Oecologia (1991) 87:473–487

Oecologia

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

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Received December 8, 1990 / Accepted in revised form April 12, 1991

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 to growth (in the cases of *Cheilopora* and *Myxilla)* or more important to growth (in the case of *Pseudochitinopoma)* than were 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; 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; Summerson and Peterson 1984; Ebeling and Laur 1985; Hershey 1985; Brönmark 1988).

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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 I, Neck Pt, Shaw I and Yellow I), 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 I (mean $= 24$ cm s^{-1}, SD $= 13$ cm s^{-1}) to moderate at Brown I (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 m^2 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 m^2 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 weaker 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 cheilostome 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 cm^2, 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 $< 10 \cdot 110$ 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.

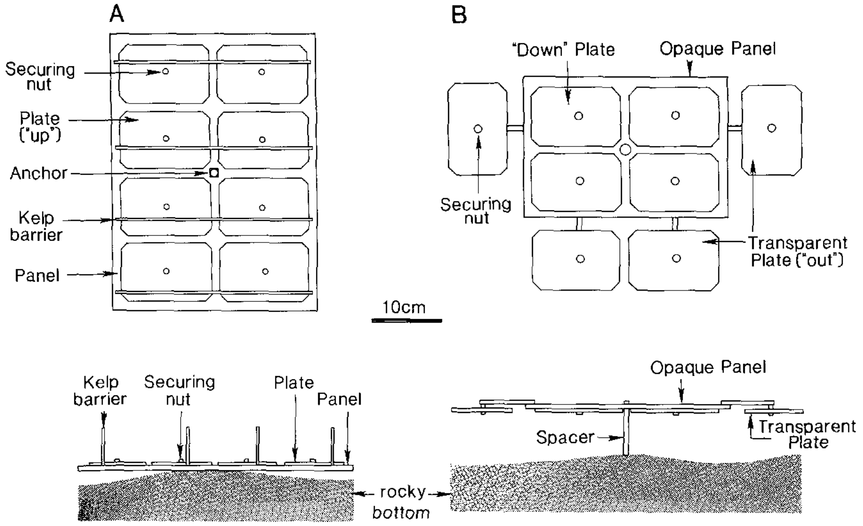

Fig. 1. (**A**) Top and side views of upward-facing PVC panels used in 1987 and 1988. (**B**) Bottom and side views of elevated, downward-facing PVC panels used in 1988 only

Plates were rephotographed in situ on 21 July. Colonies were clearly distinguishable from the background in photographs. Colonies grew in a circular pattern on plates and did not exhibit a directional bias, as has been noted on growing kelp fronds (Ryland and Stebbing 1971). However, by 21 July many colonies contained deep invaginations, probably as a result of partial predation (Harvell et al. 1990). To minimize this effect on estimates of growth, a "potential growth rate" of each colony was calculated. Potential growth was defined as the difference in areas of circles with radii equal to the maximum radius of each colony (i.e., furthest distance from ancestrula to colony edge) on 10 June and 21 July. Distances were determined from photographs using a digitizer. The use of this analytic method, rather than simple differences in total colony area, allowed us to minimize factors such as predation which would have reduced colony size only at certain points along its edge.

Juveniles of *Mytilus edulis* (which may be *Mytilus trossulus*, according to McDonald and Koehn [1988]) (mean shell height 2.07 cm, range 1.42–3.03 cm) were collected from an intertidal site, measured with vernier calipers, individually labeled by gluing a 3-mm diameter, numbered tag onto one valve, and deployed at all 4 sites on 2 June 1987. We suspected that this typically high intertidal species would be especially susceptible to predation in the subtidal (e.g., Feder 1959; Mauzey 1966; Paine 1966, 1980). To circumvent this problem, *Mytilus* on upward-facing panels were enclosed within a wide-mesh plastic screening that excluded most starfish, crabs and predatory gastropods. Seventeen mussels were enclosed within an area of 400 cm^2 on each panel. Screen material was 0.4 mm thick and formed a 10.5 mm mesh. Measurements in a flume using hot-film velocity probes (e.g., Eckman et al. 1981; Nowell et al. 1981) indicated that the screening reduced the horizontal flux of seawater over panels by 12%–18%. To minimize problems with fouling, the plastic mesh was cleaned twice a week in situ using brushes. Mussels were collected on 10 August and remeasured. Growth was defined as the change in shell height.

Balanus juveniles settled on 110 cm^2, finely sanded plexiglass plates that were attached to racks suspended at a site in the lower intertidal during April and May, 1987. Each plate was carefully scraped to reduce the density of juveniles (mean basal area 6.71 mm^2, range 1–42 mm^2) to $10\text{–}20 \cdot 110\ cm^{-2}$, labeled, photographed underwater, and deployed at Brown I, Neck Pt and Yellow I on 2 June 1987. Barnacles were deployed on the same mesh-enclosed panels as juvenile *Mytilus*. An internal partition made of the same wide mesh kept *Mytilus* from migrating onto plates with barnacles. Plates containing barnacles were rephotographed in situ on 6 August 1987. Individuals in photographs were readily distinguished from background and basal areas were determined using a digitizer. Growth was defined as the increase in basal area. Barnacles that had grown against neighbors were not considered.

Individuals of *Pseudochitinopoma* settled on 110 cm^2, finely sanded plexiglass plates from June through September, 1987. Plates were attached face downward to a rack mounted ≈20 cm above the bottom at 10 m depth. Plates were carefully brushed clean of algae, labeled, photographed underwater and deployed at Shaw I and Yellow I on 25 September. Calcareous tubes were easily distinguished from background in photographs and their lengths were determined using a digitizer. Mean tube length at deployment was 1.16 cm; the range was 0.17–2.02 cm. This species grows throughout fall and early winter. Plates were rephotographed in situ on 17 December. Growth was defined as the increase in length of the tube.

Growth of suspension feeders – 1988

In 1988 techniques were expanded to determine the extent to which growth was affected by specific effects of kelp canopies on: (1) rates of fluid and particulate flux near the bottom, (2) illumination intensity combined with the development of turfs of chain-forming diatoms, and (3) particulate deposition.

In addition to deploying animals on upward-facing panels (Fig. 1A, UP position) as in 1987, they were deployed in two new positions (OUT and DOWN, Fig. 1B) on downward-facing, opaque panels elevated 15 cm above the bottom. The design and use of these two types of panels is described in Duggins et al. (1990). Briefly, within a site and treatment (Kelp or No Kelp) organisms at all 3 positions experienced effectively equivalent levels of fluid transport relative to differences between Kelp and No-Kelp treatments, as measured by time-averaged flux of $CaSO_4$ from gypsum blocks (Table 1; see Eckman et al. [1989] for a description of the method). At each position flux was significantly reduced in Kelp relative to No-Kelp treatments. In general, average gypsum flux within No-Kelp treatments was ≈2 × that at identical positions beneath kelp canopies. This difference indicates that average flow speeds within centimeters of the substratum at each position were at least twice as fast in No-Kelp treatments. Animals in the DOWN position were underneath opaque panels and were in a similarly darkened environment in both Kelp and No-Kelp treatments. A significant difference in illumination and microalgal growth existed between the OUT and DOWN positions in No-Kelp treatments (Table 1), because the OUT plate was made of clear plexiglass and allowed illumination of the downward facing surface. Microalgal turfs developed at UP and OUT positions only within No-Kelp treatments and were absent from all positions below kelp canopies. Animals in OUT and DOWN positions were not exposed to particulate deposition in either treatment, unlike those in the UP position. Particulates deposited in 2.5–5 × greater masses beneath kelp canopies than on exposed substrata (Eckman et al. 1989). Table 2 lists

Table 1. Representative values (mean and SE, in parentheses) of gypsum dissolution from, and standing stocks of chlorophyll on, the 3 panel positions used in 1988 (Up, Down, Out) within Kelp (K) and No-Kelp (NK) treatments. B – Brown I, S – Shaw I, Y – Yellow I. See Duggins et al. (1990) for a more complete summary of these data

