Life and death beneath macrophyte canopies: effects of understory kelps on growth rates and survival of marine, benthic suspension feeders

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Summary. Experiments conducted on rocky bottoms at 7–11 m depth in the San Juan Archipelago, Washington assessed effects of canopies of understory kelps on growth of benthic suspension feeders, determined the mechanisms responsible for effects, and assessed the influence of kelp canopies on survivorship of benthic fauna. Kelp canopies influenced growth rates of diverse suspension feeders. At several sites the mussel Mytilus edulis, the barnacle Balanus glandula, and the serpulid polychaete Pseudochitinopoma occidentalis grew faster on the bottom beneath kelp canopies than on nearby exposed substrata. The cheilostome bryozoan Membranipora membranacea showed a mixed response to kelp canopies, growing faster in exposed regions at one site, but faster beneath canopies at another. There were no differences in growth of 2 other species (the cheilostome bryozoan Cheilopora praelonga and the sponge Myxilla incrustans) between kelp and no-kelp treatments; however, some processes influenced by plant canopies affected their growth. Specific mechanisms responsible for kelp effects on growth were assessed in a series of field experiments using Pseudochitinopoma, Membranipora, Cheilopora and Myxilla. Particulate deposition on the bottom, which is more intense beneath canopies, negatively affected growth of all 4 species. Kelps also reduced rates of flow and prevented development of microalgal turfs beneath the canopy. Pseudochitinopoma grew faster in the weaker flows below canopies and both Cheilopora and Myxilla grew faster where there were no microalgal turfs. These other effects of kelp canopies were at least as important as the general, deleterious effects of higher sedimentation beneath canopies.

The lower growth rates caused by higher sedimentation beneath kelp canopies did not result in higher rates of animal mortality. Surprisingly, kelp canopies typically did not influence mortality due to predation. For 7 of 12 taxa, mortality rates did not differ between kelp-covered and exposed treatments. Significantly higher mortality occurred outside canopies for only 4 of 12 taxa, and for at least 2 of these 4 differences probably were not related to predation. Mytilus, a species rare at these depths, exhibited higher mortality beneath kelp canopies due to predation by crabs. Other macrophytes in fresh and salt water, as well as some benthic animals that create complex, 3-dimensional habitats, should influence benthic organisms and assemblages in ways analogous to the kelps acting through their effects on flow, particle transport, and shading.

Key words: Kelp – Suspension feeder – Growth – Mortality – Hydrodynamics

Many shallow, aquatic environments are dominated by macrophytes. Both submerged and emergent macrophytes are common in shallow reaches of lakes, ponds and streams. In estuaries and coastal seas, seagrass meadows are widespread in shallow, boreal-to-tropical sedimentary environments, whereas kelps are an important component of rocky, nearshore regions in temperate to boreal waters. The wide distribution of fresh-and salt-water macrophytes has stimulated a great deal of research regarding their physiology and ecology (e.g., see reviews by Hutchinson 1975; Dennison and Alberte 1982, 1985; Dayton 1985; Sculthorpe 1985; Sculthorpe 1985; Carpenter and Lodge 1986; Schiel and Foster 1986), as well as their influence on associated animal assemblages. Freshwater, estuarine and marine macrophytes host unique assemblages of epiphytes (e.g., Young and Young 1978; Bernstein and Jung 1979; Gerrish and Bristow 1979; Stoner 1980; Brönmark 1985), contribute organic matter to heterotrophs both directly and through detrital pathways (e.g., Vadas 1977; Klumpp and Nichols 1983; Mann 1988; Stevenson 1988; Duggins et al. 1989), and modify intensities of predation on some resident fauna (e.g., Coyer 1979; Peterson 1982; Laur and Ebeling 1983; Dayton and Tegner 1984; Gilinsky 1984; Orth et al. 1984; Summers and Peterson 1984; Ebeling and Laur 1985; Hershey 1985; Brönmark 1988).
Marine benthic seaweeds and seagrasses also alter the hydrodynamic character of estuarine and marine waters, which may be influenced strongly by tides and waves (Jackson and Winant 1983; Jackson 1984; Peterson et al. 1984; Eckman 1987; Eckman et al. 1989). Many benthic organisms disperse through the water column as passive or weakly swimming propagules, and many feed by capturing passively dispersed particles. Consequently, effects of marine macrophytes on fluid transport and particulate fluxes in the nearshore region can significantly influence the growth, reproduction and recruitment of numerous species (e.g., Bernstein and Jung 1979; Jackson 1986; Eckman 1987; Eckman et al. 1989; Duggins et al. 1990).

Most investigations of macrophyte-animal interaction have focused on one of the suite of processes outlined above, primarily because of the logistical difficulties of executing a larger, more integrated study. In addition, some classes of macrophyte have been studied more intensely than others. Angiosperms have been the object of considerable study in both fresh- and salt-water environments. The effects of kelps on animal assemblages have been reported from studies performed primarily within forests of surface canopy plants, particularly the giant kelp Macrocystis pyrifera. Causal links between animal assemblages and canopies formed by the smaller stipitate or understory kelps have received considerably less attention (e.g., Witman 1987; Kennelly 1987, 1989; Ebeling and Laur 1985, 1988; Carr 1989). This shortcoming is unfortunate, since sub-surface canopies are common, are found in many regions where surface canopies do not exist (e.g., the north-west Atlantic), and often occur as a second layer beneath surface or overstory canopies.

