopy removal plots in Lady Bay (Adelaide, Australia) were found (Pocklington, 2003). However, further investigation revealed that microtopography was highly rugose at this site, and the canopy was patchy with short fronds (Pocklington, 2003). This suggests that both the quality of the canopy-forming alga and the alternative microhabitats available at a site can influence its role as an autogenic engineer.

Varying densities of ecosystem engineers such as fucoid macroalgae, can also be an important mechanism influencing the associated community (Schiel and Lilley, 2007; Speidel et al., 2001). For example, the density of *H. banksii* was manipulated over varying levels on a rocky shore in New Zealand, where results showed that taxon richness declined when the density of *H. banksii* was reduced (Schiel and Lilley, 2007). Additionally, densities of engineers may play an important role in relation to rehabilitation programs, as disturbances (e.g. anthropogenic or restoration programs) may move populations over important density thresholds. When densities of the fucoid, *Fucus gardneri* were manipulated, results showed robustness towards various disturbance intensities as long as a few individuals were present to maintain recruitment (Speidel et al., 2001). Therefore, when *F. gardneri* is faced with a disturbance (e.g. oil spill), and the population is completely removed, we know based on the above findings that recovery will be slow, however if a few individuals remain unaffected recovery will be much quicker (Speidel et al., 2001).

There is considerable morphological plasticity in the thallus form of *H. banksii* (Clarke

and Womersley, 1981), with broad differences between estuarine and marine habitats,

and also differences between microhabitats within these habitats (Bishop et al., 2009;

Ralph et al., 1998). However, even within morphometric forms associated with

microhabitats, particularly on eulittoral rock platforms, there is quite a lot of variability

in vesicle attributes, chain length and branching pattern (Bishop et al., 2009; McKenzie

and Bellgrove, 2008; Ralph et al., 1998). This means that the three-dimensional

structure created by *H. banksii* might vary at different sites and in different

microhabitats within sites. Therefore, the role of *H. banksii* as an ecosystem engineer

may change depending on its morphology (Bruno and Bertness, 2001; Jones et al.,

1997). For instance, Bishop et al. (2009) conducted transplant experiments of *H. banksii*

thalli from both rocky shore and estuarine habitats into a mangrove forest along the

New South Wales coast in eastern Australia. They found that while both algal types

enhanced molluscan abundance and species richness, estuarine *H. banksii*, which is

characterized by larger vesicles and longer thalli, supported higher diversity and

abundances of mollusc assemblages than did rocky shore plants. Subsequent

experiments demonstrated that thallus length was most important, but also that the

morphology of an intermediary facilitator (mangrove pneumatophores that trap floating

H. banksii thalli) may affect the epifaunal assemblages (Bishop et al., 2013).

Recovery rates of Hormosira banksii

Although Australasian studies have shown that removal of a canopy of *H. banksii* can in

some cases result in bleaching and death of understorey coralline turfs (Keough and

Quinn, 1998; Schiel, 2006; Schiel and Taylor, 1999) there is also evidence that where *H.*

banksii is weakened by intermediate levels of pollution, articulated coralline turfs can take over dominance (Bellgrove et al., 2010; Brown et al., 1990). It is possible that articulated coralline turfs and fucoid canopies are alternate community states (Petraitis and Latham, 1999) where the switch is intermediate-level pollution that disrupts dominance by *H. banksii*. Recruitment of *H. banksii* into coralline turfs could only occur when turfs had been reduced to either < 2 mm (by human trampling, Schiel and Taylor, 1999) or up to 10 mm (Alestra et al., 2014). Similarly, recovery of *H. banksii* in canopy removal plots may have been impeded by thick (30 mm) coralline turfs (Schiel, 2006) and associated bound sediments (Alestra et al., 2014; Schiel, 2006). It is therefore possible that extensive turfs (up to 40 mm thick, Bellgrove et al., 2010) of *Corallina officinalis* at sites at an intermediate distance to ocean outfalls (Bellgrove et al., 2010; Brown et al., 1990) might inhibit re-establishment of *H. banksii*, even if water quality was conducive to early development and growth. While it has been suggested that recruitment of fucoid algae is enhanced in red algal turfs because reduced wave motion facilitates strong zygote attachment and/or the turf structure traps dislodged embryos (Brawley and Johnson, 1991), it is also possible that the reduction in nutrient delivery and shading effects (Hay, 1981) inhibit photosynthesis in developing embryos. In addition, (Bellgrove et al., 2010) found coralline turfs inhibited *H. banksii* recruitment in field and laboratory studies. They suggested surface tension holding propagules above the substratum (and thus preventing attachment) as the most likely mechanism through which turfs impaired *H. banksii* recruitment, but also acknowledged the potential roles of sediment accumulation (Airoldi, 2003; Alestra et al., 2014; Schiel et al., 2006) alleopathy (Suzuki et al., 1998) and sloughing of epithallus layers (Littler and Littler, 1999).

