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Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites

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Abstract The food quality of detrital particles derived from three species of kelps was evaluated in a laboratory feeding experiment utilizing two species of suspension feeders, the serpulid polychaete *Pseudochitonopoma occidentalis* and the mussel *Mytilus trossulus*. Fresh and aged kelp particles were also evaluated, and growth in all treatments was compared to growth on ad libidum phytoplankton rations. Fresh particles from *Laminaria groenlandica*, aged particles from *Agarum fimbriatum* and *Alaria marginata*, and mixed phytoplankton promoted the highest growth rates in both consumers. Growth was inversely related to total polyphenolic concentration in the fresh kelp particles. The increase in quality of both *Agarum fimbriatum* and *Alaria marginata* particles with age corresponded with a rapid loss of polyphenolic secondary metabolites and an increase in total nitrogen.

Introduction

Marine ecologists studying nearshore foodwebs have long recognized the importance of particulate detritus derived from benthic macrophytes; however, in general, their attention has focused on detritus produced by marine angiosperms (such as marsh and eel grasses) and utilized by deposit-feeding invertebrates (Valiela 1984, and citations therein). The role of algal detritus has received considerably less attention, although a priori one might expect it to be an abundant and high-quality food source. Angiosperm tissues are comprised of a number of components, such as cellulose, waxes, and lignins, that are both difficult to digest and resistant to microbial degradation (Tenore 1983; Valiela 1984), and experiments have shown that vascular plant detritus is a relatively poor-quality food (Kirkby-Smith 1976; Williams 1981; Newell and Langdon 1986). Many algal tissues, however, are both high in nitrogen content and readily available to consumers and microflora (Findlay and Tenore 1982; Atkinson and Smith 1983). Conversely, other studies have suggested that because conversion rates of organic carbon from algal biomass to bacterial microflora are low, even aged algal particles are a poor food source (Stuart et al. 1982).

Their broad distribution, common occurrence, and high levels of production make kelp forests potentially important as sources of detritus. The relevance of kelp production to suspension and deposit feeders is predicated upon the mechanics of kelp growth and degradation. While some fraction of kelp production is exported from shallow coastal waters (either on shore as beach drift or into deeper water), a significant fraction of kelp standing-stock degrades in situ into particulate and dissolved fractions, available to a diverse assemblage of nearshore (pelagic and benthic) suspension feeders (Newell et al. 1980; Bustamante and Branch 1996). Perhaps more importantly, some kelp species are a continuous source of particulate organic carbon (POC) and dissolved organic carbon (DOC) as they grow, with DOC "leakages" estimated to be as high as 35% of net production (Khailov and Burlakova 1969; Hatcher et al. 1977) and tissue turnover rates (resulting in the sloughing of particulate material) approaching 20 times per year (Mann 1972; Duggins unpublished data).

Stable carbon isotope analyses and in situ growth experiments conducted in the north Pacific (Duggins et al. 1989) and the southeastern Atlantic (Bustamante and Branch 1996) have confirmed that kelp production is very important to a broad range of secondary con-

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sumers, including suspension feeders. However, in a field experiment comparing suspension-feeder growth rates in real versus artificial kelp stands (10 to 15 m^2; Duggins and Eckman 1994), we failed to observe any enhanced growth associated with the most common local kelp species, *Agarum fimbriatum*. In fact, the only significant difference between growth in real versus artificial kelp was higher growth for one species in the artificial kelp treatment. *A. fimbriatum* is known to contain high concentrations of polyphenolic secondary metabolites (Steinberg 1985; Van Alstyne et al. 1997) which are thought to inhibit growth (see below). Vadas (1977) demonstrated that growth and gonad development are reduced in urchins fed *Agarum* spp. compared to other algal species that are low in polyphenolics. These results led us to speculate that among kelp species considerable differences could exist with respect to the food quality of their POC and DOC, and that such differences could relate to the occurrence of polyphenolic secondary metabolites.

