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Ecological restoration using intertidal foundation species: Considerations and potential for rockweed restoration

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Abstract

Foundation species, such as trees, corals, grasses, oysters, and rockweeds, must be common and abundant to effectively modify the physical environment and increase biodiversity by buffering environmental stress. Yet many of these important species have been declining due to disease, climate change, and other factors. A prime example is the precipitous population decline of marine rockweeds, which is attributed to increased urbanization and its accompanying impacts. Rockweeds provide three-dimensional habitat in harsh rocky intertidal environments and regulate ecosystem functioning, essential roles that no substitute species are capable of filling. Recovery of impacted rockweed populations is typically slow and unpredictable due to their limited dispersal capacity. These issues have motivated efforts to conserve remaining populations of rockweeds and reestablish or enhance depleted ones. Successfully doing so requires a robust understanding of factors that affect survival of the species and the processes that influence ecosystem structure, along with rigorous scientific testing of restoration methods and the factors that affect restoration success. In this comprehensive review, we summarize the current knowledge of rockweed ecology, highlight studies that could inform restoration practices, and recommend ways to improve our ability to implement scalable restoration of rockweeds and accompanying ecosystem-wide benefits.

KEYWORDS

climate change, foundation species, fucoids, population decline, reestablish, rocky intertidal ecosystems

INTRODUCTION

Ecosystems are often characterized by conspicuous organisms referred to as foundation species (sensu Dayton, 1972) that support biodiversity, enhance ecosystem function and stability, and are often culturally valuable. In terrestrial ecosystems, foundation species range in scale from large canopy-forming trees to diminutive grasses. Similarly, marine habitats support a wide spectrum of species that structure communities, including kelps, mangroves, corals, seagrasses, mussels, and oysters. Fundamentally, the influence foundation species have on ecosystems is commensurate with their overall abundance; declines in abundance of foundation species can have cascading detrimental effects at population and community levels (Ellison et al., 2005, 2019). For example, the precipitous decline of shade-tolerant eastern hemlock trees in North America resulted in significant reductions in aquatic invertebrates as well as declines in sediment retention and productivity in streams (Degrassi et al., 2015; Ellison et al., 2005).

Rocky intertidal foundation species, such as mussels, barnacles, and seaweeds, are common in temperate regions and provide three-dimensional habitat required by other species to survive. Rockweeds, a group of conspicuous brown seaweeds (Phaeophyceae) in the order Fucales (Fucoids), are often the dominant macroalgae in temperate intertidal and shallow subtidal rocky habitats (Figure 1). Ecologically, the importance of these seaweeds in regulating ecosystem functioning and facilitating high biodiversity is well recognized, and rockweeds are increasingly being used as indicator species to assess the status of rocky intertidal ecosystems for management purposes (e.g., Maki, 1991; Murray et al., 2016; Orlando-Bonaca et al., 2008). Economically, rockweeds are valuable as commercially harvested species (Lotze et al., 2019), and they provide important ecological services supporting commercially harvested taxa, including refuge for lobsters (Schmidt et al., 2011) and nursery habitat for fish (Gullo, 2002; Vercaemer et al., 2018).

Rockweed populations, like many other species considered foundational to ecosystems, have sustained extensive degeneration and range contractions worldwide (e.g., Nicastro et al., 2013; Wernberg et al., 2011). For example, the southern range edge for the rockweed *Fucus vesiculosus* has shifted northward 1250 km from Morocco to Portugal (Nicastro et al., 2013), and the species has declined in distribution by more than 95% in the Baltic Sea (Torn et al., 2006). Globally, the causes of population declines are not well known, can result from complex interactions of multiple sources of stressors, and vary greatly among geographic locations and species. Rockweeds are known to be sensitive to both natural and anthropogenic perturbations, including severe storms (Underwood, 1998), ice scour (McCook & Chapman, 1991, 1997), pollution (Bellgrove et al., 1997), trampling (Bertocci et al., 2011), and climate change (Álvarez-Losada et al., 2020).

The decline of rockweed populations, as well as the positive effects that rockweeds have on the biological communities they inhabit, have motivated efforts to conserve remaining populations and to reestablish or enhance depleted ones (e.g., Coleman & Wernberg, 2017; Stekoll & Deysher, 1996; Whitaker, 2009; Whitaker et al., 2010). However, successful reestablishment of depleted populations requires understanding the factors that affect survival of the species along with rigorous scientific testing of outplanting methods. An understanding of community structure, including biotic interactions, is also helpful to ensure restoration is effective (Underwood, 1996). Here, we will (1) explain why rockweeds are prime subjects for restoration, (2) summarize published evidence of changes in rockweed populations, (3) identify and discuss the factors limiting population recovery, and (4) review past restoration activities and provide recommendations for future ecological restoration efforts.

