EXPERIMENTAL STUDIES OF ALGAL CANOPY INTERACTIONS IN A SEA OTTER-DOMINATED KELP COMMUNITY AT AMCHITKA ISLAND, ALASKA

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ABSTRACT

Studies on the results of competitive interactions between three kelp canopy guilds were conducted in a community in which herbivorous invertebrates have been largely removed from shallow water (approximately 20 m) by sea otters. Small sea urchins observed in the haptera of kelps all disappeared following the canopy removal, suggesting that the canopy itself offers a modest refuge from their predators. Experiments prove that the largest alga, *Alaria fistulosa*, behaves as a fugitive species with respect to *Laminaria* and *Agarum* species in spite of the structural dominance of a floating canopy. Vegetative regeneration may give *Laminaria longipes* an advantage over other *Laminaria* species, *Alaria*, and presumably *Agarum cribrosum* following disturbances in very shallow water (< 5 m). *Laminaria* species suppress *Agarum* growth (and recruitment) in moderate depths (5-20 m) where either *Laminaria* or *Agarum* suppresses growth of red algal turf beneath them, and where both *Laminaria* and *Agarum* must be removed to allow recruitment and growth of *Alaria fistulosa*. Although kelps were observed to depths of 30 m, their lower distribution appears primarily limited by sea urchin grazing.

Few natural communities are so influenced by one population as is the nearshore marine community dominated by the sea otter, *Enhydra lutris* Linn. The nearshore community at Amchitka Island, Alaska, is especially interesting in this regard because for almost 40 yr it has had a sizable sea otter population. This population has been at or near its carrying capacity for at least 20 yr (Kenyon 1969; Estes and Smith 1973), and is thus one of the few localities where the sea otter can be found in a natural balance with the rest of its community. The sea otter exerts its powerful influence in shallow water, where its predation on diverse kinds of invertebrates is remarkably efficient. In addition to drastically reducing populations of motile herbivores (McLean 1962; Ebert 1968; Lowry and Pearse 1973; Estes and Palmisano 1974), the sea otters eat many sessile animals and may release the algae from potential space competition with many potentially competitively important species such as the bivalves *Mytilus edulis*, *Modiolus modiolus*, and *Pododesmus macroschisma*, and the barnacles *Balanus* spp. The algal community at Amchitka Island, then, offers unusual opportunities to evaluate al-

gal-algal interactions in the natural absence of herbivores and animal space competitors. Such interactions might suggest important competitive components of the algal "niches."

