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Temperature and community consequences of the loss of foundation species: Surfgrass (*Phyllospadix* spp., Hooker) in tidepools

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ABSTRACT

By ameliorating environmental conditions, mediating species interactions and regulating resource availability in ecosystems, habitat-forming, foundation species underlie the structure and function of many ecological communities. Current and predicted human-induced changes to ecosystems require a mechanistic understanding of how foundation species enable the persistence of diverse, functioning ecological communities. By manipulating the abundance of a putative foundation species of rocky intertidal tidepool communities, the seagrass *Phyllospadix* spp. (surfgrass), this study assesses how surfgrass affects the thermal environment and structure of tidepool communities over a period of two years. Surfgrass removal pools experienced temperatures up to 10 °C higher than control pools during low tide. Changes in community composition of sessile organism accompanied this change in thermal regime. Over two years, removal pools saw a significant decline in the abundance of coralline crusts and bare space and an increase in the abundance of foliose red algae while control pool communities remained stable. At the level of functional groups, community similarity metrics showed pool communities became more variable in space in response to surfgrass removal, demonstrating that pool communities diverge dramatically in the absence of surfgrass. In removal pools, recovery of surfgrass was limited with less than 25% of pre-removal abundance after two years. However, removal pool communities shifted toward species compositions that favor surfgrass recruitment and suggest a mechanism by which surfgrass recovery may be enhanced over the long-term. Surfgrass clearly play a foundational role in tidepools by reducing pool temperatures and act to stabilize tidepool communities.

1. Introduction

Certain species are disproportionately important in determining the structure and function of ecological communities. While these species are known by a variety of names — e.g. keystone species (Paine, 1969; Power et al., 1996), foundation species (Dayton, 1972, 1975), and ecosystem engineers (Jones et al., 1994, 1997) — and play a variety of roles in communities, their presence is overwhelmingly important in determining composition and abundance of species in a community. In light of the many human-induced stressors impacting global ecosystems such as warming temperatures (Solomon et al., 2007), ocean acidification (Orr et al., 2005), and changes to nutrient cycles (Vitousek et al., 1997), understanding the processes determining the distribution and persistence of these important species is paramount for maintaining diverse ecological communities and their functions.

Foundation species are defined as "..hav[ing] a large effect on community structure by modifying environmental conditions, species interaction, and resource availability through their presence…" (Bruno and Bertness, 2001). In marine systems, classic examples of foundation species include salt marsh grasses (Bertness and Hacker, 1994; Bertness et al., 1999), seagrasses (Peterson et al., 1984; Beck et al., 2001), corals (Luckhurst and Luckhurst, 1978), and forest forming kelp species (Estes and Palmisano, 1974). These species affect the community by providing one or more of the following benefits to communities: generating habitat, providing refuge from predation, reducing physical or physiological stress, enhancing reproductive success or retention of offspring, and increasing food supply (Bruno and Bertness, 2001). However, the importance of a given foundation species for a community depends on the magnitude of the effect of the foundation species, the functional redundancy in that community — i.e. whether several species in a community that can perform the same functional role (e.g. Bertness and Hacker, 1994) or if only one species is capable of performing the functional role (e.g. Witman, 1985) — and the persistence of the foundation species. As such, understanding the role of foundation species in communities demands a mechanistic understanding of not only the effect of foundation species on their environment, but the factors affecting their population dynamics.

This study tests whether the temperate seagrass genus *Phyllospadix* (the surfgrasses) plays a foundational role in the rocky intertidal coasts of the northeastern Pacific by documenting the consequences

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of surfgrass removal for tidepool communities and assessing the rate and trajectory of recovery. Previous investigations have shown that surfgrasses are dominant, slow growing, long-lived marine angiosperms of exposed rocky coasts (Dethier, 1984; Turner, 1985). Living on rock benches as well as pools, they produce a dense canopy that competitively excludes most algae and sessile animals (Dethier, 1984; Turner, 1985; Menge et al., 2005). However, by generating a complex canopy and root structure surfgrass also potentially plays a key role in generating habitat for mobile invertebrates and shade tolerant algae (Stewart and Myers, 1980; Crouch, 1991).

By experimentally manipulating surfgrass abundance in tidepools, this paper assesses surfgrass' role in ameliorating thermal stress and maintaining tidepool communities and addresses the questions: (1) Does surfgrass affect the thermal environment of tidepools? (2) Does the presence of surfgrass impact the structure of tidepool communities? and (3) What are the prospects for surfgrass and surfgrass community recovery following disturbance?

2. Methods

2.1. Species description

The surfgrasses (genus *Phyllospadix*) are long-lived marine angiosperms that inhabit the rocky shores of the North Pacific Ocean. A detailed description of the three eastern Pacific species in this genus can be found in elsewhere (Turner, 1985; Turner and Lucas, 1985; Phillips and Menex, 1988; Williams, 1995; Shelton, 2008). Briefly, surfgrasses are clonal, dioecious plants with creeping rhizomes that attach directly to intertidal rocks. Surfgrasses typically form large, monospecific beds and have long, strap-like leaves (from 0.5 to 2 m long, depending on the species) that create a dense canopy and shade the substrate.