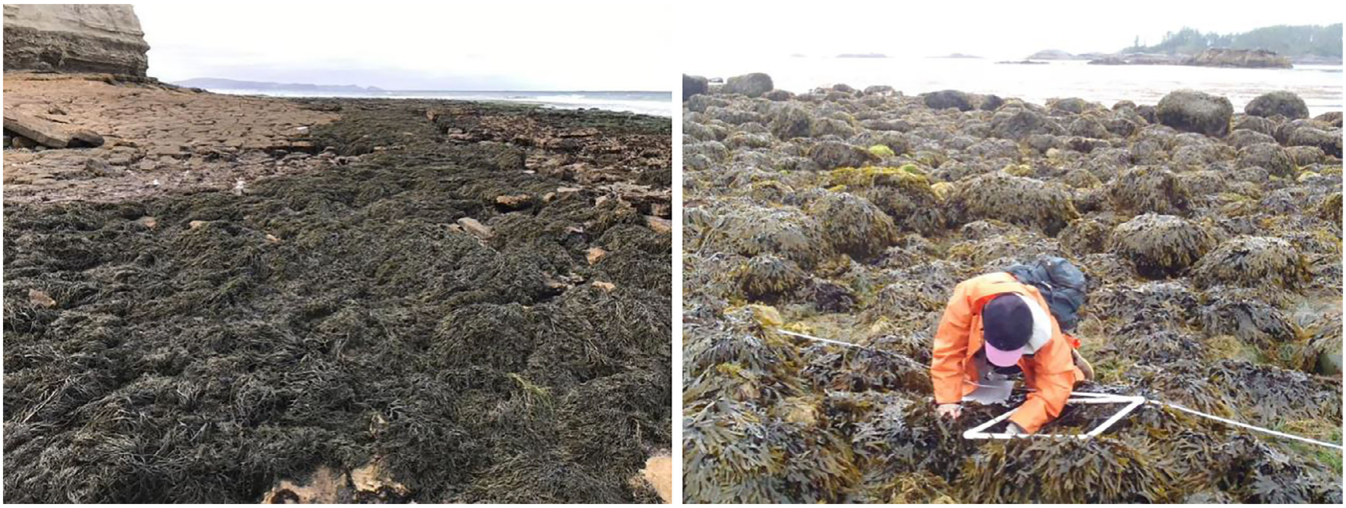

FIGURE 1 Rockweeds are often the dominant seaweed in temperate rocky intertidal ecosystems. (Left) The rockweed *Silvetia compressa* in the upper intertidal zone on the Channel Islands, California (photo credit: S. Whitaker 2021). (Right) *Fucus distichus* covers most of the mid and upper intertidal gradient on Calvert Island in British Columbia, Canada (photo credit: L. Anderson 2012).

ROCKWEEDS AS FOUNDATION SPECIES

Rockweeds play a strong role in the structuring of communities via provision of habitat and modifications to the environment (Bellgrove et al., 2017). The three-dimensional rockweed canopy provides a complex matrix of microhabitats, increasing niche availability for a high diversity of taxa (e.g., Bertness et al., 1999; Fredriksen et al., 2005; Hily & Jean, 1997; Johnson & Scheibling, 1987; Schiel & Lilley, 2011). Different sets of species can be found living in the understory of the rockweed canopy, as epiphytes attached to the rockweeds, along the edge of canopy limits, and as mobile organisms freely moving through a rockweed bed (Figure 2). Rockweed canopies modify both abiotic and biotic conditions, either directly by providing shelter or reducing environmental stress or indirectly by altering biotic interactions (e.g., Bertness et al., 1999; Beermann et al., 2013; Scrosati, 2016; Scrosati & Ellrich, 2018; Watt & Scrosati, 2013a, 2013b). Alterations to the environment can have both positive and negative effects on associated species, but, generally, rockweed facilitates the presence of long-lived taxa over opportunistic species, thereby increasing community stability, resiliency, and diversity (e.g., Eriksson, 2007; Jenkins et al., 1999; Lilley & Schiel, 2006).

Modifications to the physical environment by rockweed canopies include a reduction in the rate of evaporation and temperature change during emersion periods (Scrosati, 2016; Scrosati et al., 2021; Scrosati & Ellrich, 2018; Watt & Scrosati, 2013a, 2013b), light attenuation, and slowing of water flow. For instance, during warm periods at low tide, air temperature can be 5–16°C lower under the rockweed canopy compared to exposed rock surfaces (Beermann et al., 2013; Bertness et al., 1999; Brawley & Johnson, 1991). Similarly, evaporation rates underneath the canopy during low tides can be significantly lower than rates on the open rock (Brawley & Johnson, 1991, 1993; Bertness et al., 1999; Beermann et al., 2013). For example, in the high intertidal zone, Bertness et al. (1999) found that water loss during emersion was nearly 60% outside the canopy, while only ~5% underneath the canopy. The refuge from thermal stress and desiccation provided by rockweeds is particularly important since these are important factors affecting the ability of organisms to survive in harsh intertidal ecosystems.

Because of the canopy structure and modifications to the environment that rockweed beds provide, they harbor a biologically diverse community of epifaunal and understory species (Bertness et al., 1999; Colman, 1940; Eriksson et al., 2006; Fredriksen et al., 2005; Gunnill, 1985; Hawkins & Hartnoll, 1983; Hily & Jean, 1997; Jenkins et al., 2004; Johnson & Scheibling, 1987; Lilley & Schiel, 2006; Lubchenco, 1983; Sapper & Murray, 2003; Schiel & Lilley, 2011; Thompson et al., 1996). In England, for example, Colman (1940) identified 177 invertebrate species under the canopies provided by three species of *Fucus*.