We have been studying the influence of understory kelps (a mixed assemblage of Agarum spp. and Laminaria spp.) on the ecology of animal assemblages in subtidal waters in the Pacific Northwest, U.S.A.. Previously, we described effects of kelp canopies on fluid and particulate transport, and speculated on the significance of these effects to benthic animals (Eckman et al. 1989). We also described the influence of kelp canopies on larval settlement, and elucidated some of the specific mechanisms responsible for effects observed (Duggins et al. 1990). Here, we report on effects of understory canopies on growth and mortality of suspension feeders, as well as mortality of other benthic animals. We also describe experiments that assessed the significance of some of the specific mechanisms that may have been responsible for these effects. The specific mechanisms tested were effects of kelps on (1) rates of fluid and particulate transport, (2) illumination intensity combined with its influence on development of microalgal turfs, and (3) particulate deposition on the bottom.

Methods

Growth of suspension feeders – 1987

Our first year’s study was designed to determine the extent to which kelp canopies affected growth of diverse types of benthic suspension feeders. The study area, study sites, and layout of experimental treatments within sites are described in detail in Eckman et al. (1989) and Duggins et al. (1990). A brief review follows. Experiments described herein were carried out simultaneously with many experiments described in those reports.

Experiments were conducted on roughly horizontal rock ledges at 7–11 m below MLLW in relatively protected waters in the vicinity of the University of Washington’s Friday Harbor Laboratories (48° 33' N; 123° 01' W). Much of the bottom at these depths is covered year round by a canopy of ≈1 m long fronds of kelp, largely Agarum fimbriatum and Laminaria groenlandica. Exposed patches of rock covered by red algal crusts are interspersed among the dense canopies.

Four sites were established (Brown 1, Neck Pt, Shaw 1 and Yellow 1), separated by 1–5 km (see Fig. 1 in Eckman et al. 1989). At these sites tidal currents 1.5 m above the bottom (above the kelp canopy) ranged from strong at Shaw 1 (mean = 24 cm s⁻¹, SD = 13 cm s⁻¹) to moderate at Brown 1 (mean = 16 cm s⁻¹, SD = 8.7 cm s⁻¹) over an 8-d period with measurements taken every 10 min (Eckman et al. 1989). Three replicates each of Kelp and No-Kelp treatments were created and maintained at each site. A Kelp treatment consisted of an uninterrupted minimum 10–20 m² region of bottom completely covered by overlapping kelp fronds. Coverage of the bottom was kept at approximately 100% (typical of surrounding areas) throughout the experiment by translocating adult plants into the experimental area as needed. A No-Kelp treatment consisted of an uninterrupted minimum 10–20 m² region of exposed rock. No-Kelp treatments were created and maintained by divers on areas of rock that originally were covered by a canopy. Within each site replicate treatments were separated by distances of 5–20 m. Kelp and No-Kelp treatments were blocked within sites.

This experimental design mimicked the mosaic nature of kelp distribution in local waters, where the voracious and patchy activity of herbivorous sea urchins creates areas that are totally denuded of benthic seaweeds, interspersed among regions with total coverage of the bottom by kelps. As described by Eckman et al. (1989) and Duggins et al. (1990), relative to No-Kelp treatments the bottom beneath canopies is subjected to significantly lower flow, higher sedimentation, and is characterized by reduced development of microalgal turfs due to lower light levels.

During the summer or fall of 1987 growth rates of 4 species of suspension feeder (the chelostome bryozoan Membranipora membranacea, the bivalve Mytilus edulis, the barnacle Balanus glandula, the serpulid polychaete Pseudochitinopoma occidentalis) were measured. Pseudochitinopoma and Membranipora are abundant at these depths. Mytilus and Balanus occur at these depths only rarely, and were included in experiments to expand the modes of suspension feeding examined. Individuals or colonies of each species were obtained from a single locale, labeled, measured, and then deployed randomly among sites and treatments. Animals were placed in situ on upward-facing, PVC panels (Fig. 1A) in both Kelp and No-Kelp treatments. These treatments differed in rates of fluid and particulate transport, sedimentation, illumination, and development of microalgal turfs of chain-forming diatoms, any of which could have contributed to observed differences in growth rates. For each species, densities of individuals on panels were kept low and within narrow limits, so that results would not be biased by density effects on growth (e.g., Peterson and Beal 1989; Harvell et al. 1990). Initial sizes of individuals also were kept within narrow limits to minimize variance due to effects of size on growth (e.g., Kaufmann 1981). Moreover, any size effects were accounted for in analysis of the data (see below).

Membranipora colonies were established on 110 cm², finely sanded, plexiglass plates. During May 1987, plates were attached to racks and suspended 3 m below a floating dock, with plates facing downward. Over several weeks colonies settled and grew to diameters of 1–5 mm. Plates were scraped carefully to reduce the density of colonies to < 10 · 110 cm⁻². A label was glued to each plate and it was photographed in seawater immediately prior to deployment at all 4 sites on 10 June 1987. The mean radius of Membranipora colonies at deployment was 1.47 mm; the range was 0.59·2.65 mm.