Treatment	Position	Gypsum Flux ($mg\ cm^{-2}\ h^{-1}$) 28 April 1988		Chlorophyll a ($\mu g\ cm^{-2}$) 1 August 1988		
		B	Y	B	S	Y
K	Up	1.76 (0.06)	2.03 (0.13)	0.05 (0.02)	0.07 (0.06)	0.20 (0.09)
K	Down	2.09 (0.05)	2.38 (0.12)	0.0	0.01 (0.01)	0.0
K	Out	2.10 (0.07)	2.25 (0.12)	0.0	0.01 (0.01)	0.0
NK	Up	3.12 (0.26)	4.11 (0.35)	17.5 (1.6)	10.5 (2.7)	16.4 (2.1)
NK	Down	3.06 (0.40)	4.81 (0.31)	0.02 (0.01)	0.05 (0.01)	0.0
NK	Out	3.58 (0.15)	5.24 (0.48)	2.50 (0.60)	5.50 (1.60)	4.10 (1.60)

comparisons used to conduct each test of the specific effect of kelp canopies on growth (see also Duggins et al. 1990). As appropriate, positions were grouped to increase the degrees of freedom in a statistical analysis (see below).

Growth experiments were conducted at 2 sites (Brown I and Yellow I) only, because of the higher effort required to establish and maintain animals in 3 positions in both treatments. As in 1987, animals of 4 species (the cheilostome bryozoan *Cheilopora praelonga, Membranipora,* the sponge *Myxilla incrustans, Pseudochitinopoma*) were obtained from a single site (the same sites as in 1987 for *Membranipora* and *Pseudochitinopoma*), measured, and deployed randomly among treatments and panel positions at both sites.

Cheilopora colonies were collected during March – April 1988, as were *Membranipora* colonies in 1987. The density of colonies on each plate was reduced to $< 10 \cdot 110\ cm^{-2}$, and plates were photographed underwater immediately prior to deployment on 25 April 1988. The mean size of colonies then was 0.41 cm^2; the range was 0.04–1.66 cm^2. Plates were rephotographed in situ on 31 May 1988. Colonies did not suffer greatly from partial predation, in contrast to *Membranipora*. Consequently, growth of *Cheilopora* colonies was defined more directly as the increase in surface area, as measured from photographs using a digitizer.

Membranipora colonies were collected during June, 1988 as in 1987. Plates were treated as in 1987, and were deployed on 6 July. The mean radius of colonies at deployment was 6.77 mm; the range was 1.25–15.2 mm. Plates were rephotographed in situ on 21 July. Partial predation on colonies was again a problem, and "potential growth rates" of *Membranipora* colonies were evaluated, as in 1987.

Myxilla colonies were collected in June, 1988 from a population on the underside of a floating dock. Sponges were cut into $\approx 2\ cm \times 2\ cm$ sections that were pressed with rubber bands against pre-labeled, fine sanded, 110 cm^2 plexiglass plates. Plates were suspended facing downward on racks 2 m below the dock, and left in place for several weeks. Rubber bands were cut and sections of sponge that had not successfully attached to plates were removed with a scalpel. Plates were deployed and photographed in situ on 28 July. The initial size of colonies averaged 1.26 cm^2; the range was 0.17–3.1 cm^2. Plates were rephotographed on 23 September. The area of colonies was determined from photographs using a digitizer, and growth was defined as the increase in colony area.

Individuals of *Pseudochitinopoma* were collected and treated as in 1987. Plates were deployed on 16 August when the mean tube length was 1.98 cm; the range was 0.45–3.95 cm. Plates were rephotographed on 28 November. Growth was measured as in 1987.

We attempted to measure growth of *Mytilus* and *Balanus* again in 1988, but were unsuccessful. Racks containing plates to collect *Balanus* were destroyed either by weather or vandals. By the time the loss was discovered the settlement season had effectively passed. We collected and deployed *Mytilus* in 1988 without enclosing them in mesh screening, as we hoped to avoid the frequent dives required to keep enclosures clean. This decision proved regrettable, as mussels were quickly destroyed by crabs (see below).

Analysis of growth data

The basis for evaluation of growth data for 1987 and 1988 was a statistical model based on analysis of covariance (ANCOVA):

$$Y_{ijklm} = \beta(S_{ijklm} - \bar{S}) + \mu + \alpha_i + \gamma_j + \delta_{k(j)} + \alpha\gamma_{ij} + \alpha\delta_{ik(j)} + \theta_{l(ijk)} + \varepsilon_{ijklm} \quad (1)$$

where Y_{ijklm} is the growth rate of individual or colony m on plate or panel l within treatment i, site j and block k, β is the (single) regression coefficient representing the dependence of growth rate on size (S) of the individual or colony, μ is mean growth rate, α_i is the effect on growth rate of treatment i (in 1987 Kelp or No Kelp; in 1988 Kelp or No Kelp, Strong or Weak Flow, High Light Intensity or Low Light Intensity, Sedimentation or No Sedimentation), γ_j is the effect of site j, $\delta_{k(j)}$ is the effect of block k nested within site j, $\alpha\gamma_{ij}$ is the effect of interaction between site and treatment, $\alpha\delta_{ik(j)}$ is the effect of interaction between treatment and block, $\theta_{l(ijk)}$ is the effect of plate or panel l nested within treatment i, site j and block k, and ε_{ijklm} is the residual (Winer 1971). We suspected that plate or panel effects would be relatively unimportant, since replicates were separated by only 10's of cm. In addition, our studies of fluid transport and recruitment carried out at the same locations (Eckman et al. 1989; Duggins et al. 1990) indicated that variation at the scale of blocked treatments generally was insignificant, too. Consequently, if $F \leq 1.50$ for tests of block or plate/panel effects, then these effects were deleted from the ANCOVA. This deletion often increased the degrees of freedom in analysis of treatment effects (which were of primary interest) and, therefore, the power of statistical tests.

In order to account for variation in growth rate due to body size regression techniques were used first to search for relationships between growth rate and the size of individuals within each site and treatment. To determine the most appropriate linear function to use in ANCOVA from among the likely possibilities (Kaufmann 1981), two relationships were tested (in order): (1) growth rate vs. initial size (area or length), and (2) ln(growth rate) vs. ln(initial size), which is appropriate for linearizing a power relationship between growth and size. If either of the regressions indicated equivalent slopes among all sites and treatments, then that relationship was used to analyze growth via Eq. (1). Alternatively, if regressions indicated heterogeneity of slopes among sites, but homogeneity between treatments within a site, then ANCOVAs that tested for treatment effects were calculated separately for each site. In this case the model used was:

$$Y_{iklm} = \beta(S_{iklm} - \bar{S}) + \mu + \alpha_i + \delta_k + \alpha\delta_{ik} + \theta_{l(ik)} + \varepsilon_{iklm} \quad (2)$$

with terms as described above.

If neither of these two forms of regression indicated significant relationships within sites and treatments, the size covariate was eliminated from the model and Eq. (1) was reduced to a simpler, partially hierarchical ANOVA. In this case, untransformed growth was analyzed if it conformed to assumptions of homoscedasticity according to the *F*-max test (Sokal and Rohlf 1981); $\log_{10}$-transformed growth rates were analyzed otherwise.

In all cases $p \leq 0.05$ was assumed to indicate a significant effect; $0.05 < p < 0.10$ was taken to indicate a marginally significant effect.

Short-term mortality experiments

We assessed differences between Kelp and No-Kelp treatments in mortality of 11 species. In all cases animals were deployed on upward-facing panels (Fig. 1A) and were not enclosed by any protective screening. Thus, animals were exposed to a full suite of natural predators or disturbers, as well as burial beneath deposited sediments and overgrowth by microalgal turfs, where they occurred (cf., Young and Chia 1984).