Polyphenolic compounds are thought to serve a number of very different functions, including grazer deterrence, in a large range of terrestrial and marine plants (Paul 1992 and citations therein). One ultimate effect of these compounds is to reduce assimilation efficiency in grazers (Tugwell and Branch 1992; Boettcher and Targett 1993), although some invertebrate grazers have developed adaptations for ameliorating this problem (Steinberg and van Altena 1992; Tugwell and Branch 1992; Steinberg et al. 1995; Targett et al. 1995). At least one study suggests a similar negative effect on assimilation in a deposit feeder (Charles 1993). Thus, in the artificial versus real kelp experiment mentioned above, the poor performance of suspension feeders in the real kelp treatment could have resulted from the high concentration of polyphenolic compounds in fresh *Agarum fimbriatum* detritus.

This paper reports experiments addressing the quality of kelp particles as food for two suspension feeders, and specifically examines (1) growth differences in accordance with sources (kelp species) of particles, (2) the relationship between particle age and food quality, and (3) the interaction of source and age on levels of polyphenolic compounds in kelp particles.

Materials and methods

Experiments were conducted at the University of Washington's Friday Harbor Laboratories in the San Juan Archipelago, Washington State (USA). Rocky substrates of the shallow subtidal of this region are characterized by a diverse understory assemblage of kelps dominated by *Agarum fimbriatum* and including *Costaria costata*, *Laminaria groenlandica*, *L. complanata*, and *Pleurophycus gardneri*. Dominant rocky intertidal brown algae include *Fucus gardneri*, *Hedophyllum sessile*, and *Alaria marginata*. Three kelp species (*Agarum fimbriatum*, *Alaria marginata*, and *L. groenlandica*) were chosen for our feeding experiments based upon their frequency of occurrence and expected range of polyphenolic concentrations. Feeding experiments utilized two suspension feeders, the serpulid polychaete *Pseudochitinopoma occidentalis* and the mussel *Mytilus trossulus*.

Polychaetes were collected on settling plates deployed in the shallow subtidal, thinned to low densities (to eliminate density-dependent effects on growth) and recorded with a high resolution 8 mm video camera for later digitization. Similar-sized, small mussels (≃2 cm valve length) were collected from the intertidal zone at Argyle Lagoon, San Juan Island, measured (valve length) with a digital caliper, and individually marked. Five to ten worms (< 1.0 cm tube length) and mussels (< 2.0 cm valve length) were placed in plastic tubs, each containing 2000 ml of 1 μm-filtered seawater plus a food ration (see following subsection). Tubs were kept in a 10 °C coldroom, continuously stirred, and aerated. *Pseudochitinopoma occidentalis* were allowed to grow for 125 d, *Mytilus trossulus* for 166 d, before growth was measured. Growth was assessed using changes in *P. occidentalis* tube length (measured with NIH (National Institute of Health)-image digitizing software) and *M. trossulus* valve length. Each worm tube was dissected at the end of the experiment and only tubes containing living worms were remeasured.

Fresh particles and phytoplankton

Since we were interested in food quality rather than quantity, we attempted to provide equal-density ad libidum rations. Two 75% rations were used only to test if the 100% rations were in fact ad libidum. We assumed that if growth rate did not drop with a 25% reduction in particle concentration, the 100% ration was ad libidum. Given the low-density, small suspension-feeder size, large tub volume, and ad libidum food supply, we can assume that suspension-feeder growth was density-independent (see "Results").

There were six fresh particulate treatments: *Agarum fimbriatum*, *Alaria marginata*, and *Laminaria groenlandica*, 100% ration; cultured phytoplankton, 100% ration; *L. groenlandica*, 75% ration; and cultured phytoplankton, 75% ration. Each 100% treatment had five replicate tubs, the 75% treatments had three replicates. Fresh kelp particles were derived as follows. Every 3 d, individuals of each species was collected from the Friday Harbor Laboratories breakwater. Kelp blades were brushed and wiped to remove diatoms and epiphytes. A 20 g piece of tissue was placed in a blender with 400 ml of filtered seawater and blended until all particles could pass through a 500 μm sieve. This suspension was centrifuged at 10 000 rpm for 20 min to separate the particles from the dissolved fraction. The pelletized particles were then resuspended in 800 ml of filtered seawater in the blender, and 100 ml of this final suspension (2.50 g kelp particles per aliquot) were added to each appropriate replicate growth-tub. The three *L. groenlandica* 75% replicates received 75 ml of the suspension.