The sublittoral association of perennial algae at Amchitka has four separate canopies (Figure 1). *Alaria fistulosa* P. et R. is a conspicuous kelp with long floating fronds that form a canopy on the surface (Kibbe 1915). The thickest *Alaria* canopy is usually found in relatively shallow (< 5 m) water. The second canopy level is composed of the following stipitate *Laminaria* species: *L. groenlandica* Rosenvinge, *L. dentigera* Kjellman, *L. yezoensis* Miyabe, and *L. longipes* Bory. This canopy can be found from the intertidal to depths of approximately 20 m. The third canopy is usually composed of *Agarum cribrosum* Bory with short stripes and large broad fronds lying prostrate on the substratum. This canopy of prostrate kelp occurs between 10 and 20 m. Finally there is a turf composed of numerous species of red algae and occasional clumps of green algae, especially *Codium ritteri* Setch. et Gardn. and *Cladophora* spp. The fact that the canopies tend to occupy nonoverlapping patches in shallow (< 10 m) water suggests that there are competitive interactions between the species comprising the canopies. This paper discusses tests of a series of hypotheses
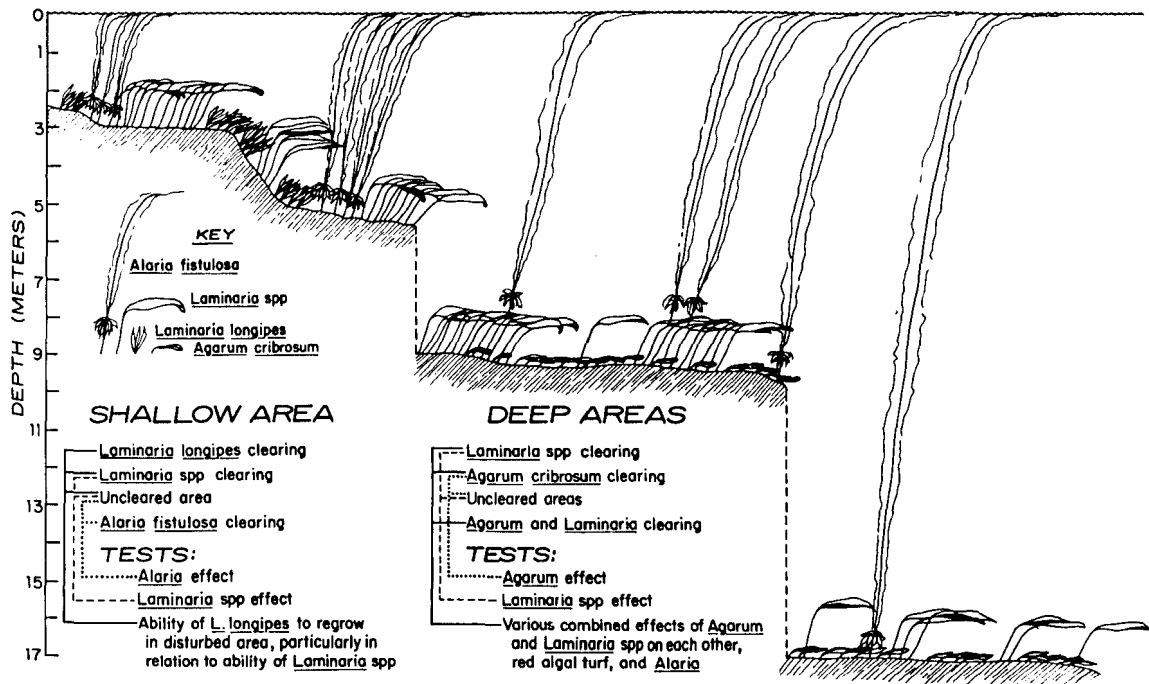
FIGURE 1.—Drawing of the kelp canopies at three different depths. *Laminaria* spp. refers to the large and very similar stipitate *L. groenlandica*, *L. dentigera*, and *L. yezoensis* which seem to occupy broadly overlapping depth profiles but form identical canopies because the stipe lengths and frond sizes are very similar. Diagrams of the experimental design testing hypotheses about the competitive effects between canopies is included for the two manipulated areas.

about the competitive effects these canopies have on each other, the role of physical disturbance in canopy composition, and a gradient of herbivore pressures in deeper waters, where the sea otter foraging becomes less efficient.

METHODS

This research was done in July 1971 and April 1972 in a small bay between the remains of the old Constantine jetty and Kirilof Point on the Bering Sea. A total of 34 dives were made during the study. There were two study sites, a nearshore shallow (< 5 m) area beside an old quarry and a deeper (> 7 m) reef about 150 m offshore. Immediately offshore in the shallow area there is a very heavy summer canopy of *Alaria* mixed with a dense growth of annual brown algae such as *Cymathere triplicata* (P. et R.) J. Ag., *Desmarestia intermedia* P. et R., and numerous species of red algae representing such genera as *Ptilota*, *Hypophyllum*, etc. Offshore from this dense algal band, but still in the shallow area, are distinct patches of *Alaria* with thick canopies floating on

the surface and patches of a very solid secondary *Laminaria* canopy. There are two *Laminaria* growth forms in the more shallow (< 5 m) area: *L. groenlandica*, *L. dentigera*, and *L. yezoensis* are solitary plants with one heavy 50-150 cm stipe per plant; *L. longipes* has thin multiple 20-40 cm stipes from a single rhizomelike holdfast (Markham 1968, 1972). The third prostrate canopy is represented in shallow water by scattered individuals of the heavy brown alga *Thalassiophyllum clathrus* (Gmelin) P. et R. The deeper offshore reef has a scattered and relatively thin (0-20%) canopy of *Alaria* and in the more shallow (7-12 m) levels a very thick canopy cover of *Laminaria* spp. With increasing depth the *Alaria* density decreases and the *Laminaria* is gradually replaced by *Agarum cribrosum* which forms the third prostrate canopy.