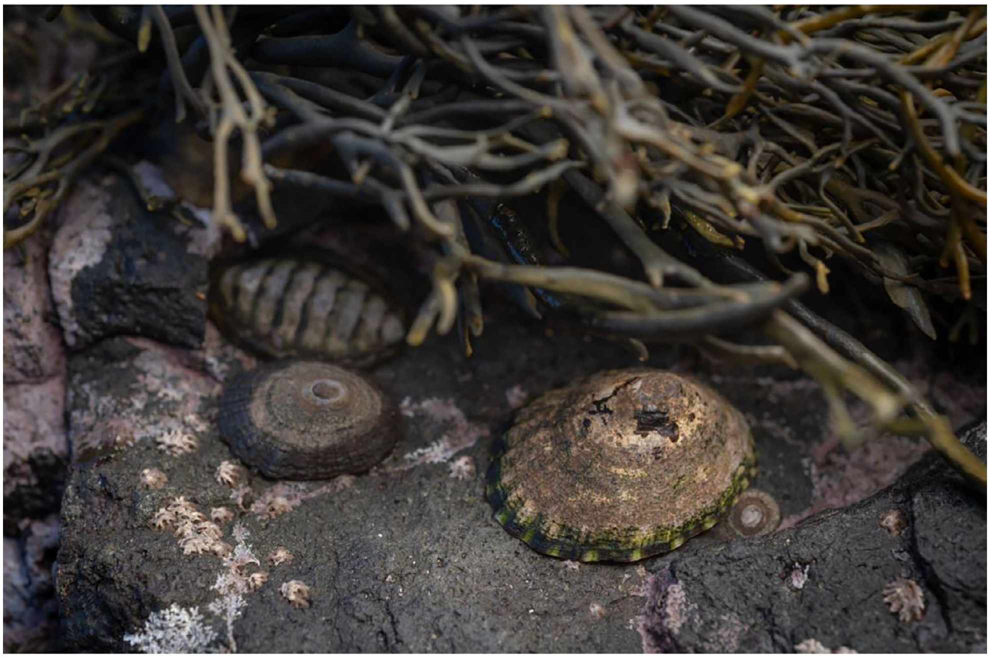

FIGURE 2 The canopy provided by rockweed supports a diverse assemblage of rocky intertidal taxa in the California Channel Islands (photo credit: M. Ready 2022).

Silvetia beds in southern California, USA, had 47 species of algae, 20 sessile invertebrate species, and 44 mobile invertebrate species for a total of 107 taxa living under the frond canopy (Sapper & Murray, 2003). In comparison, communities associated with another well-documented ecosystem engineer, the mussel *Mytilus californianus* on the eastern north Pacific coast, harbor a similar level of diversity with a range of 80–120 species found within a mussel bed within a site (Kanter, 1977, 1978, 1979; Straughan & Kanter, 1977). Rockweeds can also be important for many other taxa, including macroinvertebrates and fish that use the habitat for shorter periods of time, and birds that feed on the invertebrates found within the canopy (Hamilton, 2001; Hamilton & Nudds, 2003). For example, crabs, lobsters (Phillippi et al., 2014; Schmidt et al., 2011; Vercaemer et al., 2018), and many fishes, including some of commercial value (Gagnon et al., 2019; Gullo, 2002; Mattsson, 2019; Rangeley & Kramer, 1995; Vercaemer et al., 2018), utilize rockweed beds as feeding areas or nursery habitat.

In addition to providing habitat for the organisms that live in the understory, rockweed canopies often facilitate the recruitment of a diversity of taxa (Bertness et al., 1999; Jenkins et al., 2004), including conspecifics (Bertness & Leonard, 1997; Brawley & Johnson, 1991; Moeller, 2002; Philbrick, 2004; Vadas et al., 1990; van Tamelen et al., 1997). Recruitment, a process vital to population maintenance and long-term persistence, is typically enhanced in the presence of rockweed canopy cover because desiccation and thermal stress are reduced during periods of emersion compared to bare rock surfaces (Beermann et al., 2013; Vadas et al., 2004). During periods of immersion, the frond canopy formed by rockweeds slows water flow, which allows for gametes or larvae to settle (Dayton, 1985).

Rockweeds are also large contributors to intertidal and coastal food webs. Productivity of fucoids is considerably higher than that of many other primary producers, especially in the intertidal zone (Bordeyne et al., 2015; Golléty et al., 2008; Tait et al., 2014; Tait & Schiel, 2010). For example, in France, Bordeyne et al. (2015) found that *Fucus* beds accounted for 77%–97% of carbon dioxide flux, with gross primary productivity being 7–9 times higher than that measured in eelgrass (*Zostera noltii*) communities (Ouisse et al., 2010) and up to 44 times higher than soft bottom habitats (Migné et al., 2004) or sandy beach communities (Hubas et al., 2006). This fucoid production forms the base of many food webs (Bertness & Leonard, 1997; Jenkins et al., 2004; Lubchenco, 1983; Moore, 1977), providing food for numerous grazers, including amphipods (Moore, 1977), isopods, decapods, littorine snails (Bertness & Leonard, 1997; Lubchenco, 1983), turban snails (Steinberg, 1985), and limpets (Hawkins et al., 2008; Jenkins et al., 2004). Feeding studies confirm that grazers consume rockweeds, including *Fucus* and *Silvetia* (Kubanek et al., 2004; Steinberg, 1985). Steinberg (1985) observed that gastropods, including turban snails and periwinkle snails that commonly seek refuge in rockweed canopies, consistently preferred feeding on brown algae, including *Silvetia*, over red algal species.

Given their high productivity rates and relatively high biomass turnover, 40%–70% annually (Schmidt et al., 2011; Vadas et al., 2004), rockweeds are also major contributors to detrital pools (Bishop et al., 2010; Golléty et al., 2010; Renaud et al., 2015), providing carbon for detrital consumers. Rockweed detrital contributions are not only important within the rockweed habitat, but cross-boundary transport can export production into nearby habitats as well. For example, up to 82% of macrophyte (primarily rockweed) production was exported outside of the intertidal zone in a Canadian Bay (Vadas et al., 2004).