The phytoplankton ration was a 1:1 mixture from two phytoplankton cultures (*Thalassiosira weissflogii* and *Isochrysis galbana*). Phytoplankton cultures were inoculated every 2 wk, and were allowed to grow for 14 d before use (thus we drew from cultures that were 14 to 28 d old). A 500 ml aliquot of each culture was centrifuged for 20 min at 10 000 rpm. The phytoplankton cells were concentrated but not pelletized, the supernatant culture medium was discarded, and the concentrated cells from each culture were resuspended in 1000 ml of filtered seawater. Each full-concentration phytoplankton replicate received 100 ml of this solution, while the three 75% replicates each received 75 ml.

Aged particles

We homogenized 80 g of cleaned kelp tissue from *Agarum fimbriatum*, *Alaria marginata*, or *Laminaria groenlandica* in 800 ml filtered seawater until all particles could pass through a 500 μm sieve. This suspension was than centrifuged to remove the dissolved fraction, and the particles were resuspended in 2000 ml of filtered seawater. Each suspension was placed in a dark coldroom at 10 °C, aerated with several airstones, and continuously stirred. Each suspension was allowed to age for 1 wk before the experiment began, and was then used as a food source for a 2 wk period. New

suspensions were created every 2 wk, and thus this treatment consisted of particles that were between 7 and 21 d old. At each feeding (every 3 d- see below) 62.5 ml aliquots (2.50 g kelp per aliquot) were added to the "aged" replicate tubs. Thus, not only were consumers fed ad libidum, but particulate concentrations in all 100% kelp treatments, fresh or aged, were the same.

Phenolic assays

Phenolic concentrations (% dry weight) of whole-kelp tissues, and fresh or aged particles were determined by Dr. K. Van Alstyne using a modified Folin-Ciocalteu method described by Van Alstyne (1995). Aged particles were obtained from the particulate suspensions described above on Day 14 (half way through the aging period). In addition, a time-series was taken of phenolic concentrations immediately post-blending and 1, 2, 5, 10, and 14 d after blending.

Carbon, nitrogen, and dissolved oxygen assays

Total nitrogen (N), total carbon (C) and C:N were measured for fresh and aged (14 d) particles by means of a Perkin-Elmer 2400 elemental analyzer at the Skidaway Institute of Oceanography, Savannah, Georgia. We measured dissolved oxygen in each tub several times over the course of the experiment because of our concern that degradation of particulate detritus in some of the treatments could reduce oxygen concentration. There was no difference among any treatments ($x + \mathrm{SD} = 9.18 + 0.18$ mg l^{-1}, $F = 0.79$, $p = 0.62$) in this variable. The measurements were taken at the end of a 3 d feeding cycle, when any potential oxygen depletion would have been greatest.

Statistical analysis

This experiment was designed to be analyzed using a nested analysis of variance with replicate feeding chambers (tubs) nested within each treatment. However, due to poor settlement of *Pseudochitinopoma occidentalis* on settling plates and unexpectedly high mortality in *Mytilus trossulus* among all feeding treatments, many tubs (>25%) contained only 1 or 2 individuals at the end of the experiment. This precluded analysis of variance of the replicate-tub factor, which was designed, and assumed a priori, to be insignificant. Because of this practical constraint, the following analyses pool individuals within each treatment and consider replicate individuals as the variance-producing factor to compare with variability observed among the primary treatments (kelp species and particulate age).

Growth data were subjected to two-way analysis of variance, with both factors (kelp species and particulate age) considered fixed. Since there was no aged phytoplankton treatment, phytoplankton was excluded from this analysis. *Pseudochitinopoma occidentalis* and *Mytilus trossulus* and were analyzed separately. Where interactions between factors were highly significant ($p < 0.01$), the importance of each factor was examined using one-way ANOVA and, if appropriate, Fisher's least-significant a posteriori tests (with the phytoplankton treatment added to one-way analyses of growth on fresh particles). *t*-tests were employed to examine differences in growth between fresh and aged particles for each kelp species, since this comparison was of interest a priori.