The experimental sites were chosen on the basis of distinct patches of the respective canopies to be manipulated and on the ease of shore access and relocation. Pruning shears were used to clear areas by cutting the stipes just above the holdfasts. In every case an immediately adjacent area was monitored as a control.

Methods of estimating percent canopy cover varied. The *Alaria* canopies represent visual estimates. The 100% covers were very thick and in these cases the floating stipes seemed to form an almost impenetrable wall in the water column. A few photographs taken of the *Alaria* canopy in areas where it had less than 100% cover suggest that the visual estimates in these locations were conservative. The other percent cover estimates were made with the aid of 0.25 or 0.16 m² quadrats which, in larger areas, were placed haphazardly, and in restricted experimental areas were placed systematically in such a way that the entire experimental area was sampled. The actual measurements were usually taken planimetrically from photographs as defined earlier (Dayton 1971). There were a number of cases in which visual estimates were used because of camera malfunction, running out of film, etc. I have compared such visual estimates with planimeter measurements and found that they are usually within 5% and always within 10% of each other (Dayton 1971, 1975). The data are presented as means because the actual sample numbers varied (but except where stated, were never fewer than 10); the variance is given as standard error.

RESULTS

Shallow Area

This area is covered with an extremely thick growth of algae and is generally characterized by a conspicuous absence of herbivores (Estes and Palmisano 1974). I was surprised to find sea urchins[2] among the *Laminaria* (especially *L. longipes*) haptera and holdfasts upon removing the canopies for the experiments discussed below. The sea urchins may exist in these sheltered refuges

[2]Opinions are divided whether the Amchitka sea urchin is *Strongylocentrotus drobachiensis* or *S. polyacanthus*.

because the canopy is both very dense and relatively close (25-35 cm) to the substratum, thus seriously reducing the foraging efficiencies of their visual predators. This sea urchin-refuge hypothesis was supported by the observation that the sea urchins remained untouched in both clearings from 3 and 6 July through 8 July, but all were gone on 9 July. I suspect that they were taken by a sea otter that found the cleared patches, as one was observed foraging in the vicinity on the morning of 9 July. However, predation by the common eider, *Somateria mollissima* (Williamson and Emison 1969), and emigration are other possible explanations. At any rate, the small size (< 15 mm) and scarcity of these sea urchins do not seriously affect the contention that the herbivores have largely been eliminated from this area. The elimination of the grazing pressures makes the competition-based hypotheses discussed below more meaningful.

Hypothesis I

The *Alaria fistulosa* canopy excludes *Laminaria* spp. This hypothesis was tested (a) by cutting *Alaria* from several rocks and observing whether *Laminaria* recruited in the absence of *Alaria* and (b) by cutting *Laminaria* and observing potential *Alaria* recruitment. *Alaria* and probably *Laminaria* spp. were fertile at the time of the cutting. Significantly more *Laminaria* recruitment into *Alaria* clearings than into uncleared controls would support the hypothesis, whereas significantly more *Alaria* recruitment into *Laminaria* clearings than into the control would negate the hypothesis and suggest the truth of the converse hypothesis, that *Alaria* behaves as an opportunistic or fugitive species (Dayton 1973, 1975) in the presence of competition with the competitively dominant *Laminaria* spp. The results of such clearings at a depth of 5 m (done 3 and 4 July 1971) are presented in Table 1. The

TABLE 1.—Effects of canopies of *Alaria fistulosa* and *Laminaria* spp. on each other and on the cover of red algae in the nearshore experimental area (25 m²) at 3-5 m depth. The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean. Data presented without variance were visual estimates. Control no. 1 suffered heavy algal loss from winter storms. The mean density of *A. fistulosa* in the April 1972 *Laminaria* removal experiment was 14.7 (± 1.1, SE) in ten 100 cm² quadrats.