We did not assess mortality of *Pseudochitinopoma, Mytilus* or *Balanus* in 1987. The enclosure of mussels and barnacles in mesh screening was designed to modify natural rates of mortality by predation. The hundreds of serpulids were not examined individually in the lab after exposure in situ, as would have been necessary to assess survivorship.

Photographs of plates containing *Membranipora* colonies were taken 12 days after deployment in 1987. Photographs were censused to determine the frequency of complete disappearance of colonies from plates.

We also analyzed mortality of 2 other species in 1987 that exhibited little or no growth. Sections of *Halichondria* sp. (sponge) were prepared as were *Myxilla* in 1988 experiments. Plates were deployed at all sites and photographed in situ on 31 July 1987. Plates were rephotographed after 26 days, and the frequency of complete disappearance of colonies was assessed for each plate.

Colonies of the soft coral *Alcyonium* sp. were attached to plexiglass plates using nylon thread to hold colonies firmly against the surface (McFadden 1986). Plates with intact threads were deployed at Brown I, Neck Pt and Shaw I on 14 May 1987. Threads were cut in situ on 1 June and plates were photographed on 8 June. By this time all colonies not firmly attached had disappeared. Colonies were rephotographed after 31 days, and the frequency of complete disappearance of colonies was assessed for each plate.

In 1988 photographs of upward-facing plates containing colonies of *Myxilla* (after 28 days), *Cheilopora* (after 15 days) and *Membranipora* (after 15 days) were examined to assess the frequency of complete disappearance of colonies. Upward-facing plates containing *Pseudochitinopoma* individuals were returned to the laboratory after the 104-day deployment in 1988. Each tube was examined to determine whether or not it contained a living worm. Mortality was defined by the proportion of empty tubes on each plate.

Mortality of *Mytilus* was assessed in June 1988 by following cohorts of mussels tethered to plates using cyanoacrylate glue and monofilament line. Tethered mussels were deployed only at Yellow I. We placed 21 plates, each with 10 tethered mussels, into Kelp treatments and 21 plates into No-Kelp treatments. Survivorship of mussels on each plate was assessed after 7 days.

Mortality of *Balanus* was assessed using animals of 8–10 mm basal diameter. We collected mussels with adult *Balanus* growing on their valves, broke the valves into small chips each containing a single barnacle, and glued each chip onto a plexiglass plate using a marine epoxy. Each plate was deployed with 5 barnacles attached. Three plates were placed on upward facing panels in each of 3 Kelp and 3 No-Kelp treatments at Brown I and Yellow I during October, 1988. After 21 days we evaluated the percent mortality of barnacles on each plate.

In November 1988 scallops *(Chlamys rubida)* were tethered 5 per rod to 25 cm-long steel rods that were placed in Kelp and No-Kelp treatments at Brown and Yellow Is. Each scallop was tied to the rod by 10 cm of nylon line that was attached to a valve using cyanoacrylate glue. The percent mortality of scallops per rod was evaluated after 12 days.

To broaden the scope of the mortality study, we assessed survival of 2 species that are not suspension feeders. Shore crabs *(Hemigrapsus nudus)* (carapace width ≈2 cm) were collected from the low intertidal zone, and tethered 5 per rod to steel rods. Crabs were attached to rods with monofilament line glued onto the dorsal carapace. Rods were placed in Kelp and No-Kelp treatments in October 1988 at Brown, Shaw, and Yellow Is, and were censused daily for 2 days. We evaluated the percent mortality per rod. Similar experiments were conducted in August 1988 using juvenile *Cancer magister* (carapace width ≈2 cm) at Yellow I only. Mortality was assessed after 1 day.

Mortality data were analyzed via ANOVA using arcsine-transformed proportions. A 2-factor ANOVA (site and kelp treatment) was used where experiments were conducted at more than one site. A 1-factor ANOVA (kelp treatment) was used otherwise.

Long-term abundances and mortality

Eight sanded, 110 cm², plexiglass plates were deployed on upward-facing panels at each of the 3 replicate Kelp and No-Kelp treatments at Brown I, Shaw I and Yellow I on 4 April 1988. This deployment coincided with the start of the settlement season (Duggins et al. 1990). Plates were left undisturbed for the next 12 months, until retrieved on 31 March 1989. Each plate was placed in a plastic bag that was sealed in situ. Plates were fixed in formalin immediately, and transferred to 70% ethanol within 10 days. Plates were censused for abundances of macrofauna under a dissecting microscope at 10 × magnification.

Abundances ($\mathrm{No} \cdot 110\ \mathrm{cm}^{-2}$) of 5 taxa were analyzed for sensitivity to site and kelp treatment: *Pseudochitinopoma, Paradexiospira vitrea* (spirorbid polychaete), other spirorbids (not identified to species), *Pododesmus cepio* (bivalve) and an unidentified sabellid polychaete. Because plates were left in situ for 1 year it was not possible to evaluate sub-annual species, such as *Membranipora,* that also live in these environments but that do not overwinter. The amount of space occupied by organisms on plates averaged ≈1% and did not exceed ≈10% in any site or treatment. Thus, it was assumed that interactions among these sessile species did not greatly affect their long-term survival, and that it was reasonable to analyze abundances of each taxon separately. A 3-factor, mixed model, partially hierarchical ANOVA using $\log_{10}(x+1)$-transformed abundances was used to analyze each taxon's abundances. The model was

$$Y_{ijkm} = \mu + \alpha_i + \gamma_j + \delta_{k(j)} + \alpha\gamma_{ij} + \alpha\delta_{ik(j)} + \varepsilon_{ijkm} \tag{3}$$

with terms as defined above.

Differences between treatments in abundances on these plates reflected differential settlement and differential survival after settlement. *Pseudochitinopoma* and spirorbids secrete robust, persistent, calcareous tubes within hours of settlement, and therefore we were able to measure their rates of settlement, effectively uncontaminated by post-settlement events, in both treatments and at all 3 sites continuously from 6 April – 1 August 1988 (Duggins et al. 1990). These data were combined with measures of abundance after 12 months to estimate differences in survival post-settlement. For each site and treatment, mean abundances of *Pseudochitinopoma* and spirorbids (*Paradexiospira* plus other spirorbids) per plate were standardized to time-integrated measurements of total larval settlement during spring and summer, 1988. The resulting "survival ratio" (abundances of individuals surviving up to 12 months divided by total settlement) provided a straightforward estimate of post-settlement mortality. Theoretically, this ratio approaches 1 if there was no mortality after settlement, and approaches 0 if no animals survived. However, because our settlement experiments may not have included all of a taxon's settlement period, the calculated survival ratio can exceed 1 if mortality was low. Survival ratios were compared qualitatively between Kelp and No-Kelp treatments, but

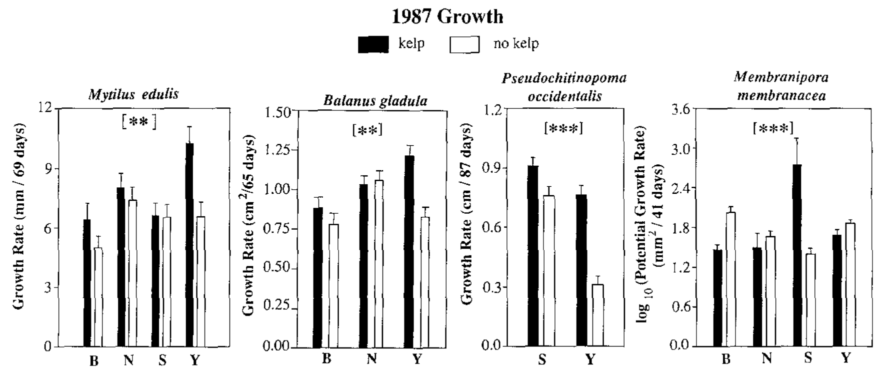

Fig. 2. Results of growth experiments in 1987. For each species mean growth and 1 SE are shown for both Kelp (shaded bar) and No-Kelp (open bar) treatments at each site. *B* – Brown I, *N* – Neck Pt, *S* – Shaw I, *Y* – Yellow I. Significance of kelp-treatment effect is indicated within brackets. NS – $p > 0.10$, no asterisks – $0.05 < p < 0.10$, * – $0.01 < p < 0.05$, ** – $0.001 < p < 0.01$, *** – $p < 0.001$

not statistically, because the variance of a ratio is not well defined for cases, as here, where both numerator and denominator have high coefficients of variation (Armitage 1977).