Results

The effect of particle concentration (100 vs 75% ration) was not significant for *Pseudochitinopoma occidentalis* fed either fresh *Laminaria groenlandica* particles ($t = 1.69$, $p = 0.09$) or phytoplankton ($t = 0.43$, $p = 0.67$). For *Mytilus trossulus*, the effect of concentration was not significant for *L. groenlandica* particles ($t = 1.69$, $p = 0.09$), but was significant for phytoplankton ($t = 3.63$, $p = 0.001$), with higher growth at the lower concentration. This result indicates that mussels on the 100% phytoplankton diet were given a ration that inhibited growth by being too concentrated for maximally efficient feeding. While this should not affect comparisons of different kelp diets, where particle concentration was held constant among treatments (and where effect of concentration was insignificant), comparisons between growth on kelp versus phytoplankton rations in this species must be interpreted cautiously.

Two-way analyses of growth for both suspension feeders resulted in a highly significant interaction between source (kelp species) and age of particles (*Pseudochitinopoma occidentalis*: $F = 10.69$, $p < 0.001$; *Mytilus trossulus*: $F = 5.04$, $p = 0.007$). Consequently, we proceeded to one-way analyses of each of these effects. Source of fresh particles was a highly significant factor for both suspension feeders. *P. occidentalis* growth rates were more than twice as high when food was fresh *Laminaria groenlandica* particles or phytoplankton than when it was fresh *Agarum fimbriatum* or *Alaria marginata* particles [($F = 14.10$, $p < 0.001$; Fig. 1)]. A posteriori tests revealed no difference in food quality between *L. groenlandica* and phytoplankton ($p = 0.33$) or between *Agarum fimbriatum* and *Alaria marginata* ($p = 0.98$). A similar pattern was observed for *M. trossulus* ($F = 6.53$, $p < 001$, Fig. 2), but a posteriori differences between *L. groenlandica* and *Agarum fimbriatum* or *Alaria marginata* were less distinct ($p = 0.08$, and 0.07 respectively). For *M. trossulus*, phytoplankton appears to be a higher-quality food than does *L. groenlandica* ($p = 0.06$).

The effect of particulate age is generally similar between suspension feeders (Figs. 1 and 2) but with some

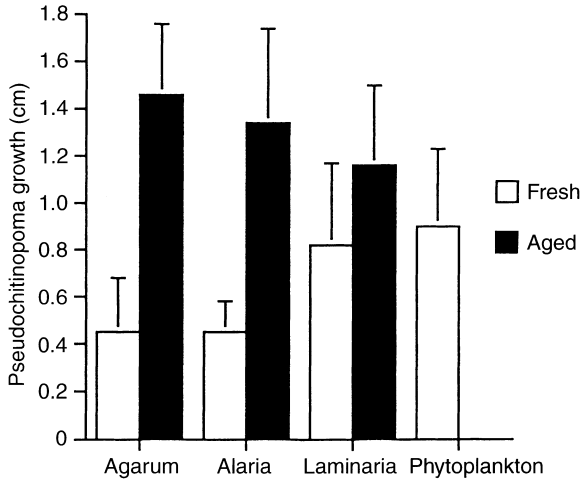

Fig. 1 *Pseudochitinopoma occidentalis.* Growth (mean ± SE, cm of tube elongation) of polychaetes fed fresh and aged kelp particles (*Agarum fimbriatum*, *Alaria marginata* and *Laminaria groenlandica*) and phytoplankton

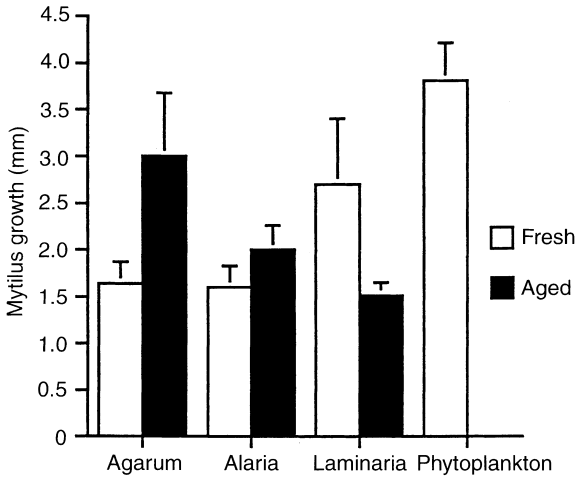

Fig. 2 *Mytilus trossulus.* Growth (mean ± SE, mm of valve elongation) of mussels fed fresh and aged kelp particles (*Agarum fimbriatum*, *Alaria marginata* and *Laminaria groenlandica*) and phytoplankton

