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Mature and developing kelp bed community composition in a glacial estuary

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ABSTRACT

The assembly and maintenance of biological communities is influenced by environmental factors, which are predicted to shift with climate change. Glaciers are melting at increasing rates, delivering sediment and fresh water to coastal habitats. We hypothesized that environmental factors related to glacial discharge would be correlated to the initial recruitment and colonization of sessile communities in kelp beds, and to the abundance of mobile epibenthic invertebrates and adult kelp. To test these hypotheses, cleared rocks were placed at six sites at 10-m depth across a gradient of glacial-influence in Kachemak Bay, Alaska and the percent cover of the initial recruitment and the subsequent progression of the sessile community was monitored over 18 months. Small mobile invertebrates (such as limpets and chitons) were also monitored on these rocks for 18 months. Lastly, larger invertebrates (such as sea stars) and adult kelp were surveyed over the same time period along transects in the immediate vicinity of the cleared rocks. Environmental factors (sedimentation rates, salinity, temperature, irradiance, and nutrient concentration) were concurrently monitored at each site. Recruitment and subsequent colonization varied along the glacial gradient. At sites with higher sedimentation rates, recruitment and the subsequent developing community was dominated by barnacles with little or no kelp recruits and other macroalgae and high temporal variation in availability of bare space. At more oceanic sites, these communities were characterized by a slow increase in cover of encrusting and upright macroalgae, also with high variability among sites. Mobile invertebrates and adult kelp were more abundant at oceanic sites than the glacial sites. Using distance-based linear models, inorganic sedimentation rate was correlated to patterns of kelp bed recruitment and colonization and to the abundance of mobile invertebrates and adult kelps in the surrounding area. Changes in inorganic sedimentation with climate change may alter how kelp beds are distributed and structured in glacial estuaries.

1. Introduction

Kelp beds are important ecosystems around the world. Kelp beds support a wide range of commercial, recreational and subsistence fish and invertebrate species (Efird and Konar, 2014; Hamilton and Konar, 2007; Markel and Shurin, 2015). The primary productivity in kelp beds is large, and as such, kelp beds feed nearshore and offshore communities via detritus and through kelp drift (Abdullah et al., 2017; Duggins et al., 2016; Yorke et al., 2013). Kelp is harvested for subsistence and commercial use, as well as for herring roe, which use kelp blades for substrate (Holen et al., 2012; van Tamelen and Woodby, 2001; Vásquez et al., 2012). Hence kelp beds are important to nearshore and offshore ecosystems and to human communities.

Kelp beds naturally experience environmental and biological disturbances that result in space being cleared for recruitment. Recruitment can be affected by larval or propagule supply, environmental conditions, and biotic interactions. Hydrodynamic factors such as upwelling variability and current direction can affect propagule supply and the pool of species that can recruit to an area (Billot et al., 2003; Menge, 2000). Environmental conditions such as high sedimentation may also prevent certain organisms from establishing (Balata et al., 2007). Kelp microscopic stage growth, survival, and subsequent recruitment may be inhibited by high temperature, low nutrient conditions (Ladah and Zertuche-Gonzalez, 2007; Mabin et al., 2013; Nielsen et al., 2014) and interactions between temperature and salinity (Fredersdorf et al., 2009). The effects of eutrophication and disturbance on kelp recruitment can vary by species, resulting in compositional changes to kelp beds (Carnell and Keough, 2014). The study of initial recruitment and early colonization can give clues to ecological processes such as propagule supply, competition, and disturbance (Benes and Carpenter, 2015; Gagnon et al., 2005; Konar and Iken, 2005; Maggi et al., 2012). Recruitment is critical for sustaining populations, so understanding the effects of multiple stressors on recruitment is needed to assess population and community stability (Perkol-Finkel and Airoldi,

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2010).

Contrasts between communities in recently disturbed patches and more established communities can indicate environmental factors that affect adult populations. The community that persists to reproduce may be very different than the community that initially recruits. Localized mortality of macroalgae and invertebrates sometimes follows influxes of sediment or fresh water (Branch et al., 1990; Karsten, 2007). Kelp responses to warming can vary among co-existing species, potentially leading to changes in kelp bed species composition with future temperature increases (Hargrave et al., 2017). Kelp beds may be replaced by filamentous turf communities under persistent high sedimentation rates and elevated temperature (Bogen, 2009). Sea star movement and feeding can be inhibited by low salinity conditions (Agüera et al., 2015; Held and Harley, 2009). Variation in epibenthic invertebrate assemblages has been attributed to organic sedimentation, sediment type, and wave exposure (Eddy and Roman, 2016). Persistent changes in environmental conditions, such as increasing temperature at an ocean warming hotspot, can result in large scale changes in kelp biomass and species composition of kelp communities (Filbee-Dexter et al., 2016).