Tentacle heights

We considered it possible that the level of extension of feeding organs above the bottom could have influenced growth responses by some suspension feeders to rates of fluid transport, sedimentation, or development of microalgal turfs. Accordingly, we measured and compared the vertical extension of tentacles of *Pseudochitinopoma* (≈2 cm tube length) and lophophores of *Membranipora*. Animals were placed in seawater in the laboratory and viewed from the side with a stereomicroscope equipped with a calibrated ocular micrometer. Measurements were obtained from 20 worms and 1 extended lophophore near the center of each of 12 bryozoan colonies. Differences in tentacle height between the 2 species were evaluated by student's *t*-test using $\log_{10}$-transformed data.

Results

1987 Growth experiments

Kelp canopies significantly affected growth of all 4 species in 1987 (Table 3). For all species significantly higher growth occurred below kelp canopies at one or more of the sites.

Growth of *Mytilus* was not significantly related to the size of animals within the range used. At all 4 sites the mean growth rate was higher beneath kelps (Fig. 2). The kelp effect was highly significant ($F_{1,221} = 7.85$, $p = 0.005$) as was the site effect ($F_{3,221} = 4.68$, $p = 0.003$). The interaction of site and kelp treatment was not significant.

Growth rates of *Balanus* were higher beneath kelp canopies at Brown and Yellow Is, though there was essential parity in growth rates between treatments at Neck Pt. The effect of kelps on growth was highly significant ($F_{1,90} = 8.66$, $p = 0.004$), as were site effects ($F_{2,90} = 5.83$, $p = 0.004$) and the interaction of site and kelp treatment ($F_{2,90} = 5.69$, $p = 0.005$).

Growth rates of *Pseudochitinopoma* were independent of animal size within the range studied. Mean growth rate at both sites was higher beneath kelp canopies than on exposed portions of rock (Fig. 2). The kelp effect was highly significant ($F_{1,29} = 12.85$, $p = 0.001$) as was the site effect ($F_{1,29} = 9.77$, $p = 0.004$). The interaction term was not significant.

Potential growth rates (i.e., rates corrected to account for predatory loss) of *Membranipora* were independent

Table 2. Summary of tests performed in 1988 for effects of physical and biological variables on growth. The composition and microtopography of surfaces on which animals were deployed were held constant in all treatments, in addition to other variables listed

Effect (Treatment)	Comparison	Principal variables held constant between treatments
Kelp	UP plates in kelp vs. UP plates out of kelp	surface orientation
Flow	DOWN & OUT plates in kelp (low flow) vs. DOWN plates out of kelp (high flow)	light-microalgae (all shaded); sedimentation (eliminated, all down-facing); surface orientation
Sediment	DOWN & OUT plates in kelp (no sedimentation) vs. UP plates in kelp (high sedimentation)	light-microalgae (all shaded); flow (all in low flow environment)
Light-microalgae	DOWN plates out of kelp (shaded) vs. OUT plates out of kelp (illuminated)	sedimentation (eliminated, both down-facing); flow (both in high flow environment); surface orientation

of colony size. Growth rates were higher by more than an order of magnitude beneath kelp canopies at Shaw I, but were greater by a factor of 4 in No-Kelp treatments at Brown I (Fig. 2). At Yellow I and Neck Pt potential growth rates were essentially equivalent in both treatments. The kelp effect was highly significant ($F_{1,8} = 46.7$, $p < 0.001$) as was the interaction of kelp and site effects ($F_{3,8} = 482$, $p < 0.001$), due to differences between Brown and Shaw Is. The site effect was not significant.

1988 Growth experiments

Table 3 summarizes overall effects of kelp canopies on growth in 1988, and the importance of effects of kelps on flow, light intensity and development of microalgal turfs, and sedimentation.

Growth rates of *Cheilopora* were independent of the size of colonies within the range studied. In tests of the overall kelp effect (i.e., on upward facing surfaces, as in 1987), growth was not significantly affected by the presence of a kelp canopy (Fig. 3), and neither site nor interaction effects were significant. There were no detectable effects of flow, site or site × flow interaction on growth of *Cheilopora*. Growth was significantly lower in environments with higher illumination and microalgal cover (Table 3, Fig. 3; $F_{1,28} = 7.23$, $p = 0.01$), and was significantly higher at Brown I in this comparison (site effect: $F_{1,28} = 21.1$, $p < 0.0001$). The site × light interaction was not significant. Effects of particulate deposition on growth appeared to be negative but were only marginally significant ($F_{1,4} = 5.72$, $p = 0.075$). The weak significance was due, in part, to the inclusion of a significant blocking factor in the ANOVA, which greatly lowered the denominator degrees of freedom and the power of the test for sediment effects. Neither site nor interaction terms were significant in this comparison.

Table 3. Overall direction of effects of kelp canopies on growth in 1987, and effects of kelp canopies, flow, light and microalgal turfs, and sediments on growth in 1988. (+) indicates a significant positive effect of the treatment at $p \leq 0.05$, (−) indicates a significant negative effect at $p \leq 0.05$, (+/−) indicates that both positive and negative effects were detected among sites at $p \leq 0.05$. A sign enclosed in square brackets ([ ]) indicates marginal significance ($0.05 < p < 0.10$). (0) indicates that the treatment effect was not significant. Flow, light and sediment effects were not tested in 1987

	Treatment effect			
	Overall kelp	Flow	Light & Microalgae	Sediment
1987				
Mytilus	+			
Balanus	+			
Pseudochitinopoma	+			
Membranipora	+/−			
1988				
Cheilopora	0	0	−	[−]
Membranipora	[+/−]	0	0	−
Myxilla	0	0	−	−
Pseudochitinopoma	+	−	+	−

Potential growth rates of *Membranipora* varied directly and significantly with colony size. Regression slopes were equivalent among sites and treatments. There was a marginally significant effect of kelps on potential growth rates ($F_{1,11} = 4.46$, $p = 0.058$). As in 1987, the treatment that exhibited higher growth rates differed between sites (Table 3; Figs. 2, 4) and potential growth rates were higher in No-Kelp treatments at Brown I. Neither site nor interaction terms were significant. Tests for effects of flow and light/microalgae were weakened by the survival of only two colonies in the DOWN position in No-Kelp treatments at Yellow I. This low survival prohibited use of ANCOVA, and assessment of these two treatment effects was therefore possible for Brown I only. Potential growth rates at Brown I were not significantly affected either by the strength of flow or the intensity of light and microalgal cover (Table 3, Fig. 4). The ANCOVA indicates that there was a significantly negative effect of sediment deposition on growth ($F_{1,17} = 4.67$, $p = 0.045$), but that site and site × sediment interaction were not significant.