ROCKWEED DECLINES

Fucoids are declining locally and regionally on temperate rocky shores in the northern hemisphere (Davies et al., 2007; Strain et al., 2014; Wahl et al., 2015). There is also evidence of range contractions (Duarte et al., 2013; Nicastro et al., 2013) and localized extinctions (Duarte et al., 2013; Fales & Smith, 2022; Fernández, 2016; Lamela-Silvarrey et al., 2012; Martínez et al., 2012; Viejo et al., 2011) of rockweeds in multiple regions. Large declines in subtidal fucoids, such as *Sargassaceae*, have also been documented (reviewed by Falace et al., 2010).

In a thorough literature search on changes in populations of true rockweeds in the family Fucaceae, we found many examples of local extinctions, range shifts, and population declines (Table 1). We did multiple searches across several databases, including Web of Science, ProQuest, and Google Scholar, to find literature pertaining to long-term population declines in the family Fucaceae. Search terms included "rockweed, fucoid, *Ascophyllum, Fucus, Pelvetia, Pelvetiopsis, Silvetia*" and "change, declines, and population decline," among other key terms. Though we also performed targeted searches for studies reporting stability or increases in fucoid populations, fewer examples were found, which in part may be due to publication bias (Appendix S1: Table S1). Studies that fit the inclusion criteria are included in Table 1, categorized by species, region, and the hypothesized driver of change, if described. Most of the studies did not experimentally or quantitatively evaluate the cause of declines or local extinctions but rather qualitatively discussed the likely drivers or causes of change. Nevertheless, these insights may help focus future analyses and experiments.

TABLE 1 Studies observing population changes of multiple species of rockweed from the family Fucaceae from four regions and the discussed causes of change.

		Discussed causes of change						
Species	**Type of change**	**I**	**II**	**III**	**IV**	**V**	**VI**	**Studies**
Northeast Pacific								
Silvetia compressa	Decline		X	X				Barry et al. (1995), Gerrard (2005), Goodson (2003), Graham et al. (2018), Sagarin et al. (1999), Whitaker et al. (unpublished manuscript), and Widdowson (1971)
Pelvetiopsis californica	Decline; Local extinctions		X				X	Fales and Smith (2022) and Thom and Widdowson (1978)
Fucus distichus	Decline		X	X				Barry et al. (1995), Driskell et al. (2001), and Weitzman et al. (2021)
Northeast Atlantic								
Ascophyllum nodosum	Decline	X	X					Davies et al. (2007)
Fucus guiryi	Decline; Local extinctions; Range change		X					Riera et al. (2015)
Fucus serratus	Decline; Range change	X	X					Álvarez-Losada et al. (2020), Duarte et al. (2013), Fernández (2016), Reichert and Buchholz (2006), and Fernández and Anadón (2008)
Fucus spiralis	Decline; Local extinctions	X	X					Lamela-Silvarrey et al. (2012)
Fucus vesiculosus	Decline	X	X					Fernández (2016), Lamela-Silvarrey et al. (2012), and Piñeiro-Corbeira et al. (2016)
Pelvetia canaliculata	Decline; Local extinctions	X	X					Lamela-Silvarrey et al. (2012)
Baltic Sea								
Fucus vesiculosus	Decline			X				Kukk and Martin (1992) and Mäkinen et al. (1984)
Mediterranean								
Fucus virsoides	Decline	X		X	X	X		Battelli (2016), Munda (1982), Munda (1993), and Rindi et al. (2020)

Note: The discussed causes of change are indicated by roman numerals: I, herbivory; II, climate change; III, water quality, pollution, oil spill, sedimentation; IV, habitat loss; V, introduced species; VI, other impacts.

The causes of declines in rockweed populations varied across regions and time (Table 1). Eutrophication or decreased water quality in the Baltic Sea played a role in many subtidal rockweed declines documented in the 1980s, while climate change or extreme climate events and stressors from multiple sources were more frequently associated with declines in the 1990s and onward, particularly in the northeast Pacific and Atlantic. Most of the discussed causes of rockweed declines were anthropogenic in origin, including climate change, water quality, habitat loss, and introduced species, with the exception of increased herbivory documented in the Mediterranean, northeast Atlantic, and the Baltic Sea (Table 1). Unfortunately, very few studies have evaluated the mechanisms driving these declines, so further work is needed to disentangle the complex causes of global declines.

FACTORS AFFECTING POPULATIONS AND LIMITING RECOVERY

Fucoid functioning and fitness are influenced by numerous natural and anthropogenic stressors (e.g., Schiel & Foster, 2006; Wahl et al., 2015 and references therein).

Natural abiotic stressors include low (Pearson & Davison, 1993, 1994) and high (Bell, 1993; Kübler & Davison, 1993) air temperature, decreased humidity (Brawley & Johnson, 1991), variations in nutrient supply (Korpinen et al., 2010), irradiance (Martínez et al., 2012; Schonbeck & Norton, 1980) and osmotic shock, and extremes in sea temperature, wave energy, and nutrients (Pielou, 1981; Vadas et al., 1990). Human-caused stressors include urbanization (Coleman & Wernberg, 2017), eutrophication (Bellgrove et al., 1997), trampling (Araújo et al., 2009; Bertocci et al., 2011; Denis, 2003; Irvine, 2005; Keough & Quinn, 1998; Schiel & Taylor, 1999), coastal sedimentation (Schiel et al., 2006), petroleum spills (Crowe et al., 2000), harvesting (Boaden & Dring, 1980), invasive species (Sutherland et al., 2014), and climate change (Keser et al., 2005; Sagarin et al., 1999). Individually, each of these abiotic drivers imposes serious impacts on fucoids. Collectively, the effects are likely to be synergistically detrimental (Hurd et al., 2014).