Canopy species	Alaria removal		Laminaria removal		Control no. 1		Control no. 2	
	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Alaria fistulosa	[1]75	20.3 ± 20.0	5	100	45	100	10	5
Laminaria spp.	35.7 ± 15.0	39.2 ± 12.1	[1]87.2 ± 7.9	0	[2]100 ± 0	25.3 ± 20.0	100 ± 0	100 ± 0
Red algal turf	40.4 ± 10.7	45.6 ± 13.6	15.3 ± 8.6	45.5 ± 4.6	10.2 ± 5.8	40.2 ± 12.0	5.4 ± 5.3	15.8 ± 7.9

[1]Signifies that the canopy was experimentally removed.
[2]Canopy ripped out during winter storms.

Alaria forming a 75% canopy were removed from a 25 m² area and no significant change was observed in the *Laminaria* or red algal turf canopies by April 1972. But the removal of an 87% cover of *Laminaria* produced dramatic (5-100%) increases in the *Alaria* cover and a significant ($P<0.001$) increase in the red algal turf covers (*t*-test run on data normalized with an arcsine transformation). The 100% *Laminaria* cover in Control no. 1 suffered heavy damage when two large boulders, rolled about by winter storms, reduced *Laminaria* densities and resulted in significant increases in recruitment of *Alaria* and red algal turf covers ($P<0.01$). In addition to the extremely heavy *Alaria* recruitment in the *Laminaria* removal areas, there were also patches of *Rhodymenia palmata* (L.) Greville, *Ptilota* spp., *Desmarestia* spp., *Cymathere triplicata*, *Chaetomorpha melagonium* (Weber et Mohr) Jutz., and *Coilodesme* spp. No significant changes were observed in Control no. 2. To a certain extent these observations could be explained by a very slow growth rate of *Laminaria* spp. But certainly the hypothesis that *Alaria* dominates in competition over *Laminaria* was negated, and these data strongly support the conclusion that despite the expected competitive advantage gained by forming a surface canopy, *Alaria fistulosa* is not a competitive dominant, but a fugitive species colonizing areas released from competition with the dominant *Laminaria* canopy.

Hypothesis II

The rhizoidal growth pattern of *Laminaria longipes* allows an efficient recovery following a disturbance (Markham 1968). The hypothesis suggests that the removal of an *L. longipes* canopy results in the area being succeeded by its own extensive vegetative regrowth, in contrast to the invasion of many individuals of fugitive species seen following the removal of a mixed species canopy of *Laminaria groenlandica*, *L. yezoensis*, and *L. dentigera*. This hypothesis was tested by cutting the stipes near the holdfasts of a 100% cover of *L. longipes* from a 10 m² patch at a depth of 3 m on 7 July 1971. Fifteen ¼ m² quadrats observed after the 100% canopy was removed showed the following mean substratum covers: 57% (± 4.9, SE) *L. longipes* holdfasts, 7% (± 1.8, SE) sponges and compound tunicates, and 22% (± 5.2, SE) coralline algae, mainly *Clathromorphum* spp.

They also showed mean ¼ m² densities of the sea urchin, *Strongylocentrotus* sp., of 17.5 (± 3.8, SE) and the asteroid, *Leptasterias aleutica*, of 1.0 (± 0.3, SE). Spores of the three other *Laminaria* species and of *Alaria* were potentially available from many plants on rocks on three sides of the clearing.