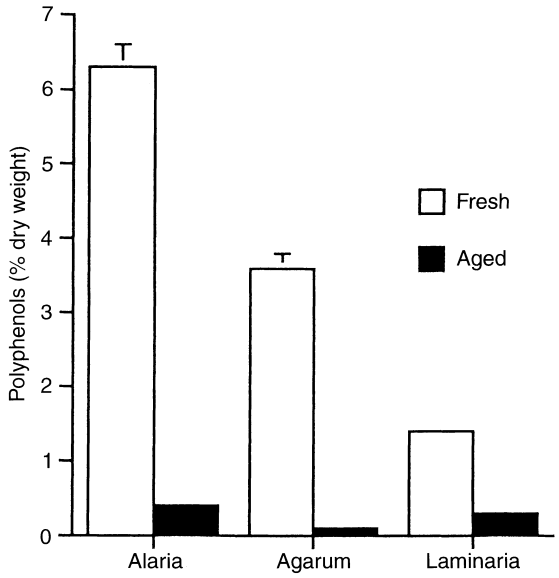

Fig. 3 *Agarum fimbriatum*, *Alaria marginata* and *Laminaria groenlandica.* Polyphenolic concentration of fresh kelp tissues, and aged kelp particles (mean ± SE). Aged particles were sampled 14 d after homogenization

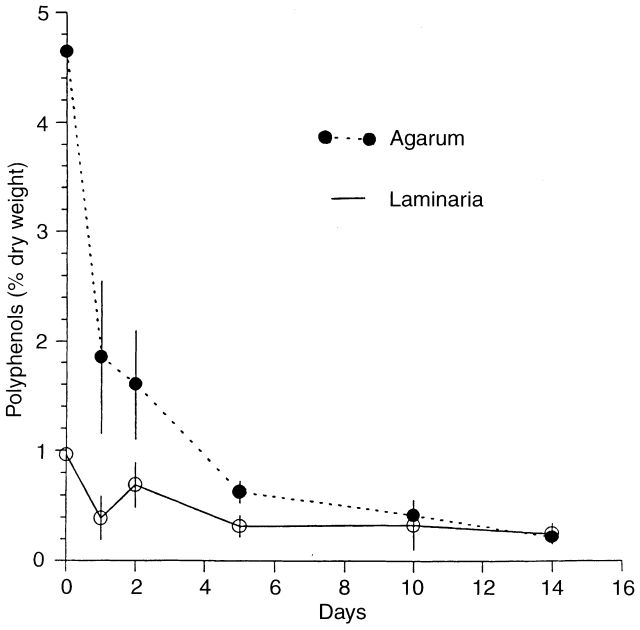

Fig. 4 *Agarum fimbriatum* and *Laminaria groenlandica.* Polyphenolic concentration for particles from two kelp species over 14 d aging period (mean ± SE)

interesting differences. The polychaetes (Fig. 1) grew ~300% faster when fed aged versus fresh particles originating from *Agarum fimbriatum* or *Alaria marginata*, and on the order of 50% faster on aged versus fresh particles originating from *Laminaria groenlandica*. All pairwise comparisons between growth on fresh versus aged particles were significant (*Agarum fimbriatum*, $t = 12.71$, $p < 0.001$; *Alaria marginata*, $t = 7.94$, $p < 0.001$; *L. groenlandica*, $t = 2.52$, $p = 0.019$). In contrast, the direction of the effect of particle age on *Mytilus trossulus* growth (Fig. 2) was dependent on kelp species. Mussels fed *Agarum fimbriatum* particles grew significantly faster on aged material ($t = 2.02$, $p = 0.04$). Mean growth rates were higher on aged versus fresh *Alaria marginata* particles, but the difference was not significant ($t = 1.09$, $p = 0.28$). The pattern was reversed on *L. groenlandica* particles, and the difference was nearly significant ($t = 1.86$, $p = 0.06$). The effect of aging reversed the order of quality amongst kelp species in both suspension feeders; *L. groenlandica* was clearly better than *Agarum fimbriatum* or *Alaria marginata* when fresh particles were compared, but worse than either when aged (Figs. 1, 2).