Growth rates of *Myxilla* were independent of the size of colonies within the range used. *Myxilla* exhibited negative growth in some treatments (Fig. 5), as is typical of many sponges seasonally or under adverse conditions (e.g., Palumbi 1985). Growth rates on all upward facing surfaces were relatively low. There was no net effect of kelp canopies on growth of sponges in this orientation (Table 3, Fig. 5), and neither site nor interaction terms were significant. Similarly, there was no direct effect of

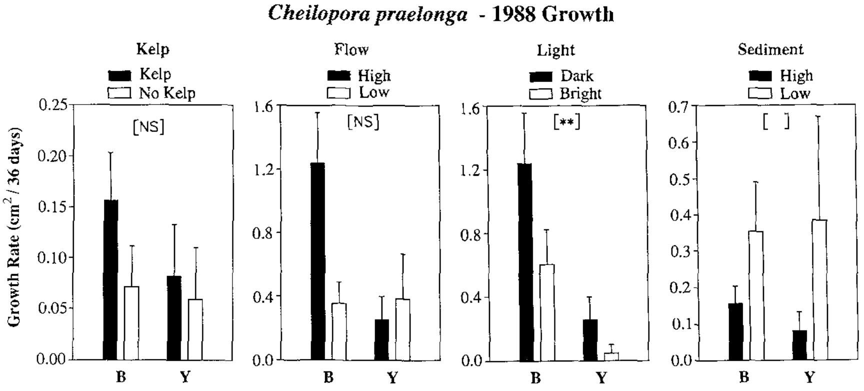

Fig. 3. Results of growth experiments on *Cheilopora* in 1988. Interpretation as in Fig. 2

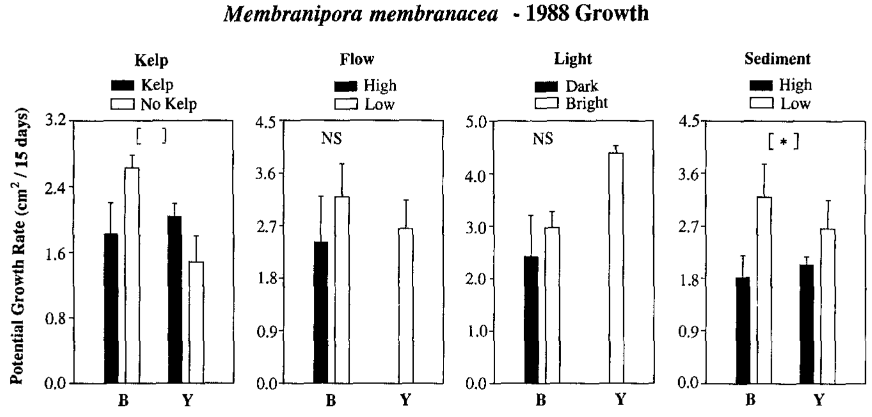

Fig. 4. Results of growth experiments on *Membranipora* in 1988. Mean growth and SE for standard colony of 1.75 cm^2 initial area, as predicted by ANCOVA. Significance of flow- and light-treatment effects are indicated for Brown I only. Other interpretations as in Fig. 2

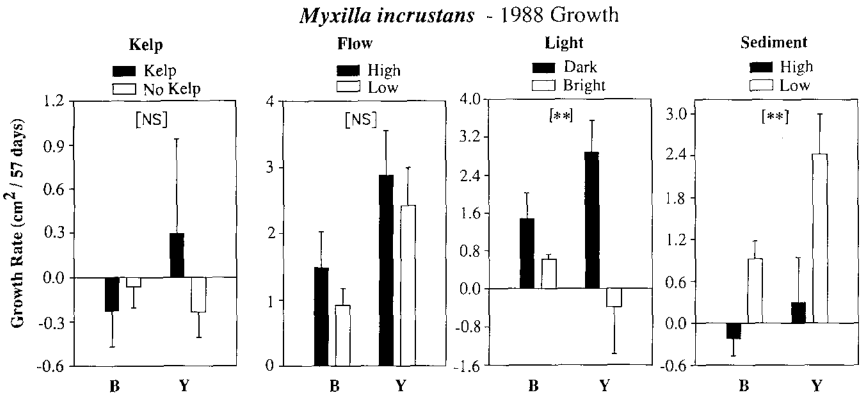

Fig. 5. Results of growth experiments on *Myxilla* in 1988. Interpretation as in Fig. 2

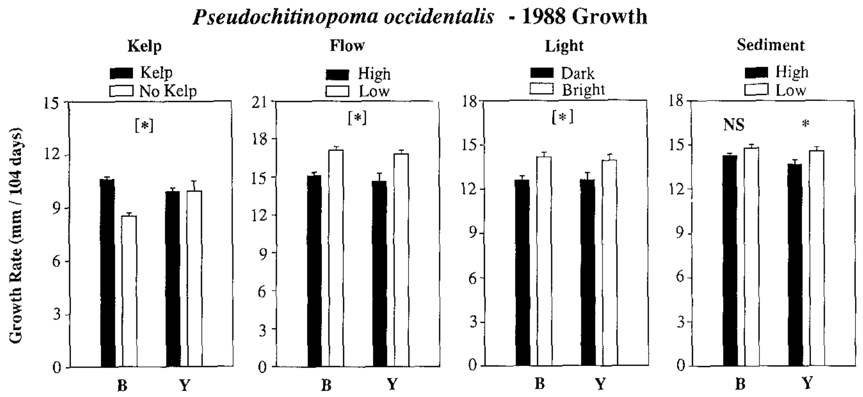

Fig. 6. Results of growth experiments on *Pseudochitinopoma* in 1988. Mean growth and SE for standard individual of 1.9 cm initial tube length, as predicted by ANCOVA. Test results for sediment effect are indicated separately for Brown and Yellow Is. Other interpretations as in Fig. 2

flow on sponge growth, and site and interaction terms again were not significant. Growth was significantly higher in darkened environments with no microalgal cover (Table 3, Fig. 5; $F_{1,28} = 8.12$, $p = 0.008$), but site effects and the interaction of site and light/microalgae were not significant. There was a significant negative effect of sediment deposition on growth ($F_{1,14} = 9.41$, $p = 0.008$). Site effects and the interaction of site and sedimentation were not significant.

Growth rates of *Pseudochitinopoma* varied significantly and directly with the size of tubes. Regression slopes were equivalent among sites and treatments for all but the sedimentation effect. As in 1987, the net effect of kelp canopies on growth of the serpulid was significantly positive ($F_{1,4} = 14.7$, $p = 0.018$; Fig. 6; Table 3). Although the site effect was not significant, there was a marginally significant site × kelp interaction ($F_{1,4} = 6.47$, $p = 0.064$). The interaction derived from the clear effect of kelps on growth at Brown I in contrast to the essential parity in growth between treatments at Yellow I (Fig. 6). Growth was significantly and negatively related to the strength of flow ($F_{1,4} = 8.10$, $p = 0.047$) and positively related to the intensity of light and microalgal cover ($F_{1,3} = 9.7$, $p = 0.05$). The site and interaction terms were not significant for either of these comparisons. For the sediment effect, regression slopes were different between sites, so separate ANCOVA's were run. There was a significant negative effect of sedimentation on serpulid growth at Yellow I ($F_{1,2} = 21.7$, $p = 0.043$), but no effect of particulate deposition at Brown I.