Rockweeds lack the ability to reliably disperse over long distances, which affects the ability of their populations to recover following declines. Dispersal of rockweeds is mostly limited to the movement of early life stages, including propagules and zygotes (Schiel & Foster, 2006), and is generally low, since the propagules are relatively large, released near the substratum (Dudgeon et al., 2001; Hays, 2006; Johnson & Brawley, 1998), and adhere to the substratum with a polyphenolic adhesive shortly after fertilization (Vreeland et al., 1993). For some species, the distance spores are capable of traveling is further reduced by the thick mucilage that surrounds them and slows their movement (Pearson & Brawley, 1996). Their propensity to time gamete release to periods of calm environmental conditions, such as low tide or low water motion, putatively sensed via carbon acquisition (Pearson et al., 1998), also limits dispersal in fucoids (Pearson & Brawley, 1996). Dispersal distance can vary among different rockweed taxa but is generally less than 30 m (Chapman, 1995) and more often less than 10 m (Serrão et al., 1996; Williams & Di Fiori, 1996). For example, propagules of the rockweed *Ascophyllum nodosum* can disperse up to 6 m from the parent source (Dudgeon et al., 2001), while *Silvetia compressa* recruits typically within <3 m, but mostly less than 1 m from the parent (Williams & Di Fiori, 1996). Longer distance dispersal is possible through drifting of detached reproductive fronds and is common for species in the family Sargassaceae (Fucales) that are neutrally or positively buoyant due to floating pneumatocysts (Chapman, 1995; Deysher & Norton, 1981; Hawes et al., 2017; Norton & Mathieson, 1983; Schiel, 1985). The importance of drifting as a dispersal method for other taxa, including rockweeds, has been hypothesized, but strong evidence is lacking (McKenzie & Bellgrove, 2009).

Rockweed recovery can also be inhibited or slowed due to temporal and spatial limitations in settlement and recruitment. Rockweeds typically are reproductive during relatively short periods during specific seasons, and, although they tend to be highly reproductive with very high fertilization rates (>95%; Brawley, 1992; Pearson & Brawley, 1996), early postsettlement (EPS) life stages have extremely high mortality rates (e.g., Brawley & Johnson, 1991; Chapman & Johnson, 1990; Gunnill, 1980; Johnson & Brawley, 1998; McLachlan, 1974; Moeller, 2002; Vadas et al., 1992). For example, Moeller (2002) found that EPS mortality during peak egg production was more than 99.99%. Lamote and Johnson (2008) found the density of recruits from three rockweed species to be exponentially higher under the canopy during all three years of their study, while Moeller (2002) found peak egg production for *Silvetia* to be markedly higher underneath the canopy than areas outside the rockweed bed. EPS mortality due to desiccation is particularly high when the rockweed canopy is limited in extent or absent (Johnson & Brawley, 1998; Lamote & Johson, 2008; Moeller, 2002). At the same time, EPS survival is reduced under the rockweed canopy due to mechanical dislodgement caused by the sweeping motion of fronds (Johnson & Brawley, 1998). For example, Johnson and Brawley (1998) observed settlement of EPS *Silvetia* recruits to be 1–2 orders of magnitude greater under the adult canopy, yet juveniles were most abundant outside of the canopy.

As a result of short-distance dispersal and temporal and spatial constraints on successful recruitment, recovery of fucoids is highly variable following disturbances (Bellgrove et al., 2017; Jenkins et al., 1999, 2004; Underwood, 1998, 1999). Recovery time can also be affected by numerous other factors, including the intensity and frequency of perturbations, the size of the area disturbed or proportion of the population removed, and the timing and frequency of disturbance (Bertocci et al., 2005; Farrell, 1989; Foster et al., 2003; Kim & DeWreede, 1996; Paine & Levin, 1981; Sousa, 1979, 1984). Frequent disturbances can inhibit fucoid recovery because a large population with a contiguous canopy can never form as individuals are being repetitively removed over time. The timing of the disturbance can also be important, depending on, for example, whether recovery of a disturbed area occurs during optimal environmental conditions or when fucoids are in peak reproductive periods (Kim et al., 2017; Kim & DeWreede, 1996). In the Gulf of Maine, disturbance timing has been proposed to determine whether a fucoid-dominated system can recover or shift to an alternative stable state dominated by mussels and barnacles (Petraitis & Dudgeon, 1999, but see Bertness et al., 2002). An alternative stable state can also be induced by the severity of the disturbance, such as a stable *Ascophyllum*-dominated community shifting to a stable *Fucus*-dominated community when a large area of *Ascophyllum* has been manually removed (Menge et al., 2017).

Recovery times for fucoids are further complicated by alterations in biotic interactions as a consequence of the disturbance itself or due to indirect, cascading effects from the removal of the canopy-forming rockweed (e.g., Kim, 1997). For example, canopy removal and resulting decreased whiplash can result in an increase in barnacle recruitment and space occupancy, inhibiting subsequent recruitment of fucoids (Kordas & Dudgeon, 2009). In another study, removal of an *A. nodosum* canopy resulted in a cascade of events that inhibited the rockweed from fully recovering more than 12 years after removal (Jenkins et al., 1999, 2004). Without the protection of the *Ascophyllum* frond canopy from desiccation stress, understory turf-forming seaweeds disappeared, which resulted in an increase in limpets that grazed down subsequent rockweed recruits and other seaweeds within which rockweeds settle (Jenkins et al., 1999).