2.2. Tidepool manipulation

To test the effect of the presence of surfgrass on the environmental conditions and community composition of tidepools, surfgrass was removed from tidepools and the response of temperature and tidepool communities was documented. In June 2007, 10 pools at Shi Shi, Washington State, USA (48°17.0′N, 124°41.0′W), were identified for surfgrass removal. Pools were in close proximity to one another, similar in tidal height, and volume (estimated as half an ellipsoid, Table 1). All pools had abundant surfgrass (primarily *Phyllospadix serrulatus*, although some *P. scouleri* was present in some pools) with all pools having greater than 80% of the pool surface consisting of dense surfgrass leaves. Surfgrass rhizomes occupied 0.46 ± 0.03 (mean ± SE) of the rock substrate before manipulation (range: 0.30 to 0.60).

The percent cover of all sessile species in each pool was surveyed on four occasions: immediately prior to surfgrass removal (June 2007) and 2, 11, and 24 months after the surfgrass removal (August 2007, May 2008, and June 2009, respectively). For community surveys, organisms were identified down to the lowest taxonomic level feasible in the field (typically genus or species). The percent cover of each group was estimated visually with the aid of a 1 cm grid. These censuses produced a time-series of community composition in each tide pool. However, because the primary interest was in broad patterns of community composition rather than individual species responses, species were grouped into nine functional groups: erect coralline algae, encrusting coralline algae (crusts), branched red algae, flat red algae, brown algae, green algae, bare space, sedentary animals, and surfgrass. For all comparisons of communities, only the non-surfgrass component of the community was compared. To make the relative proportion directly comparable between control and removal treatments, the analysis used the raw percent cover data for removal pools but rescaled the proportion cover of non-surfgrass groups by dividing by (1-proportion surfgrass). This made the proportion of non-surfgrass groups sum to 1 and make removal and control pool directly comparable. While surveys of mobile invertebrates were conducted each census and a survey of tidepool fishes was completed in June 2009, mobile species were either too rare or too variable in abundance between treatments and among sample dates for informative, statistically valid comparisons. Therefore, analyses were restricted to sessile groups. In addition, surfgrass seedling recruits were surveyed at 11 and 24 months.

Table 1
Descriptors of the ten tidepools used in this study. Pool volume was estimated by assuming the pool was an ellipsoid in shape. See text for methods used in estimating effective shore level.

Pool	Treatment	Pool volume (m^3)	Effective shore level (ESL; meters)
1	Control	0.115	1.25
2	Removal	0.193	1.16
3	Control	0.156	1.52
4	Removal	0.445	1.34
5	Control	0.235	1.40
6	Removal	0.143	1.43
7	Control	0.048	0.61
8	Removal	0.044	0.61
9	Control	0.081	1.10
10	Removal	0.048	1.01

To understand how the presence of surfgrass affected environmental conditions in tidepools, a HOBO® temperature logger (Onset Computer Corporation, Pocasset, MA) was installed into each pool. Loggers were installed in the deepest point of each pool and recorded the water temperature of every 10 min to an accuracy of 0.10 °C. Loggers recorded data for approximately one month in early summer 2007, from June 13 to July 19, and again in summer 2008, from May 9 to June 8. Temperature loggers were installed a week before surfgrass removal in 2007, enabling a comparison of the temperature profiles of pools before and after the surfgrass removal. Both monitored intervals coincided with some of the largest tidal fluctuation of the year with low tides occurring during daylight hours. As a result, the study bracketed a period of the year known to produce some of the highest temperatures for intertidal organism in Washington State. Since the survival of organisms is often better predicted by extremes of physiological stress than by the average conditions (Harley, 2003; Stillman, 2003), documenting potential extremes of environmental conditions is appropriate (Helmuth et al., 2002; Harley et al., 2006).

2.3. Statistical analyses

2.3.1. Temperature

The thermal environment of each pool was summarized as the maximum temperature reached on each day. To understand the effect of surfgrass removal on the pool environment, other factors known to affect pool temperatures, such as the timing of high and low tides, the tidal height of the pool, and the weather had to be accounted for. To account for the timing of the tides and pool tidal height, the effective shore level (ESL) of each pool was calculated (Harley and Helmuth, 2003). The ESL uses the temperature time-series of each pool and tidal height measurements from nearby sites to determine the relative tidal elevation of pools. The time-series of temperature from each pool and tidal height from a nearby NOAA tide gauge at Neah Bay, Washington (48°22.1′N,124°37.0′W) was used to estimate each pool's ESL. Because the temperature of tide pools rose gradually during low tides when pools are isolated from the ocean and dropped rapidly when the incoming tide flooded with cool ocean water, times at which each pool's temperature dropped precipitously (greater than 1.5 °C in 10 min) were used to identify times as times at which the pool was flooded by a rising tide. By matching the time at which pools flooded with the tidal height measured at Neah Bay 45 min later (the time lag in tidal height between Shi Shi and Neah Bay as predicted by NOAA), the ESL of each pool relative to Neah Bay's tide gauge was calculated. Many days did not have a temperature drop of sufficient rapidity and therefore were not used to