Significant differences were observed amongst kelp species and between particulate age with respect to polyphenolic concentration. Again, the two-way analysis resulted in a highly significant interaction effect between kelp source and age ($F = 57.16$, $p < 0.001$), and we examined each factor separately. In fresh material, these compounds were significantly lower in *Laminaria groenlandica* than in either of the other two kelp species ($F = 33.64$, $p = 0.001$), but in aged material these differences became trivial (with concentrations at or below the level of resolution of our assay; Fig. 3). In all three pairwise comparisons, the effect of aging particles was to significantly reduce polyphenolic concentration ($p < 0.001$ in all cases). The speed with which these concentrations changed is illustrated in Fig. 4. Within 24 h of grinding, polyphenolic concentration was reduced by more than 50% in both a high and a low phenolic species. Within 3 to 4 d, levels were at or below the levels of resolution of our assay.

The nitrogen content (Fig. 5) of kelp particles also varied with species, but only amongst aged particles (effect of species in fresh material, $F = 0.28$, $p = 0.763$). In all three kelp species, total nitrogen was significantly higher in aged particles (*Agarum fimbriatum*, $t = 3.29$,

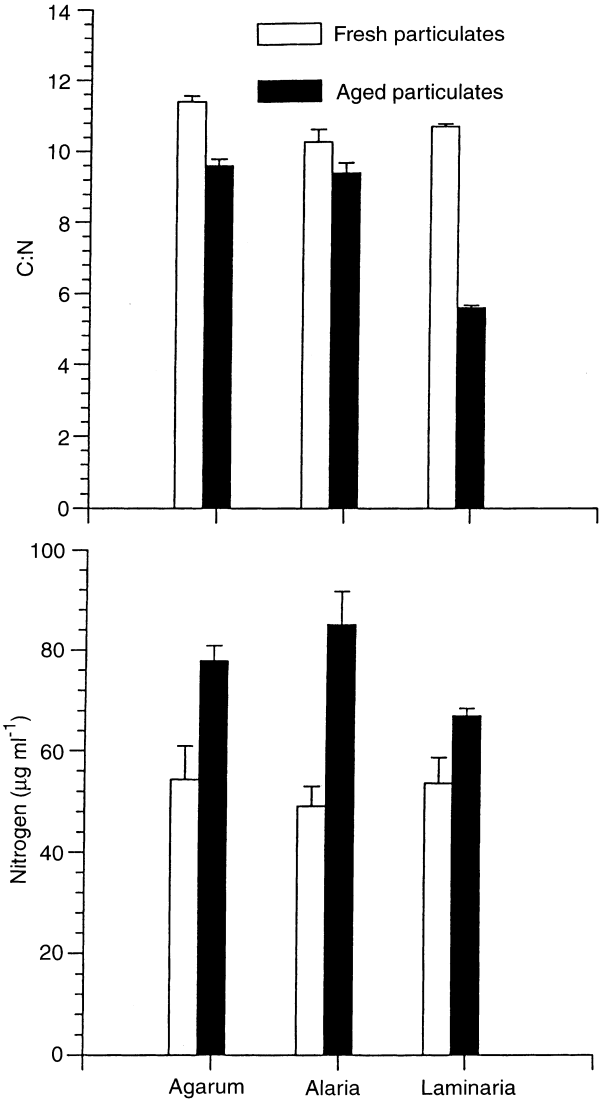

Fig. 5 *Agarum fimbriatum*, *Alaria marginata* and *Laminaria groenlandica*. Carbon:nitrogen ratios and total nitrogen (expressed as mass per unit volume particulate suspension) for fresh and aged particles derived from three kelp species (mean ± SE)

$p = 0.017$; *Alaria marginata*, $t = 4.69$, $p = 0.003$; *Laminaria groenlandica*, $t = 2.52$, $p = 0.046$), with the greatest differences in the two species that also had the largest change in polyphenolic concentration with aging (*Agarum fimbriatum* and *Alaria marginata*).