Table 4. Summary of analyses of mortality. Reported for each species is time period (in days) over which mortality was assessed, mean mortality rate (expressed as % d^{-1}) in Kelp (K) and No-Kelp (NK) treatments at each site, and, for analysis of the kelp effect, F values (F), degrees of freedom (d.f.) and probability levels (p)

	Days	BROWN I.		NECK PT.		SHAW I.		YELLOW I.		KELP EFFECT		
		K	*NK*	*K*	*NK*	*K*	*NK*	*K*	*NK*	*F*	*d.f.*	*p*
1987												
Membranipora	12	3.38	5.03	4.70	3.38	2.43	1.38	2.66	0.43	0.99	1,58	0.32
Halichondria	26	3.44	1.07	0.90	2.30	0.25	0.60	2.40	1.12	1.04	1,60	0.31
Alcyonium	31	0.13	0.32	0.03	0.21	0.10	0.69	–	–	3.98	1,45	0.05
1988												
Mytilus	7	–	–	–	–	–	–	10.8	5.31	11.3	1,40	0.002
Balanus	21	2.77	2.64					1.37	2.86	2.06	1,32	0.16
Pseudochitinopoma	104	0.52	0.65	–	–	–	–	0.30	0.76	19.9	1,19	<0.001
Myxilla	28	2.57	0.75	–	–	–	–	1.94	1.33	1.94	1,17	0.18
Cheilopora	15	0.00	0.85	–	–	–	–	0.53	1.83	7.19	1,19	0.015
Membranipora	15	0.83	0.44	–	–	–	–	2.44	4.60	0.15	1,19	0.71
Chlamys	12	6.20	6.20	–	–	–	–	1.71	1.92	0.01	1,8	0.94
Cancer	1	–	–	–	–	–	–	58.4	35.6	1.83	1,10	0.21
Hemigrapsus	2	28.7	25.6	–	–	19.0	15.3	29.4	29.2	0.11	1,16	0.74

Table 5. Abundances of animals on plates (No · 110 cm^{-2}) deployed for ≈1 year. Listed for each taxon are means and 1 SE (in parentheses), back-transformed from $\log_{10}(x+1)$-transformed abundances, in both Kelp (K) and No-Kelp (NK) treatments at all sites. *P* gives probability level for kelp effect

Species or taxon	BROWN I.		SHAW I.		YELLOW I.		*p*
	K	*NK*	*K*	*NK*	*K*	*NK*	
Pseudochitinopoma	1.58 (0.40)	0.18 (0.10)	16.9 (2.90)	0.07 (0.05)	4.12 (1.12)	0.00 (0.00)	0.0003
Paradexiospira	1.31 (0.35)	0.03 (0.03)	7.18 (1.19)	0.17 (0.13)	0.52 (0.21)	0.00 (0.00)	0.0004
Other spirorbids	0.57 (0.18)	0.00 (0.00)	0.80 (0.23)	0.00 (0.00)	0.36 (0.13)	0.00 (0.00)	0.0024
Pododesmus	0.62 (0.50)	0.96 (0.66)	0.62 (0.38)	0.58 (0.42)	0.50 (0.13)	0.33 (0.12)	0.80
Sabellid	0.35 (0.14)	0.03 (0.03)	1.46 (0.56)	0.00 (0.00)	0.83 (0.29)	0.04 (0.04)	0.0095

Short-term mortality experiments

In 1987, colonies of *Membranipora* and *Halichondria* suffered relatively high mortalities in both treatments at most sites (> 1% d^{-1}, Table 4). There were no significant differences between Kelp and No-Kelp treatments for either species, but for *Halichondria* the site effect was significant ($F_{3,60}=3.98$, $p=0.012$). In contrast, *Alcyonium* colonies experienced relatively low rates of mortality at all sites. Mortality was significantly higher in more exposed areas than beneath kelp canopies (Table 4), but the site effect was not significant.

In 1988, 6 of 9 species (*Balanus, Myxilla, Membranipora, Chlamys, Cancer,* and *Hemigrapsus*) exhibited no differences in mortality between Kelp and No-Kelp treatments (Table 4). All of these species exhibited mortality rates that averaged > 1% d^{-1}. Differences between sites existed for *Chlamys* only ($F_{1,8}=7.24$, $p=0.03$).

Significantly higher mortality rates occurred in No-Kelp treatments for *Pseudochitinopoma* ($F_{1,19}=19.9$, $p<0.001$) and *Cheilopora* ($F_{1,19}=7.19$, $p=0.015$) (Table 4). There were no significant site effects for these 2 species, and mortality rates for both were relatively low.

Mytilus was the only species that exhibited significantly higher mortality beneath kelp canopies than in No-Kelp treatments ($F_{1,40}=11.3$, $p=0.002$; Table 4). Mortality rates were high and clearly due to predation, as evidenced by an abundance of cracked shell fragments.

Long-term abundances and mortality

Table 5 lists mean abundances of 5 taxa on upward-facing plates after 12 months. 4 of 5 taxa (*Pseudochitinopoma, Paradexiospira,* other spirorbids, the sabellid) were significantly more abundant ($p<0.01$, in all cases) beneath kelp canopies than in No-Kelp treatments (Table 5). There were also significant site effects for *Pseudochitinopoma* ($F_{2,134}=31.6$, $p<0.001$), *Paradexiospira* ($F_{2,134}=45.6$, $p<0.001$) and the sabellid ($F_{2,134}=4.21$, $p=0.02$).

Survival ratios (i.e., the ratio of individuals surviving after 1 year to the average number of settlers measured) indicate that probabilities of survival of both *Pseudochitinopoma* and total spirorbids were orders of magnitude greater beneath kelp canopies that in No-Kelp treatments (Fig. 7). These results are consistent with the higher rates of mortality observed in exposed areas in short-term mortality experiments (Table 4).

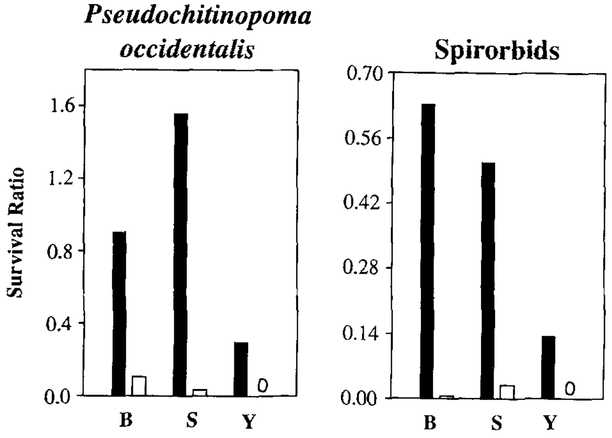

Fig. 7. Survival ratios for *Pseudochitinpoma* and spirorbids in Kelp *(shaded bar)* and No-Kelp *(open bar)* treatments at Brown I (*B*), Shaw I (S) and Yellow I (*Y*). "0" at base of graph indicates no survival in that site and treatment

Tentacle heights

Tentacles of *Pseudochitinopoma* extended an average of 2.05 mm above the substratum (SE = 0.146 mm, back-transformed from $\log_{10}$-transformed data), whereas lophophores of *Membranipora* extended an average of 1.15 mm above the bottom (SE = 0.088 mm, back-transformed). This difference is highly significant ($t = 5.74$, 30 d.f., $p < 0.0001$).

Discussion

Growth rates of marine invertebrates are subject to both environmental and genetic controls. Genetic controls may result in intrinsic effects of size on growth rate (Kaufmann 1981) and may impose an upper limit on the size of organisms (e.g., Sebens 1987). The influences of environment may be multifaceted and perhaps are most obvious from the substantial differences in growth rates of suspension feeders among sites separated in space (e.g., Seed 1976; Sebens 1984, 1987; Thompson 1984; Hilbish 1985; Page 1986; Bricelj et al. 1987; Duggins et al. 1989; Peterson and Beal 1989). These differences have been attributed to variability in times spent feeding (e.g., Suchanek 1978; Griffiths 1981; Peterson and Black 1987, 1988), gradients over large and small spatial scales in the quality and rate of supply of food to animals (e.g., Sebens 1984; Duggins et al. 1989; Fréchette et al. 1989; Grizzle and Lutz 1989; Grizzle and Morin 1989), and localized selection for specific alleles (Hilbish 1985; Peterson and Beal 1989). Significant differences in growth rates among sites were not an uncommon result in our study. However, no obvious pattern emerged from site effects. No individual site was associated with consistently high or low growth rates among species, or, in 1988, among the various treatments for any one species. Our study was not designed to focus on and elucidate mechanisms responsible for site effects, but it is reasonable to suspect that, over the kilometers that separated sites, significant differences existed in qualities or concentrations of suspended particulate organic matter used by suspension feeders.