By April 1972, the clearing had been completely recolonized by *L. longipes*, despite the proximity of large plants of the other species. The recovery was so complete that the clearing could only be recognized after a long search located a few "landmarks" (sponges, compound tunicates, and a *Laminaria yezoensis* holdfast with the stipe cut by pruning shears) photographed the previous year. This strongly supports the hypothesis that the rhizoidal growth pattern of *L. longipes* is an effective adaptation for the recovery of its canopy following a disturbance and is in marked contrast to the heavy *Alaria* recruitment following the removal of a nearby *Laminaria* spp. canopy. I was unable to test the obvious hypothesis that this capacity for vegetative growth gives *L. longipes* an advantage over the other *Laminaria* spp. in a disturbed area, but loses a competitive advantage in less disturbed areas because the other *Laminaria* species have a higher, more effective canopy.

Offshore Area

An exploratory dive was made on the deeper offshore reef to investigate the relationship between sea urchin densities and the various algal canopies. Samples were taken from haphazardly placed ¼ m² quadrats. Five samples taken in the 12-15 m range showed means of 44% (± 23.3, SE) cover of *Laminaria* spp. and 62% (± 15.7, SE) cover of *Agarum cribrosum*, and a mean density of 11.2 (± 3.8, SE) sea urchins per ¼ m². In the 15-21 m depth range five samples provided means of 36% (± 13.0, SE) canopy cover of *Laminaria* and 80% (± 4.9, SE) canopy cover of *Agarum* with a mean sea urchin density of 6.4 (± 3.2, SE) per ¼ m². Few identifiable foliose algae were seen below 21 m, but there was a high mean sea urchin density of 30.4 (± 3.7, SE) per ¼ m². In these deeper areas there was almost a complete substratum cover of the encrusting coralline algae *Clathromorphum* spp. and the green alga, *Codium ritteri*. Only four *Alaria* plants were encountered in these 17 samples; all were growing from the top portion of one Laminaria stipe at 11 m.

On 11 and 12 July 1971, a study site was chosen and the data in Figure 2 labelled July 1971 were collected. The differences between these data and those given in the preceding paragraph give an idea of the variation in this area. The inverse relationship between the percent cover of *Laminaria* and *Agarum*, in which the *Laminaria* decreases and the *Agarum* increases with depth and sea urchin density, suggests that in shallow water *Laminaria* competition suppresses the growth of *Agarum*, but that *Agarum*, which has been demonstrated to be highly distasteful to *Strongylocentrotus drobachiensis* (Vadas 1968), is

more successful in the presence of a moderate density of grazers. Finally, *Agarum* itself may also have an important competitive effect against *Alaria* and the foliose red algal turf. Grazing pressure and limiting light conditions probably cause the severe reduction of foliose algae in deeper water. These data demonstrating high densities of sea urchins at depths below 20 m agree with the observations of Barr (1971), Estes and Smith (1973), and Estes and Palmisano (1974). This suggests that sea otters at Amchitka do not forage effectively below 18-20 m.

That the experimental area could not be continuously monitored meant that it was not possible to manipulate the sea urchin density, but competitive effects of the algae at this depth were readily testable by selective removal of algal species.

Hypothesis III

The presence of *Laminaria* spp. has no effect on other algae. This hypothesis was tested by removing a 2-m wide strip of *Laminaria* from the area where the data in Figure 2A were collected. The hypothesis was negated as both *Agarum* and the foliose red algae canopies significantly increased their covers (Figure 2B, C). The spectacular increase in the cover of the *Agarum* canopy certainly resulted partially from growth of the fronds; however, samples taken in April 1971 and repeated in July 1972 at approximately the same spots along the experimental *Laminaria* removal strip, showed that the mean *Agarum* density increased significantly from 4.1 ($\pm$ 0.6, SE; ten ¼ m² samples) plants to 15.6 plants per ¼ m² (was calculated from ten 1/16 m² samples with a mean of 3.9; $\pm$ 0.4 SE). The increase in canopy cover of the red algal turf was less spectacular, but a one-tailed Wilcoxon matched-pairs signed-ranks test of mean percent canopy cover at all depths considered shows a significant ($P<0.005$) general increase after the *Laminaria* were removed, this despite the fact that April may be early in the season for red algal growth. Thus the *Laminaria* canopy in the presence of an *Agarum* canopy has an important effect on other algal species.