RESTORATION

Restoration ecology is a relatively new discipline, which may be why it is inherently expensive and associated with somewhat high uncertainty of success and feasibility. This is particularly true for marine restoration, which, in comparison to terrestrial systems, is still in its infancy (Bayraktarov et al., 2016; De Groot et al., 2013). Comparably few studies involve marine restoration (Benayas et al., 2009; Blignaut et al., 2013), even though these systems have often been heavily urbanized and degraded (Halpern et al., 2008). For example, in a sample of 224 ecological restoration studies published from 2004 to 2013, marine habitats were the least represented (~15%) relative to terrestrial and freshwater environments (Kollmann et al., 2016). Although restoration can be expensive, the cost of restoration is not necessarily correlated with success. Bayraktarov et al. (2016) found the most successful restoration efforts to be highly contingent upon ecosystem type, site selection, and techniques applied rather than cost. Despite costs and variable levels of success, restoration ecology has strong potential to be a promising tool for repairing degraded ecosystems, particularly as ecological theory evolves and is used more consistently to inform restoration practices (Peterson et al., 2003). Opportunities for practicing restoration will undoubtedly continue through legally mandated responses to impacts on natural resources (e.g., US Congress, 1980, 1990).

To date, a substantial amount of marine restoration studies has focused on a few select taxa, such as seagrasses, corals, oysters, and kelp, all of which are considered to be ecosystem engineers. Notably rare, however, are studies on restoration of other ecologically important canopy-forming macroalgal engineers, such as rockweeds. Certainly, the marked global decline of fucoid algae (Piñeiro-Corbeira et al., 2016; Vogt & Schramm, 1991; Wahl et al., 2015) and their influence on community structure have spurred an increased urgency in developing strategies to halt and reverse their loss. Thus far, fucoid restoration has predominantly focused on nonrockweed, subtidal taxa, such as *Sargassum* and *Cystoseira* (Campbell et al., 2014; La Fuente et al., 2019; Lardi et al., 2022; Perkol-Finkel et al., 2012; Yoon et al., 2014); only a handful of studies have focused on the restoration of intertidal rockweeds in the family Fucaceae (e.g., Gao et al., 2017; Jonsson et al., 2006; Kautsky et al., 2019; Stekoll & Deysher, 1996; Tronske, 2020; Whitaker et al., 2010).

To reverse losses of fucoids, a wide range of human-mediated actions have been applied with variable levels of success, including passive restoration approaches that involve removing the source of the impact. However, the causes of declines are often unclear or multifactorial (Piñeiro-Corbeira et al., 2016). In cases where the causes of fucoid losses are known, there is some support for the efficacy of passive restoration. For example, in the Baltic Sea, where large declines in subtidal rockweeds were caused by eutrophication (Kautsky et al., 1986; Torn et al., 2006; Vogt & Schramm, 1991), substantial recovery has occurred following reductions in nutrient loads (Eriksson et al., 1998; Nilsson et al., 2004). However, in other regions where water quality has improved, recovery of fucoid populations has failed to occur (Coleman et al., 2008; Díez et al., 2009; Soltan et al., 2001), potentially due to low standing stock or other discussed processes limiting rockweed resilience. In harvested rockweed populations, the implementation of sustainable management strategies, including equipment regulations, harvest limits, maximum cutting heights, and longer periods between harvests, has resulted in reduced impacts (Gendron et al., 2018; Ugarte & Sharp, 2001).

In cases where rockweeds have failed to recover naturally, active restoration techniques have been applied, consisting primarily of transplantation of individuals from the wild, cultivating outplants, constructing artificial habitat or substrate, and seeding with fertile branches or propagules (Campbell et al., 2014; Kautsky et al., 2019; La Fuente et al., 2019). Transplantation of whole individuals, or thalli, in particular, has been relatively successful (Figure 3). For example, Gao et al. (2017) attributed the recruitment of ~1000 rockweed individuals to a transplant method they applied involving the attachment of fertile rockweed thalli to polyethylene rope, which, in turn, was affixed to the substratum.

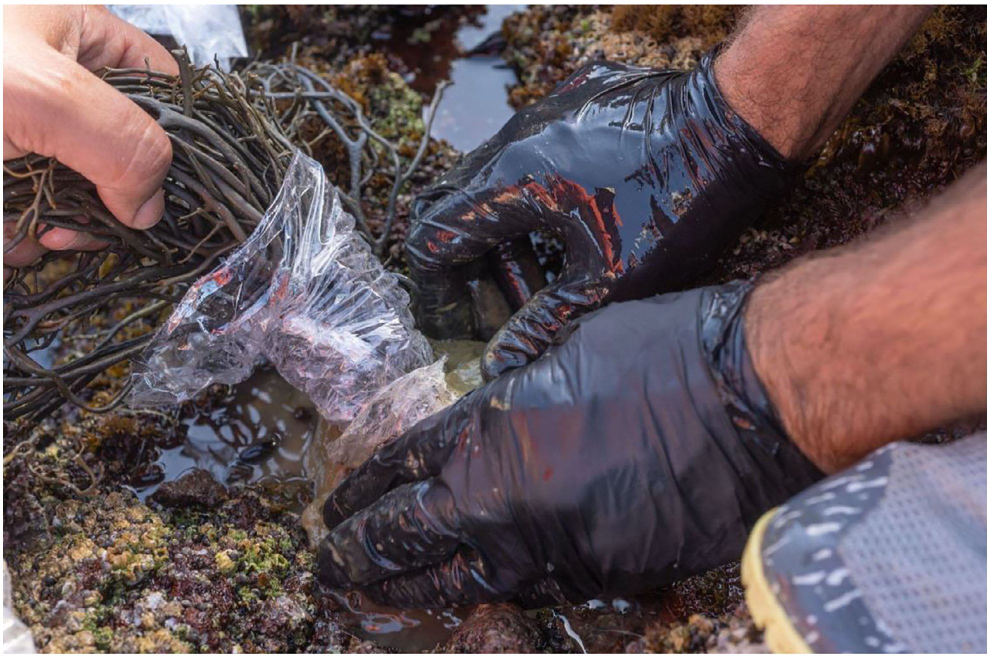

FIGURE 3 Rockweed transplant being attached via marine epoxy (photo credit: M. Ready 2022).