Because we studied short-term growth of juveniles or immature colonies, our results were not biased by genetic limitations on maximum sizes. For this same reason, our assumption that net increases in food energy were directed largely toward changes in size of animals also was reasonable; there should have been comparatively little diversion of energy reserves to gonadal production in juveniles. We hoped to minimize biases in growth measures resulting from localized selection for alleles by obtaining animals from a single source, by subsequently distributing them randomly among sites and treatments, and by separating our primary treatments of interest (i.e., kelp cover, flow speed, microalgal turfs, sedimentation) by no more than a few meters. Thus, our experiments were well suited to determine the extent to which somatic growth of suspension feeders was controlled by several potentially important properties of the environment that, in turn, were controlled by the structure of subtidal kelp canopies.

Our results allow us to make several generalizations. First, it is clear that kelps exerted pronounced effects on growth of suspension feeders. In general, kelps exerted an overall positive influence on growth of animals on roughly horizontal, upward-facing surfaces. This pattern held among species that feed by greatly different mechanisms, including strong ciliary-driven circulation (*Mytilus* in 1987), active cirral sweeping or passively deployed cirral fans (*Balanus* in 1987; cf., Trager et al. 1990), and relatively sessile tentaculate arrays that utilize weak ciliary currents (*Pseudochitinopoma* in 1987 and 1988, *Membranipora* at Shaw I in 1987 and Yellow I in 1988). In contrast to this more general pattern, a net negative effect of kelps on growth was observed in only one species, and then at only 1 of 4 sites (*Membranipora* at Brown I in 1987 and 1988).

Only 2 species were tested in both 1987 and 1988, and results were consistent between years. *Pseudochitinopoma* grew at significantly faster rates beneath kelp canopies in both years (Table 3). The overall effect of kelp canopies on growth of *Membranipora* was significant in 1987 and marginally significant in 1988. In both years growth rates were higher in No-Kelp treatments at Brown I, but higher beneath canopies at another site.

The *net* effect of kelps on growth was not significant for 2 other species in 1988 (*Cheilopora* and *Myxilla*). This result does not indicate that their growth was unaffected by kelp canopies, however. On the contrary, some effects of kelps on the environment significantly impacted growth of all species tested in 1988. The parity in growth of *Cheilopora* and *Myxilla* between kelp treatments indicates only that, for these species, significant negative and positive effects of kelps effectively counterbalanced one another to produce no net differences at the 2 sites studied. The opposing effects of kelps on growth relate to the influence of plant canopies on sedimentation and development of microalgal turfs, as described below.

A second generalization that emerged from our results is that the deposition of particulates on benthic suspension feeders, which is greatly increased beneath kelp canopies (Eckman et al. 1989), reduced growth rates of all 4 species studied in 1988. This result is consistent with Kennelly's (1989) observations on sponges and Young and Chia's (1984) report that short-term survival of juvenile ascidians was reduced in environments subject to sedimentation. Their results and ours suggest that negative effects of particulate deposition are widespread among encrusting benthic suspension feeders. This experimental evidence supports similar suggestions based on observational distributions of animals (e.g., Seed and O'Connor 1981). However, the universally negative effects of higher sedimentation beneath kelp canopies presents an apparent paradox, since for 2 of the 4 species there was some evidence that growth rates were higher on upward facing surfaces beneath canopies than several meters away on more exposed regions of the bottom. We resolve this apparent paradox later in the Discussion.

Although effects of sedimentation on growth always were negative, the extent of growth depression varied interspecifically. A comparison of mean growth rates in high- and low-sediment treatments (Figs. 3–6) indicates that *Pseudochitinopoma* was not greatly affected by particulate deposition relative to the pronounced reductions in growth noted in *Cheilopora, Membranipora* and *Myxilla.* We suspect that the lower sensitivity of the serpulid to sedimentation was tied to its ability to extend feeding tentacles higher into the water column than can the bryozoans. Moreover, the high sensitivity of *Myxilla* to sedimentation is reasonable, as only a thin veneer of deposited particulates might clog ostia.

A third generalization that emerged from our results is that growth of most species was affected by the development of microalgal films occurring outside of kelp canopies (Table 3). However, the direction of the effect was not consistent among species. The higher growth rates of *Cheilopora* and *Myxilla* in darkened environments suggest that these species were affected negatively by algal overgrowth, as has been demonstrated for ascidians (Young and Chia 1984; Kennelly 1989). In contrast, *Pseudochitinopoma* grew at significantly higher rates in illuminated environments. The relatively high extension of its feeding tentacles into the water column may prevent this species from being affected adversely by microalgal films. The higher growth of serpulids in illuminated regions suggests that this species may feed directly on benthic microalgae or on particulate matter trapped within the algal turf. In either case, a revision of the current dogma that serpulids are exclusively suspension feeders (Fauchald and Jumars 1979) may be required. Our study offers no direct evidence that growth of *Membranipora* was affected significantly by microalgal films, but this particular test was weakened because an evaluation of microalgal effects was possible at only 1 of 2 sites.

A fourth generalization that emerged from our results is that growth of most species was not affected by differences in flow between kelp-covered and exposed environments. Of the 4 species examined, growth of *Pseudochitinopoma* only was sensitive to the intensity of flow (Table 3). It grew faster in environments where rates of fluid transport within centimeters of the substratum were, on average, at least 50% slower. A likely explanation for this pattern is that particle capture by serpulids was inhibited at higher flow speeds, as has been demonstrated directly for several other tentaculate suspension feeders that obtain food either passively or via weak ciliary currents (Okamura 1984, 1985; Patterson 1984; McFadden 1986; Leonard et al. 1988; Leonard 1989). This explanation is not compromised by the lack of a significant flow effect for *Membranipora* or *Cheilopora.* In an identical environment, lophophores of the bryozoans would encounter seawater and particles moving at a slower rate than would the tentacles of *Pseudochitinopoma,* because lophophores do not project as far into the bottom boundary layer. Moreover, interspecific differences can be expected in sensitivities to flow speed. The bryozoans may be particularly well adapted to feed successfully in stronger flow regimes, since they occur typically on the thalli of kelps (e.g., Ryland and Stebbing 1971; Bernstein and Jung 1979; Yoshioka 1982; Cancino et al. 1987) that project meters or more above the substratum.

Our experiments implicate strong flow as a factor negatively affecting growth of the serpulid. However, our experimental design does not allow us to reject unequivocally an alternative hypothesis. Our flow-treatment comparisons also included variation in the presence/absence of a kelp canopy (Table 2). Kelps slough off particulate organic matter, and the plants or their particulates release dissolved organic matter (e.g., Khailov and Burlakova 1969; Mann 1973; Linley et al. 1981). It is possible that significant gradients in concentrations of suspended particulate and dissolved organic matter existed over the few meters that separated strong and weak flow treatments, due to the reduced rate of flushing of water beneath canopies (Eckman et al. 1989). If such gradients existed, they may have contributed to the higher growth of *Pseudochitinopoma* in weak flow treatments. Such gradients would represent a small-scale analog to Duggins et al.'s (1989) observation in the Aleutian I chain that over hundreds of kilometers growth rates of suspension feeders varied due to differences in the supply of kelp-derived organic matter.

We consider this alternative explanation less likely than that based on differences in flow speed between treatments. We suspect that differences in concentrations of dissolved or particulate organic matter between flow treatments would have produced some evidence of similar differences in growth rates of other suspension feeders, yet growth of other animals was not significantly different between flow treatments. However, this *a posteriori* reasoning is not fully satisfactory, and we are conducting experiments to evaluate directly the influences of flow speed and kelp-derived organic matter on growth.