Discussion

In order that particulate detritus originating from kelps be a significant contributor to nearshore secondary production, both the quantity and quality of material must be high. The quantity of kelp biomass produced along the world's temperate coastlines is considerable. Kelp forests achieve both high standing stock and, at least in many cases where appropriate studies have been performed, high levels of production (Mann 1972, 1973; Duggins 1980 a, b). The dynamics of nearshore marine systems guarantee that some portion of benthic primary production will be exported into deep-water or deposited on shore. Kelp biomass exported to deeper water may constitute a significant resource for deep-water organisms, but is probably of no further consequence to shallow-water organisms. Kelp biomass washed ashore may be consumed by littoral and supralittoral herbivores, or it may return to nearshore waters during periods of high tide or storm conditions as drift (relatively large), particulate, or dissolved material. Drifting kelp is subject to rapid degradation to particulate and dissolved components in the turbulent and abrasive shallow-water environment, but perhaps the most significant source of particles from kelps results from normal growth and in situ senescence. Algae such as *Laminaria groenlandica* erode (as dissolved and particulate material) from the distal portion of a strap-like blade while growing from the meristematic region at the base of the blade (Mann 1973; Duggins 1980 b). Many species, such as *Costaria costata*, senesce by gradual loss of the blade (as particulate material) from distal to proximal portion until nothing is left but a stipe and holdfast. Unfortunately, there are few quantitative studies on the fate of kelp biomass (see Branch and Griffiths 1988 for review of such studies in one ecosystem). Our premise that it remains in the nearshore region – in appropriate forms and density to constitute an important source of nutrition for benthic and pelagic suspension feeders – is based largely on comparisons of secondary production between areas differing greatly in kelp standing-stock (Duggins et al. 1989).

If we know little about the quantitative fate of kelp particles, we know even less about the differences in the qualitative value of such particles among kelp species, or about qualitative changes during the time a detrital particle remains in the water column. That all kelp species are not of comparable quality as a source of food to suspension feeders was suggested by the results of our previously published field experiment (Duggins and Eckman 1994), in which consumers did not experience higher growth rates when exposed to fresh kelp particles. The key to understanding these results involves: (1) among-species differences in particulate quality, (2) temporal changes in particulate quality, and (3) the spatial scales and physical processes involved in particle transport.

Very large differences in particulate quality were observed among the three kelp species used in our feeding experiments. These differences closely parallel the differences in polyphenolic concentration observed in fresh tissues and particles from these species. A large literature indicates that polyphenolics can reduce food quality in marine and terrestrial plants by reducing assimilation efficiency in grazers. Our results indicate similar results in suspension feeders fed particles of different polyphenolic content. Other differences influencing quality may exist among particles derived from different kelp

species, but the importance of polyphenolics is further supported by the relationships among particle age, polyphenolic concentration, and food quality. Particles from the high-polyphenolic kelp *Agarum fimbriatum* exhibited very rapid reduction of polyphenolic concentration over time (≃60% of the polyphenolics were lost within the first 24 h following grinding). Simultaneous with this reduction in polyphenolic concentration was an increase in food quality of particles from both kelp species with initially high polyphenolic levels. We do not know the mechanism behind this reduction, but simple leakage is an obvious possibility. Within 4 d, polyphenolic concentrations were at or below the resolution of our assay, and probably below the level likely to affect food quality.

A second possible connection exists between polyphenolic concentration and particulate food quality. Polyphenolic compounds are thought also to function as antibacterial and antifouling agents (Ragan and Glombitza 1986 and citations therein; Steinberg 1992). Consequently, the loss of polyphenolic compounds may act to enhance the colonization of particles by microflora. The ultimate consequence of this synergism would probably be the enhancement of total nitrogen that accompanies the development of detrital microflora and an increase in food quality. Particles from all three kelp species increased in total nitrogen content over time, with the greatest increase occurring in the two species that exhibited the largest reduction in polyphenolic concentration.