Experimental transplantation of *S. compressa* by chipping off rock pieces with rockweeds attached from donor sites and affixing the rock to the substrate at restoration sites using marine epoxy resulted in survival rates as high as ~60% (Tronske, 2020; Whitaker et al., 2010). Success was particularly high when transplants were placed on sloped surfaces protected from direct sunlight and trampling by visitors. More than a decade later, at a site where rockweed had become locally extinct for well over two decades, despite only <70 rockweed thalli being transplanted (Whitaker et al., 2010), the small population has expanded in 2022 to include well over a thousand individuals (Figure 4). More recent efforts by the authors to outplant *Silvetia* at several locations have shown early success with high survivorship (>75% after ~4 months) and subsequent recruitment of new individuals.

Some rockweed restoration studies have utilized seeding, construction of artificial substrates, or a combination of these techniques to stimulate or enhance recruitment of rockweeds. Whitaker (2009) collected fertile receptacles of *Silvetia* and affixed them to the substrate in mesh containers, while Stekoll and Deysher (1996) attached entire fertile *Fucus gardneri* individuals to erosion control netting and inoculated the plots with a solution of zygotes. More recently, the authors have preliminarily tested attaching fertile branches to the substrate, stimulating gamete release in the field, and outplanting of discs with germlings from laboratory gamete release. Though these studies found that seeding techniques were unsuccessful, similar approaches have been found to be successful for other Fucales that are predominantly subtidal, such as *Cystoseira* (Verdura et al., 2018) and *Sargassum* (Yu et al., 2012). Although Stekoll and Deysher (1996) were unable to enhance recruitment via seeding erosion control netting, they observed that moisture retention facilitated by the netting may have enhanced recruitment of zygotes from the surrounding *Fucus* population. In a factorial field experiment, Whitaker et al. (2010) found that the presence of artificial canopy significantly enhanced survival of *Silvetia* transplants.

The deployment of artificial substrates or structures that mimic the positive effect of a rockweed canopy by reducing desiccation and facilitating natural recruitment warrants further exploration. Studies employing the use of artificial substrate for restoration of fucoids have primarily been conducted on subtidal species, but the techniques utilized may also be applicable to rockweed restoration. These studies have largely focused on cultivating germlings on artificial substrates in vitro, then outplanting the substrate into the wild. For instance, Chai et al. (2014) cultured *Sargassum* germlings in vitro on “breeding boards” that were then mounted on concrete blocks and placed at the restoration site. The germlings survived and, after one year, had grown to an average length of ~15 cm. Growth of *Gongolaria* germlings in laboratory conditions also showed promise for use in restoration efforts (Lardi et al., 2022), though outplanting of germlings has not been tested. A similar technique could potentially be utilized in rockweed restoration by cultivating rockweed germlings in vitro onto artificial substrates

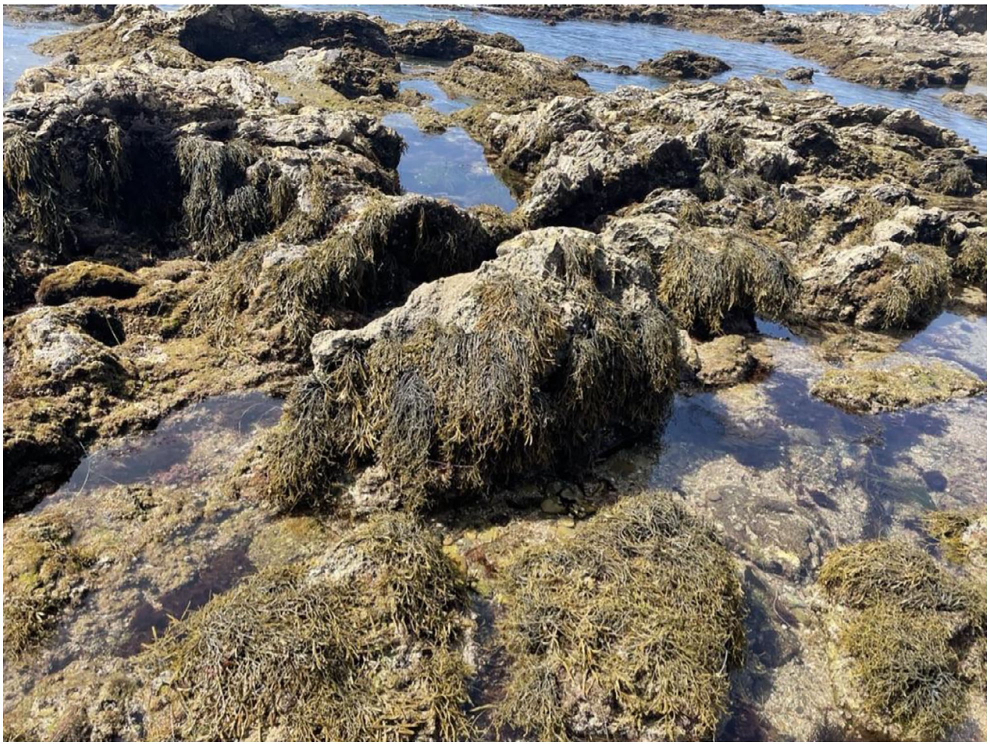

FIGURE 4 *Silvetia compressa* at Little Corona del Mar in Newport Beach, California, 14 years after restoration (photo credit: J. Smith 2021).