A fifth generalization that emerged from our results is that kelp canopies typically did not influence animal mortality due to predation. A parity in mortality rates between kelp treatments characterized 7 of 12 taxa tested (the 11 species listed in Table 4, plus spirorbids [Fig. 7]). Moreover, differences observed in mortality of some other species may not have been related to predation (see below). The influence of kelp canopies on mortality was much less than we expected given an abundance of previous evidence that complex, vegetated habitats in fresh water, estuaries and coastal seas reduce the effectiveness of predators (see references cited in Introduction; also Orth 1977; Nelson 1979; Heck and Thoman 1981; Blundon and Kennedy 1982; Crowder and Cooper 1982; Peterson 1982; Stoner 1982; Ebeling and Laur 1985; but for exceptions see Bernstein and Jung 1979; Gaines and Roughgarden 1987). For 4 of 12 taxa, the mortality observed was clearly the result of predation. Bivalves (*Mytilus* and *Chlamys*) and small crabs (*Hemigrapsus* and juvenile *Cancer*) were crushed by predators, such as *Cancer productus* or various fish, with portions of valves or exoskeleton left as evidence of predation. In contrast to results from most vegetated habitats, there was no reduction in the mortality of these 4 species beneath kelp canopies (Table 4). In fact, *Mytilus* suffered significantly higher rates of predation beneath kelps.

Four taxa, of diverse sizes and morphologies (*Alcyonium, Cheilopora, Pseudochitinopoma,* spirorbids), exhibited significantly higher rates of mortality in the more exposed environments. Although this pattern is expected if kelps provided a refuge, we suspect that for at least 2 of the 4 taxa predation outside of kelp canopies was not the cause of higher mortalities. For *Alcyonium* this result may have been an experimental artifact. Colonies were attached to plates with varying degrees of tenacity following our grafting procedures (see Methods). Since plates deployed outside canopies were in a significantly stronger flow environment (Eckman et al. 1989), dislodgement by lift and drag forces may have been responsible for the greater loss of colonies in this treatment. In the well-lighted environments outside of canopies *Cheilopora* colonies often were overgrown by filamentous algae that used zoecia as substrates for attachment. We suspect that algal overgrowth probably resulted in colony death (cf., Young and Chia 1984). Although we have no direct evidence, the higher mortality of *Pseudochitinopoma* in No-Kelp treatments probably was due to predation. Individuals of this species may be too large to suffer significantly from overgrowth by chain-forming diatoms. In fact, the serpulid grew significantly faster in well-lighted environments.

The mortality data help us to interpret a paradox described above: sedimentation beneath kelp canopies depressed growth rates of all suspension feeders tested in 1988, yet for *Pseudochitinopoma* and *Membranipora* in 1988, in addition to other species in 1987, there was evidence of faster growth rates on upward facing surfaces below kelp canopies, where sedimentation is more intense. Our results indicate that the depression of growth by sedimentation was not associated with increased mortalities. Clearly, deleterious effects of sedimentation on growth either were sublethal, or as a source of reduced growth and mortality were no more important, or were less important, than microalgal overgrowth, predation, disturbance, or flow-inhibited feeding. This conclusion is supported by patterns of abundance on upward-facing plates deployed in situ for 1 year. *Pseudochitinopoma* and spirorbids were virtually absent from No-Kelp treatments, but they, as well as a sabellid polychaete, persisted in significantly higher abundances beneath canopies where sedimentation is more pronounced (Table 5, Fig. 7).

In this respect, our results differ significantly from those of Young and Chia (1984). They reported that mortality of juvenile ascidians was significantly increased by sedimentation between 4 and 15 m depth in the same area that we worked, and that sediment deposition resulted in greater mortality than overgrowth by microalgae. We suspect that the differences between their conclusions and ours in part derive from differences in experimental techniques. Young and Chia studied mortality of ascidians that were translocated into petri dishes. Sediment deposition probably was more intense within these dishes having negative relief than it was onto the plexiglass plates of slight positive relief (Fig. 1) that we deployed. Thus, differences between our results and those of Young and Chia support the contention that mortality of benthic organisms may be modified significantly by microtopography (e.g., Shanks and Wright 1986; but see Wethey 1984 for an exception).

The differential abundances of *Pseudochitinopoma* and spirorbid polychaetes between Kelp and No-Kelp treatments after 1 year were not simple reflections of differential settlement. Overall, both taxa settled in significantly higher abundances below kelp canopies (Duggins et al. 1990). However, survival of these 2 taxa post-settlement was 1–2 orders of magnitude (or more) higher beneath kelp canopies than in more exposed environments located only a few meters away (Fig. 7). These results clearly indicate that the combined influences of microalgal overgrowth, predation, and flow-inhibited feeding outside of kelp canopies served to magnify differences established originally at settlement. A similar phenomenon has been reported for hard clams that recruit into and survive within seagrass meadows at higher rates than within adjoining bare sand flats (Peterson 1986). The simplest explanation for these patterns is that environmental factors affecting larval settlement operate in a similar fashion on juveniles and adults. In fact, our settlement experiments (Duggins et al. 1990) indicate that sediment deposition and, for some species, microalgal growth, affect larval settlement and growth in similar fashions. We are also tempted to suggest that selection has favored animals whose larvae recognize environmental cues associated, however directly or indirectly, with higher probabilities of mortality after settlement, and avoid settling in areas having these cues.

In summary, our results clearly indicate that understory kelps exerted an important influence on growth and mortality of suspension feeders in shallow, rocky marine environments. Growth rates and survival were enhanced beneath canopies for many species, though positive net effects of canopies on growth and survival were not exhibited by all species or at all sites. The deposition of particulates on the bottom reduced growth rates of all species tested. By itself, this universally negative effect of sedimentation appears to contradict animal responses to kelp canopies, since sedimentation is increased below canopies, where many species exhibited increased growth and survival. The solution to this apparent paradox derives from the role of kelps in lowering rates of flow and preventing development of microalgal turfs beneath the canopy. These latter effects each tended to increase growth rates of one or two species below canopies, and these effects clearly were at least as important or were more important to growth and survival than were growth-inhibiting effects of sedimentation.

We do not reject the hypothesis that kelp beds can offer refuges from predation (e.g., Coyer 1974; Dayton and Tegner 1984; Ebeling and Laur 1985), but we note that the converse is not uncommon (Bernstein and Jung 1979; Gaines and Roughgarden 1987, *Mytilus* in this study), and that this mechanism was not generally important in the survivorship of species we studied. Understory kelps clearly affected other factors, such as siltation and overgrowth by filamentous microalgae, that influenced survivorship in addition to predation efficiency. Furthermore, while some organisms may find refuge from predation in kelp stands, the protected species may themselves be predators, leading to increased mortality of their prey.

We conclude by noting that many of the mechanisms by which kelp forests influence associated assemblages of organisms will be shared by other macrophytes in fresh and salt water, as well as by some animals that create complex three-dimensional habitats, such as worm tubes, hard corals, and beds of gorgonians. In marine and estuarine waters, streams, rivers, and shallow reaches of lakes and ponds exposed to wind-generated waves, the obvious influence of biologically generated habitat complexity on predation, and the creation of microhabitat, is greatly augmented by the influence of such habitat complexity on hydrodynamics. The influence of biological structures on fluid transport near the bottom, sedimentation, and particulate resuspension can be expected to significantly influence the dispersal, settlement, growth, and survival of associated biota.

Acknowledgements. We gratefully acknowledge contributions of many people who assisted us in the lab and field, particularly Mark Hallmark and Dave Edinger. The Herculean efforts of Amy Sewell were instrumental to the completion of this research. Helpful comments on earlier versions of this manuscript, and multifaceted support, were provided by Megan Dethier and Roberta Marinelli. Comments by Mark Hay, Beth Okamura, C.H. (Pete) Peterson and two anonymous reviewers also helped to improve the manuscript. Finally, we thank A.O.D. Willows, Director of the Friday Harbor Laboratories, and the staff of the Labs, for providing us with critical support and assistance. This research was supported by NSF grants OCE–8515697 and OCE–8911116.

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