Hypothesis IV

The *Agarum cribrosum* canopy alone has no effect on the other algae. This hypothesis was tested by clearing 45-85% covers of *Agarum* from 4 m²
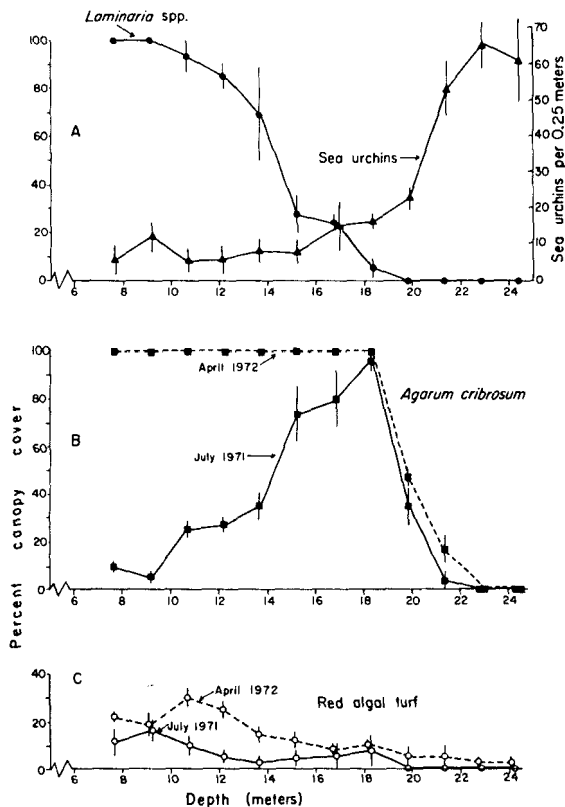
FIGURE 2.—Mean sea urchin densities and percent covers of *Laminaria*, *Agarum*, and red algal turf canopies at increasing depths before (July 1971) and after (April 1972) the *Laminaria* canopy was removed. Figure 2A contrasts the decreasing *Laminaria* cover with increasing sea urchin density in July 1971. Note that the *Agarum* canopy cover at that time shown in Figure 2B is nearly complete only at those depths at which there is reduced *Laminaria* coverage and relatively low sea urchin density. After removal of *Laminaria*, the *Agarum* canopy increased dramatically at the shallower depths. The increase of red algal cover after *Laminaria* removal is shown in Figure 2C. Variance is presented as the 95% confidence interval around the mean.

plots at 9.1- and 16.8-m depths in July 1971. In both cases a 100% canopy of *Laminaria* persisted throughout the experiment. A slight recovery of the *Agarum* population was observed the following April (Table 2), but no significant differences were observed in the numbers or percent cover of the other species. Thus there is, at present, no reason to negate the hypothesis.

Hypothesis V

The *Agarum cribrosum* canopy in the absence of the *Laminaria* canopy has an important effect on the other species of algae. This hypothesis was tested by removing both *Agarum* and *Laminaria* canopies from 4 m² plots at 9.1- and 16.8-m depths. These clearings were then compared to those in the adjacent *Laminaria*-only removal experiments at the same depths (Figure 2C). A strict interpretation of this comparison suggests that either a *Laminaria* or *Agarum* canopy or both is sufficient to prevent an increase of red algal turf cover because there is, at those two particular depths, no significant increase of red algal turf in either the *Laminaria*-only or *Agarum*-only removal experiments (Figure 2C, Table 2). This interpretation is equivocal, however, as Hypothesis III demonstrated a slight but significant *Laminaria* effect on the red algal turf. There is no equivocation regarding the effect of the combined *Laminaria* and *Agarum* canopies on the red algal turf which increased from 7 to 49% at 9.1 m and 1 to 38% at 16.8 m (Table 2). These are much more dramatic increases than were observed in the *Laminaria*-only removal areas and convincingly argue for a strong *Agarum* effect in the absence of *Laminaria*. Some of the red algae in this experiment were *Ptilota asplenoides* (Esper) C. Ag., *Laingia aleutica* Wynne, *Hypophyllum*