Glaciers are important features in high latitudes with direct connections to the nearshore environment (tidewater glaciers) or indirect connections through rivers fed by glaciers. Glaciers are melting at accelerating rates (Neal et al., 2010), resulting in increased glacial discharge that reduce water temperatures and salinities, increase sedimentation rates, reduce light availability (Wiencke et al., 2007), and degrade substrate quality (Spurkland and Iken, 2011). These environmental changes have been observed to diminish benthic biodiversity and macroalgal abundance (Spurkland and Iken, 2011; Wlodarsk-Kowalczuk and Weslawski, 2001); however, it is not yet understood whether these declines are due to differences in survival of initial recruits or drivers impacting subsequent colonization. This study investigated the role of environmental factors in a glacial estuary in structuring several components of kelp bed communities including 1) the recruitment and subsequent colonization of the sessile community on bare rocks over a time period of 18 months, and 2) mobile epibenthic invertebrate and adult kelp abundance. Identifying potential drivers of kelp beds among the environmental factors affected by glacial melt will aid in selecting variables for further study. This study also contributes to the discussion of how environmental drivers structure kelp bed communities in glacial estuaries.

2. Material and methods

2.1. Study site

Kachemak Bay, Alaska, is a high latitude estuary whose kelp beds are exposed to an environmental gradient influenced by glaciers. It is divided into an inner and outer bay at the Homer spit, which extends several kilometers into the bay (Fig. 1). Oceanic water from the Alaska Coastal Current enters the outer bay along the southern shore and flows counter-clockwise to then exit along the northern shore (Schoch and Chenelot, 2004). The outer, southern bay is free of glacial sediments while the inner bay has a sedimentation gradient along the coast with lower light and salinity and greater inorganic sedimentation at the head of the bay (Abookire et al., 2000; Spurkland and Iken, 2011). The counter-clockwise circulation carries some glacial fresh water and sediment westward along the bay's north shore toward the mouth (Gatto, 1982). Six sites at 10-m water depth were established to encompass the range of glacial exposure in Kachemak Bay (Fig. 1). Three sites were in the more oceanic outer bay (O1, O2, and O3) and three were in the glacially fed inner bay (I1, I2, and I3). These sites were chosen to visually have similar bottom slope and substrate composition. At each site, several components of the biological community and various environmental factors associated with glacial melt were sampled.

2.2. Sampling of recruitment of the sessile community and of mobile invertebrates and adult kelp over time

Six bare slate rocks were placed at each site to estimate recruitment of the sessile community (invertebrates and macroalgae) and the presence of mobile invertebrates over time. For this, 72 rocks were collected from two intertidal sites located mid-bay (Kasitsna Bay and Jakolof Bay). The rocks were scraped clean with a wire brush, placed in the sun for 48 h to eliminate any spore bank, and individually tagged with white-out paint. All rocks were approximately 5 cm thick, 25 cm wide and 35 cm long with two flat surfaces, one facing down to ensure that the rock did not roll and one facing up for settlement. Six rocks were randomly assigned to each site. Rocks were haphazardly placed along a 10-m permanent transect along the 10-m isobath at mean lower-low water marked with a plastic-coated steel cable.

Percent cover was visually estimated for all recruiting sessile invertebrates and macroalgae. Individual kelp were also counted and pictures were taken of the rocks so that rock area could be calculated using Image J (Schneider et al., 2012). Counts were standardized to rock surface area by dividing the raw count by the surface area. The first set of rocks was deployed in March 2013. A subsequent set was deployed in April 2014 to examine temporal variability in recruitment and colonization. After deployment, all rocks were surveyed in April of both years, and biweekly from May to September in 2013 and 2014 using SCUBA. No surveys were conducted from October to March due to inclement weather. Initial recruitment and colonization were examined over the first 1–6 months for rocks deployed in 2013 and 2014 and from 12 to 18 months for the rocks deployed in March 2013.

At each site, the density of small mobile invertebrates (such as limpets and chitons) was monitored by counting all individuals present on each experimentally cleared rock. These small invertebrates were identified to the lowest taxonomic level possible in the field (usually to class or lower). Counts were standardized to rock surface area by dividing the raw count by the surface area and expressed as density per m^2.

Larger invertebrates (e.g., sea stars such as *Asterias amurensis*) and adult kelp were counted along two haphazardly-placed replicate 2 × 10-m transects at each site. Transects started 1 m from each end of the permanent transect where cleared rocks were placed and the direction of each transect was chosen haphazardly. All invertebrates and kelp along these transects were identified to the lowest taxonomic level possible. Fish were not surveyed because of the logistical challenges of visual surveys in low visibility conditions.

2.3. Environmental factors

At each site, environmental factors directly related to glacial discharge were monitored, including sedimentation rate, bottom water temperature, irradiance, salinity, and nutrient concentrations [nitrate (NO_3^+), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicate (SiO_4^{2-})]. Sediment traps were used to determine sedimentation rates at each site from March to September 2013 and April to September 2014. These traps consisted of three polyvinyl chloride pipes with a height: diameter ratio of 5:1 to prevent resuspension (Hargrave and Burns, 1979) and were placed with the mouth of the trap approximately 0.7 m above the bottom. Once per month, traps were retrieved and replaced with new ones. Particulate mass flux was quantified by filtering the trap samples onto pre-weighed Whatman GF/F glass microfiber filters (0.7 μm). Filters were dried for 24 h at 60 °C to obtain dry weight. Filters were then burned for 6 h at 500 °C and re-weighed to determine organic content as the ash-free dry weight. Inorganic content was estimated as the remaining content after the organic content was burned off.

Bottom temperature and irradiance (photon intensity per area) were recorded hourly at each site using Honest Observer by Onset (HOBO) Pendant data loggers (Onset Computers, Bourne, Massachusetts) fixed