A number of studies have demonstrated variable recovery of *H. banksii* in Australia and New Zealand and at different spatial scales, suggesting different mechanistic processes. Cover of *H. banksii* was reduced from ~ 60 % to < 5 % on a Sydney shore by a severe storm in 1974, but had recovered to ~ 60 % cover by 1979 (Underwood, 1999). However, recovery was highly variable even on small scales and was dependent on the amount of damage done to holdfasts and the activities of grazers: recovery was much slower when holdfasts were removed than when they were undamaged; grazing molluscs and seastars slowed the rate of recovery but did not prevent it altogether (Underwood, 1998).

In an experimental test of the effects of trampling on *H. banksii* at two sites separated by 320 km (Kaikoura and Moeraki) in southern New Zealand, despite almost 100 % reduction in cover in some treatments, *H. banksii* recovered to control levels at both sites in all treatments except one at Moeraki (where final cover was ~ 25 % less than controls) within 21 months of the original pulse disturbance (Schiel and Taylor, 1999). However, larger scale (3 × 3 m plots) experimental canopy removals of *H. banksii* at the same sites resulted in very different patterns of recovery between sites (Lilley and Schiel, 2006). Plots had recovered to control levels (almost 100 % cover) at Kaikoura after 2 y, but at Moeraki cover was only ~ 20 % (c.f. ~ 100 % in controls) after 2 y. Furthermore, although *H. banksii* had recovered to form almost a closed canopy similar in cover to control plots at both sites 8 y after initial canopy removals, density and biomass of *H. banksii* fronds was significantly greater in 0.25 m^2 quadrats at Kaikoura than Moeraki, and control plots always had higher frond densities and biomass than pulse and press plots (Schiel and Lilley, 2011). It is worth noting that where community data were recorded for the New Zealand example, the communities in removal plots

were still very different from those in controls (as in Hawkins and Harkin, 1985; Lilley and Schiel, 2006; Schiel and Lilley, 2011) even when canopy recovery was complete. This suggests that the residence time (Bruno and Bertness, 2001; Jones et al., 1994, 1997; Konar, 2000) might be particularly important for benthic communities that rely on recruitment (and associated variability) of component species.

In Victoria, Australia, canopy recovery in response to different levels of trampling was also variable, where high trampling plots only returned to 50 % of the initial cover after 420 days (Povey and Keough, 1991). Sites subject to heavy trampling may never recover fully because of annual pulses of trampling pressure (Povey and Keough, 1991). When these shores were examined over longer temporal scales, large site-to-site differences in recovery were seen for trampling experiments at sites separated by only 1 km (Keough and Quinn, 1998). Two sites on the same large rock platform showed a series of pulse responses to repeated pulse disturbances, but a third site 1 km away showed a press response to repeated pulse disturbances over a 5 y period.   At the end of the 5 y experiment the two adjacent sites had comparable canopy cover in all treatments, but the third site cover was < 10 % cover in high trampling treatments and 60 – 70 % in intermediate trampling treatments (c.f. > 90 % in controls) (Keough and Quinn, 1998). We do not currently fully understand the causes for these large differences in recovery between sites (Keough and Quinn, 1998; Lilley and Schiel, 2006), although there is evidence that differences (of 0.4 m) in height on the shore can affect recovery rates (Schiel, 2006). However, it is clear that monitoring programs focusing on *H. banksii* (and potentially other fucoid algae), including those designed to monitor restoration success, must account for the potential variability between sites in recovery of this species, by using well-designed monitoring programs with multiple control/impact sites

and replication at meaningful temporal and spatial scales (Chapman et al., 1995;

Keough and Quinn, 1998).