These results give us a framework for interpreting the results of our previous field experiment (Duggins and Eckman 1994), in which the comparison between suspension-feeder growth-rate in stands of artificial kelp and stands of *Agarum fimbriatum* (the dominant understory kelp in the Friday Harbor region) was made in relatively small-scale experimental units (10 to 15 m^2) isolated from natural kelp stands. Fresh particles from this high-phenolic species were not a high-quality food. The small size of these units, coupled with the strong tidal fluxes in the San Juan Archipelago, made it unlikely that particles generated within the "real kelp" experimental units would remain there for any significant length of time (probably only a few hours). Consequently, even though the particles would eventually be aged to a high-quality state, in all likelihood they would have been exported from the experimental unit well before such a transformation could take place. Any enhancement of detrital food concentration in the real treatment (relative to the artificial kelp treatment) would have resulted from an increase in the relatively poor-quality fresh *A. fimbriatum* particles.

In general, understory kelp distribution is patchy due to the patchy nature of the biological and physical disturbances that are so important in determining plant density. For a suspension feeder, the potential advantage of association with kelp stands involves a series of tradeoffs (Eckman and Duggins 1991; Duggins and Eckman 1994) mediated by lower water velocities but substantially higher sedimentation rates within stands. Advantages of association stemming from availability of autochthanous (fresh) kelp particles depend upon the specific type of kelp and its quality as a food source. For low-phenolic species such as *Laminaria groenlandica* or *Costaria costata*, detrital material is of immediate high value as it sloughs from the plant. Association with a high-polyphenolic species such as *Agarum fimbriatum* would not enhance growth by any increase in the availability of autochthanous kelp particles (i.e. fresh and consequently of low quality). However, association with any kelp stand is likely to enhance availability of allochthanous (aged) particles through the stand's effects on rates of sedimentation (Eckman et al. 1989; Eckman and Duggins 1991). Along the west coast of North America, more than 50% of the species in the order Laminariales and virtually all the species of algae in the order Fucales have polyphenolic levels high enough to be of consequence to food quality (Van Alstyne et al. 1997). However, the turbulent, well-mixed nature of most of this coastline means that some particulate material will remain in suspension long enough for even high-polyphenolic species to become a source of high-quality particulate food.

Assessing the trophic importance of kelp-derived particles relative to phytoplankton is beyond the scope of this paper, but several observations seem warranted. The comparison is complicated by the significant effect of phytoplankton concentration on one of our two suspension feeders.

For *Pseudochitinopoma occidentalis*, effects of concentration were insignificant for both *Laminaria groenlandica* particles and phytoplankton. We believe that these worms were fed ad libidum in all treatments, and that the comparable growth rates on fresh *L. groenlandica*, all aged particles, and on phytoplankton are realistic reflections of relative food quality.

For *Mytilus trossulus* fed fresh *Laminaria groenlandica* particles, the effect of concentration was insignificant (and we thus assume mussels were at ad libidum ration levels). However, growth was significantly greater in the 75% phytoplankton treatment, suggesting that the 100% concentration was actually inhibiting growth. Thus, the significantly higher growth rate for *M. trossulus* fed phytoplankton may be an underestimation of real treatment differences. These results are consistent with at least two laboratory studies. Cranford and Grant (1990) found that consumption rates are lower for aged algal particles than for phytoplankton, and Stuart et al. (1982) argued that algal detritus is a poor food because conversion of organic carbon to bacteria is low in these particles. Our results suggest, however, that for some kelp species (with low polyphenolics) microfloral conversion is not necessary for kelp particles to be of food value comparable to phytoplankton. Furthermore, where aging increases food quality, changes over time may have as much to do with the loss of secondary metabolites as with the development of microflora.

In many mid- and high-latitude marine habitats, phytoplankton production is highly seasonal, with winter abundances falling to very low levels. During winter months, many kelps are senescing, storms are taking their toll on kelp biomass, and the production of kelp particles may reach its highest levels. This winter contribution by kelps to food-web dynamics may be of particular importance.

The role of kelp forests in the nearshore marine ecosystem is complex and multifaceted (Duggins 1988). In addition to providing habitat and altering hydrodynamic characteristics, kelp detritus is likely to be a significant source of nutrient input to grazer, deposit feeder, and suspension feeder food-web linkages in nearshore regions where kelp forests are extant. The extent to which this influence is diluted with distance from the source of production remains unknown, but in well-mixed waters, this influence could extend well beyond the margins of the kelp-dominated habitat.

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