ruprechtianum Zinova, *Constantinea rosamarina* (Gmelin) P. et R., *Pantoneura juergensii* (J. Ag.) Kylin, *Cirrulicarpus gmelini* (Grunow) Tokida et Masaki, *Turnerella* sp., *Callophyllis flabellulata* Harvey, and *Nienburgia prolifera* Wynne.

The most impressive effect of the *Agarum* canopy in the absence of *Laminaria* was its inhibition of *Alaria* recruitment. In each of the two quadrats from which both *Laminaria* and *Agarum* were removed, the *Alaria* cover, consisting of a heavy recruitment of juvenile plants, increased from 0 to 100% canopy cover (Table 2). The *Alaria* response was particularly impressive because the dense *Alaria* recruitment completely filled, but was perfectly contained within, the *Agarum*-and-*Laminaria* removal patches. The mean density increased from 0 to 22.8 *Alaria* plants per 1/16 m² ($\pm$ 3.5, SE). In contrast to this result in the *Agarum*-and-*Laminaria* removal area, there was no *Alaria* recruitment in the rather extensive area from which *Laminaria* alone was removed (Figure 2). This result also contrasts sharply with those of the shallow *Laminaria* removal experiments (Table 1), in which no *Agarum* canopy level existed. An adjacent control was monitored for each experimental clearing; no changes were observed in any of the controls.

The above comparisons demonstrate that both the secondary *Laminaria* canopy and the tertiary *Agarum* canopy individually can significantly reduce the recruitment of *Alaria*, the species which forms the primary surface canopy. Further evidence of the intense competition in the deeper area where both understory canopies exist is provided by the observation that, of 100 *Alaria* plants surveyed, 79 were utilizing secondary substrata with their holdfasts attached high on *Laminaria* stipes (Figure 1).

TABLE 2.—Effects of *Agarum cribrosum* and combined *Agarum-Laminaria* spp. canopies on each other, red algal turf, and *Alaria fistulosa* at 9.1-m and 16.8-m depths in the offshore study site. Each experimental clearing area was 4 m². The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean; data presented without variance are visual estimates.

| Canopy species | Depth: 9.1 m | | | | Depth: 16.8 m | | | |
| | Agarum (only) removal | | Agarum and Laminaria removal | | Agarum (only) removal | | Agarum and Laminaria removal | |
	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Laminaria	100 ± 0	100 ± 0	¹100 ± 0	0	100 ± 0	100 ± 0	¹100 ± 0	0
Agarum	¹65.3 ± 23.4	11.5 ± 10.2	¹45.5 ± 16.1	25.8 ± 11.9	¹85.2 ± 33.4	17.5 ± 7.1	¹77.4 ± 12.7	11.5 ± 4.0
Red algal turf	11.5 ± 12.9	8.4 ± 10.7	7.0 ± 4.9	49.2 ± 14.0	2.1 ± 5.6	0	1.2 ± 4.0	37.5 ± 10.2
Alaria	0	0	0	100 ± 0	0	0	0	100 ± 0

¹Signifies that the canopy was experimentally removed.

DISCUSSION

The pattern emerging from these and other (McLean 1962; Lowry and Pearse 1973; Estes and Palmisano 1974) studies of sea otter-dominated communities is that by consuming the populations of invertebrate herbivores, the sea otter has an extremely important role in maintaining the structure of shallow algal communities. In this study, high densities of sea urchins are found below 18-20 m, suggesting that this depth is the lower limit of effective sea otter foraging in this area. It is interesting to note that this depth is much more shallow than the 30-fathom profile speculated by Kenyon (1969). In addition, this seems to be a much more shallow limit to efficient foraging than is exhibited by the California population of sea otters, as I have seen evidence of their foraging to at least 30 m in the Carmel Bay region.