Discrepancies in knowledge from experimental field ecology and application by restoration ecologists

Despite the important role that habitat-forming species play in structuring communities

and ecosystems, ecological research has focused more on negative interactions (*e.g.*

competition and predation) than positive interactions between species (Bertness and

Leonard, 1997; Bertness et al., 1999; Bruno and Bertness, 2001; Jones et al., 1994).

This is also true for intertidal rocky shores that have been the focus of a plethora of

experimental studies and development of current ecological theory. Bruno and Bertness

(2001) surveyed publications in the prominent marine ecological journal, *Marine*

Ecology Progress Series, from 1994 – 1996 and found a 5:1 ratio of papers examining

predation compared to ecosystem engineers (facilitators) (Table 1). They made a plea

for more research to help us understand the strength and importance of interactions

between ecosystem engineers and associated species. However, 20 years on and the

focus on the roles of ecosystem engineers has declined. A survey of the papers in

Marine Ecology Progress Series from 2003 – 2005 showed only 1.5% of papers

focussing on the roles of ecosystem engineers and then ten years later from 2013 – 2015,

the percentage of papers dropped to 0.5%. The predation: ecosystem ratio in the later

years has changed to an approximately 11:1 (Table 1). The picture is not much different

if we look at broader ecological journals, such as *Ecology, Oikos* and *Oecologia,* where

the percentages of papers focusing on ecosystem engineering from 2003 – 2005 are

4.1 %, 2.5 % and 2.5 %, respectively. However, a decade later (2013 – 2015) the

percentages have slightly increased (5.5 %, 5.9 % and 4.7 %, respectively). In contrast, 22 % of papers published in *Restoration Ecology* from 2003 – 2005 focused on restoring ecosystem engineers to facilitate restoration of associated assemblages, but overtime this trend has dramatically decreased to 1.8 % from 2013 – 2015, with a shift in emphasis to studies focusing on sampling techniques for restoration (Table 2). Additionally, Byers *et al.* (2006) proposed that incorporating ecosystem engineers into restoration efforts may result in cheaper, easier, faster and more sustainable restoration. This suggests that managers and restoration ecologists have to make decisions about best practice for biogenic habitat restoration, without necessarily a sound understanding of the interactions between species and the conditions in which these interactions may be strongest.

It is also important to note that restoration of ecosystem engineers, regardless of how much is known of the positive and negative interactions between species, is unlikely to be successful unless the physico-chemical environment is conducive to sustaining the restored populations (Nienhuis et al., 2002). Less than 10 % of studies published in *Restoration Ecology* since 2003 have focussed on restoring the physico-chemical environment, but this exceeds those focusing on the restoration of biotic habitats in recent years (Table 2).

Restoration and future directions

For sound management of our coastal ecosystems we must understand the role of individual species and their interactions within communities (Marzinelli et al., 2014; Schiel, 2006; Wahl et al., 2015). Management decisions to focus on the re-establishment of important ecosystem engineers such as canopy-forming fucoid algae,

should result in effective restoration of rocky intertidal ecosystems (Benedetti-Cecchi et al., 2001; Bruno and Bertness, 2001; Byers et al., 2006; Crain and Bertness, 2006; Jones et al., 1994, 1997; Nienhuis et al., 2002; Wahl et al., 2015; Wright and Jones, 2006). In temperate Australasia, *H. banksii* has many characteristics that suggest it is an important ecosystem engineer: it forms extensive, long-lived and stable canopies; it integrates and may modulate many abiotic resources (slows flow, decreases heat and desiccation, decreases UV radiation, provides microhabitats) in the physically and physiologically stressful environment of the rocky intertidal zone; has direct and indirect, positive and negative interactions with a wide range of species and undoubtedly increases biodiversity on seascape scales (Jones et al., 1994, 1997). However, for a full understanding of the ecosystem function of *H. banksii* and other fucoid algae, it will be important to conduct carefully planned manipulative experiments to assess the types and strength of interactions with associated species (Díez et al., 2013; Jones et al., 1997; Menge et al., 1994), the influence of the quality of canopy cover and the environmental conditions under which these interactions vary (Bertness et al., 1999; Bruno and Bertness, 2001; Crain and Bertness, 2006; Jones et al., 1997; Wright and Jones, 2006).