such as ceramic tiles or epoxy discs, which may then be affixed to the reef with bolts or marine epoxy. Early efforts by the authors show that *Silvetia* can be stimulated to release gametes with germlings settling on discs in the laboratory, but germlings on outplanted discs have not survived. Several additional studies have utilized in vitro propagation of fucoids onto artificial substrates with varying levels of success (Choi et al., 2003; Falace et al., 2006; Kautsky et al., 2019; La Fuente et al., 2019; Leung et al., 2014; Terawaki et al., 2003; Verdura et al., 2018; Yoon et al., 2014; Yatsuya, 2010, and references therein).

Continued exploration of restoration techniques for rockweeds is needed, particularly with the use of seeding and lab cultivations. Though, as previously discussed, transplanting entire thalli has been one of the more successful techniques implemented in rockweed restoration, it also has a potential impact on the donor population. This is a particularly important consideration for those species that have experienced steep population declines and have limited distribution. Seeding and outplanting techniques limit the amount of material harvested from the donor population, as fertile receptacles (Whitaker, 2009), branches (Verdura et al., 2018), or even drift material (Yatsuya, 2010) can be collected and used to propagate individuals in vitro or be placed at a restoration site to establish a source of propagules that may facilitate natural recruitment.

CONCLUSIONS AND RECOMMENDATIONS

Fucoid declines are predicted to increase in frequency and intensity in the future, with rising temperatures accompanying climate change (Kay et al., 2016; Keser et al., 2005; Rugiu et al., 2018; Takolander et al., 2017; Wilson et al., 2015). Recovery of damaged rockweed populations is slow and unpredictable (Hill, 1980; Vesco & Gillard, 1980) since dispersal is limited and early life stages experience extreme mortality (Moeller, 2002). Recovery is particularly limited when perturbations result in low abundances or local extirpations because of insufficient adult sources for recruitment and reestablishment. Assisted recovery can facilitate a return to stable populations, particularly for those populations with low abundances, whose inhibited recovery may otherwise result in continued declines and eventual extirpation. Because they are foundational species, rockweed recovery can increase the biodiversity of the entire rocky intertidal ecosystem that depends on them. For these reasons, rockweeds are optimal candidates for restoration. Although restoration in rocky intertidal habitats is in its infancy, with very few examples of tested approaches, some methods for successfully restoring rockweeds have been identified through rigorous empirical testing (Gao et al., 2017; Whitaker et al., 2010).

Scaling up rockweed restoration remains a central challenge. Although some work has been done in support of this goal (e.g., seeding and cultivation), these studies were largely unsuccessful (e.g., Stekoll & Deysher, 1996; Whitaker et al., 2010). Cultivation techniques for rockweeds have been developed (e.g., Pearson et al., 1998), but extremely high levels of mortality for early life stages of rockweed species require vast numbers of propagules or cultivation to larger sizes to enable successful restoration. More research and development are needed to effectively cultivate rockweed to stages that are resistant to mortality in large enough numbers to be used in restoration projects.

In the face of climate change, relying on historical reference states as a target for restoration may be ineffective if the changing climate is a major factor contributing to habitat degradation and species decline. Current regulatory frameworks understandably emphasize conserving essential species within their indigenous range, and the concept of assisted migration, also known as managed relocation (Richardson et al., 2009) or assisted colonization (Hällfors et al., 2014), is controversial. For restoration to be successful in a rapidly changing climate, nevertheless, the specific environmental requirements of individual species and the possible impacts of such management actions should be seriously considered (Harris et al., 2006).

Rocky intertidal ecosystems have tremendous value through the provision of significant economic benefits for tourism, fisheries, and real estate, vital ecosystem services, such as shoreline stabilization and protection, and a rich environment for education, research, and recreation. As a result, rocky shores have long had great cultural and historical significance, including for tribal nations. However, rocky intertidal ecosystems are vulnerable to impacts of human activities, such as urbanization (Vogt & Schramm, 1991), overexploitation (Harley & Rogers-Bennett, 2004), pollution (Eriksson et al., 1998, 2002; Kangas et al., 1982; Kautsky et al., 1986; Kukk & Martin, 1992; Mäkinen et al., 1984; Middelboe & Sand-Jensen, 2000; Nilsson et al., 2004; Torn et al., 2006), and climate change (e.g., Barry et al., 1995; Sagarin et al., 1999). Many rocky shore ecosystems, particularly near urban centers, are already degraded, and that trend will continue as coastal development progresses. Thus, effective and quantifiable restoration is needed to maintain habitat health and resilience as well as the valuable services that rocky intertidal ecosystems provide. Restoring key foundation species, such as rockweeds, is an efficient way to achieve broader benefits to ecosystem integrity. It is critically necessary to identify effective methods for restoring rocky intertidal communities at meaningful spatial scales to counter future large- and small-scale impacts on this ecologically important and valuable marine ecosystem. Restoring foundational rockweeds and their associated communities is one of them and will help buffer against the impacts of climate change and other catastrophic events in the future, as well as prevent larger scale losses of intertidal communities.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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