Strong competitive interactions between species of benthic algae appear well expressed in the shallow nearshore waters of the Aleutian Islands which have sea otters. The shallower (3-5 m) waters, subject to severe storm disturbance, are functionally dominated by *Laminaria* species. When the larger *Laminaria* spp. (*L. groenlandica*, *L. dentigera*, and *L. yezoensis*) are removed, either experimentally or by natural storm disturbance, their space is quickly utilized by *Alaria fistulosa*. In contrast, the rhizomelike holdfast with multiple meristems of *L. longipes* appears to be an effective adaptation to disturbance, as it allowed quick regrowth of stipes and fronds after their experimental removal. In deeper water (12-20 m), where there are many sea urchins, *Agarum cribrosum* is one of the dominant algal species. *Agarum*, however, loses in competition for light to solid canopies of *Laminaria* spp., which have erect stipes supporting their fronds above the nearly prostrate *Agarum*. When freed from *Laminaria* competition, *Agarum* significantly increases its cover and abundance. When both *Laminaria* and *Agarum* are removed, there is a bloom of red algal turf and of *Alaria fistulosa*. These tests of competition-based hypotheses are probably valid despite the various depth-related changes in the physical environment because each was compared to immediately adjacent controls.

It is interesting to note that despite having potentially long-lived individuals and the competitively superior adaptation of a floating canopy, *Alaria fistulosa* behaves as a fugitive species with its densest distribution in the highly disturbed immediate offshore area, occurring farther offshore only in areas where two understory canopy levels are removed or by growing on *Laminaria* stipes. This is surprising because quite the opposite situation seems to exist in the southern California kelp community, where *Macrocystis pyrifera* forms a heavy surface canopy which may inhibit the growth of the understory species (North and Shaeffer 1964; Dayton unpubl. data). Although *Alaria* was observed in depths of over 25 m, its lower distribution appears to be restricted primarily by sea urchin grazing.

Other research (Estes and Palmisano 1974; Palmisano in prep.) contrasts the nearshore and intertidal communities of Amchitka with nearby otter-free islands and convincingly demonstrates the powerful role the sea otters have in structuring the nearshore community. This paper has experimentally demonstrated competitive trends between different canopy guilds in an algal community which contains an unusually high number (four) of *Laminaria* species which have semirigid stipes. It is tempting to speculate an evolutionary hypothesis in which the sea otters reduce the herbivore pressure and thus allow a competitive differentiation of niches of these large stipitate kelps. Such hypothetical evolutionary thought has the common and serious flaw of ignoring the roles of extinct species, many of which may have left large and important "vacant niches" (such as those left by the mammal extinctions of the late Pleistocene discussed in Martin and Wright 1967). This problem is particularly acute in the Bering Sea, as Steller in 1751 (reference in Gard et al. 1972) reported the giant sea cow, *Hydrodamalis gigas* (Zimmermann 1780), eating algae in the nearshore and tidal beaches of the Komandorskiye Islands. The large populations reported by Steller and various Russian and German sailors of this huge (ca. 10 tons, Scheffer 1973) kelp-eating (Stejneger 1936) sirenian surely had important consequences to the kelp populations that weaken any present day speculation of the evolutionary consequences of kelp competition. It may be reasonable, however, to pose the hypothesis that by consuming invertebrate herbivores, particularly sea urchins, the sea otter was indirectly responsible for the high productivity of large algae necessary to maintain the sea cow populations. Such an hypothesis is supported by the overlap of the otter

and sea cow populations in the Pleistocene (Jones 1967; Kenyon 1969; and Gard et al. 1972). This relationship is nicely diagrammed in Scheffer's (1973) touching story of the last day of the sea cow.

ACKNOWLEDGMENTS

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