Additionally, to facilitate effective restoration of canopy-forming fucoid algae and their associated communities affected by anthropogenic disturbances such as sewage effluent discharge, we must first have a thorough understanding of the factors that lead to the initial demise of these populations at polluted sites (as suggested in Wahl et al., 2015), including effects on early life-history stages as well as established plants (e.g. Sales et al., 2011). Only then can we set realistic water quality targets for restoration efforts.

Finally, for restoration of both fucoid engineers and associated species we must understand the connectivity and the patterns of gene flow between populations (Coleman et al., 2011; McKenzie and Bellgrove, 2006, 2008, 2009; Schiel, 2004), and the variability in, and factors that may limit, the associated processes. This will allow us to make informed predictions about the probability of natural re-establishment and the conditions under which it might be maximised. Finally, in order to assess the success of intertidal restoration projects, we need to carefully design monitoring programmes that are replicated over appropriate spatial and temporal scales to detect positive or negative effects of restoration over and above the high degree of variability that naturally exists in these systems (Chapman et al., 1995; Keough and Quinn, 1998; Schiel, 2006).

Acknowledgements

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Table 1. Number of papers and percentage of total in each study type published in *Marine Ecology Progress Series* from 1994 – 1996, 2003 – 2005 and 2013 – 2015. Data for 1994 -1996 are from Bruno and Bertness (2001).

nr, not recorded.

Study Type	1994 – 1996		2003 – 2005		2013 – 2015	
	Number	%	Number	%	Number	%
Population Ecology	nr	nr	412	18.0	226	15.1
Predation/Herbivory/Parasitism/ Scavenger	133	10.6	139	6.1	79	5.3
Physiology/Behaviour	144	11.5	284	12.4	205	13.7
Diet/Feeding Ecology	nr	nr	122	5.3	114	7.6
Consumers/Food Webs	nr	nr	37	1.6	101	6.7
Supply side ecology	76	6.1	114	5.0	87	5.8
Morphology, Biomechanics, Structure, Composition	14	1.1	62	2.7	110	7.3
Biogeochemistry	nr	nr	296	12.9	92	6.1
Management, Conservation, Monitoring, Marine Reserves	35	2.8	80	3.5	80	5.3
Migration/Movement Patterns	nr	nr	151	6.6	70	4.7
Disturbance	53	4.2	87	3.8	49	3.3
Ecosystem Engineers (Facilitation)	**27**	**2.2**	**36**	**1.5**	**7**	**0.5**
Natural/Life History	231	18.5	146	6.4	60	4

Genetics, phylogeny	32	2.6	92	4.0	56	3.7
Global Warming/Climate Change	nr	nr	9	0.4	46	3.1
Introduced/Invasive spp.	nr	nr	33	1.4	27	1.8
Pollution, Bioassay	45	3.6	40	1.7	13	0.9
Mortality Patterns/Diseases/Virus	nr	nr	37	1.6	23	1.5
Sediment Transport/Erosion/Sedimentation	nr	nr	16	0.7	16	1.1
Metal concentration/trace metals/metal uptake	nr	nr	25	1.1	3	0.2
Intracellular Symbiosis	6	0.5	7	0.3	7	0.5
Competition	15	1.2	32	1.4	12	0.8
Impact of antifouling	nr	nr	6	0.3	nr	nr
Other	441	35.2	31	1.3	14	0.9
Total	1252	100	2294	100	1497	100

Table 2. Number of papers and percentage of total in each study type published in *Restoration Ecology* from 2003 – 2005 and 2013 – 2015.

Study Type	2003 – 2005		2013 – 2015	
	Number	%	Number	%
Restoration of ecosystem engineers/facilitators	**69**	**21.6**	**6**	**1.8**
Disturbance (Natural/Human) +ve and -ve effects on restoration.	50	15.7	52	15.4
Population Ecology	40	12.5	35	10.4
Ecological theory to restoration ecology/Management/Monitoring/	35	11.0	22	6.5
Society & Environment/ Development/Conservation			35	10.4
Restoration of the physio-chemical environment	31	9.7	24	7.1
Introduced/Invasive/Exotic Species	25	7.8	16	4.7
Predators/Grazers/Competition/ Dispersal/Recruitment	23	7.2	29	8.6
Plant Life Histories/Germination	11	3.5	25	7.4
Addition of single charismatic or rare species (including Endangered/Threatened species)	10	3.1	8	2.4
Restoration Success (Theory)	9	2.8	11	3.3
Sampling techniques for restoration treatments/methods for monitoring restoration success	7	2.2	54	16.0
Genetics of restoration/Gene flow	3	1.0	4	1.2

Food Web Management	3	1.0	6	1.8
Land Uses	2	0.6	5	1.5
Other	1	0.3	5	1.5
Total	319	100	337	100

Figure captions

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 direct positive (solid) and

negative (dashed) interactions with other organisms and ecological processes are

indicated by black arrows. Indirect interactions are implied by the series of arrows.

Fig. 2.   Schematic diagram expressing the current understanding of the effects of

treated sewage effluent disposed into the marine environment on rocky intertidal

communities (see text for further explanation and citations). Solid arrows indicate direct

positive interactions, dashed arrows indicate direct negative interactions and perforated

dashed arrows indicate indirect negative interactions. Cross indicates no interaction;

question mark indicates that the possibility of an interaction has not yet been thoroughly
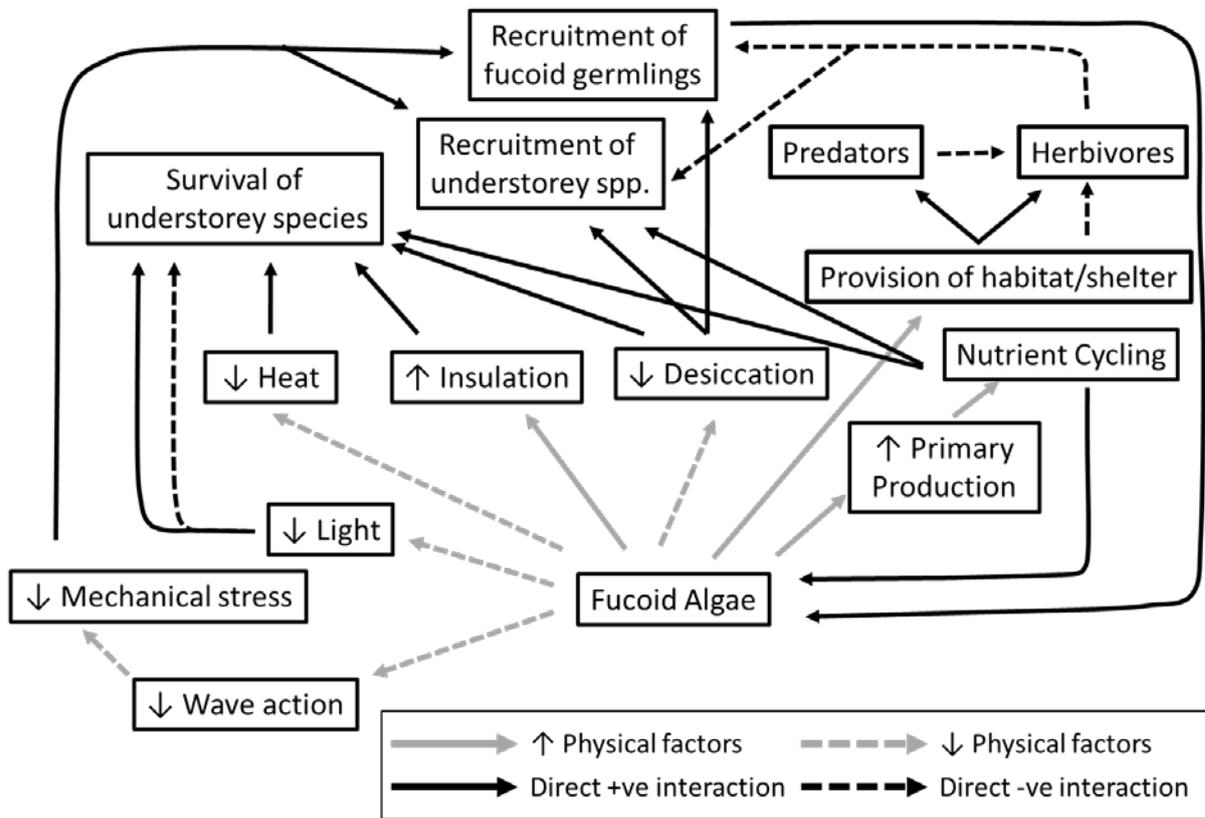
explored and is thus unknown.

Fig. 1.

Fig. 2