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**EFFECTS OF THE INVASIVE SEAWEED  
*SARGASSUM MUTICUM* ON NATIVE MARINE  
COMMUNITIES IN NORTHERN  
PUGET SOUND, WASHINGTON**

**Karen Giver**

**May 1999**

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EFFECTS OF THE INVASIVE SEAWEED *SARGASSUM MUTICUM*  
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by

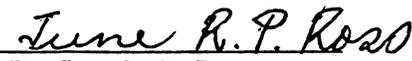
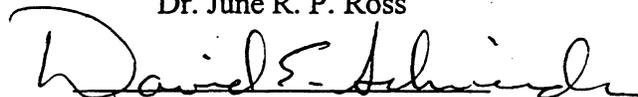
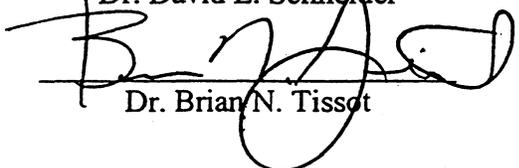
Karen J. Giver

Accepted in Partial Completion  
of the Requirements for the Degree  
Master of Science



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EFFECTS OF THE INVASIVE SEAWEED *SARGASSUM MUTICUM*  
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IN NORTHERN PUGET SOUND, WASHINGTON

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A Thesis  
Presented to  
The Faculty of  
Western Washington University

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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science

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by  
Karen J. Giver  
May 1999



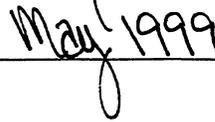
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**EFFECTS OF THE INVASIVE SEAWEED *SARGASSUM MUTICUM*  
ON NATIVE MARINE COMMUNITIES  
IN NORTHERN PUGET SOUND, WASHINGTON**

by Karen J. Giver

**ABSTRACT.** The epibiont community associated with *Sargassum muticum* in northern Puget Sound (San Juan Islands) was examined from May to September, 1997. Abundance and species richness of epibiont communities were determined as well as the relationships between faunal abundance and plant size, particulate load, and polyphenolic concentration of *S. muticum*. One hundred and seven epifaunal taxa were identified from *S. muticum*. Faunal communities on *S. muticum* were compared with those on *Laminaria saccharina*, a native alga displaced by *S. muticum*. *S. muticum* is able to support a more abundant and species rich community than the native alga *L. saccharina* (mean of 20 species/plant compared to 10 species/plant on *L. saccharina*) because of its high degree of morphological complexity. Only two species never occurred on *S. muticum* that were common on *L. saccharina* whereas 15 species were common on *S. muticum* but never found on *L. saccharina*. Abundance of fauna increased as *S. muticum* biomass increased through time. No relationship was found between polyphenolic concentration (1 – 2% dry weight) and herbivore abundance. The particulate load on *S. muticum* was heavy and consisted primarily of diatoms. Epibiont diversity and abundance increase in areas invaded by *S. muticum* because of the increased habitat, productivity, and complexity that *S. muticum* provides. For this reason, elimination of *S. muticum* is not recommended based on the impact *S. muticum* has on epifauna. *S. muticum* may affect water movement, light penetration, sediment accumulation, and anoxia at night. Further research is needed before management decisions can be made regarding *S. muticum*.



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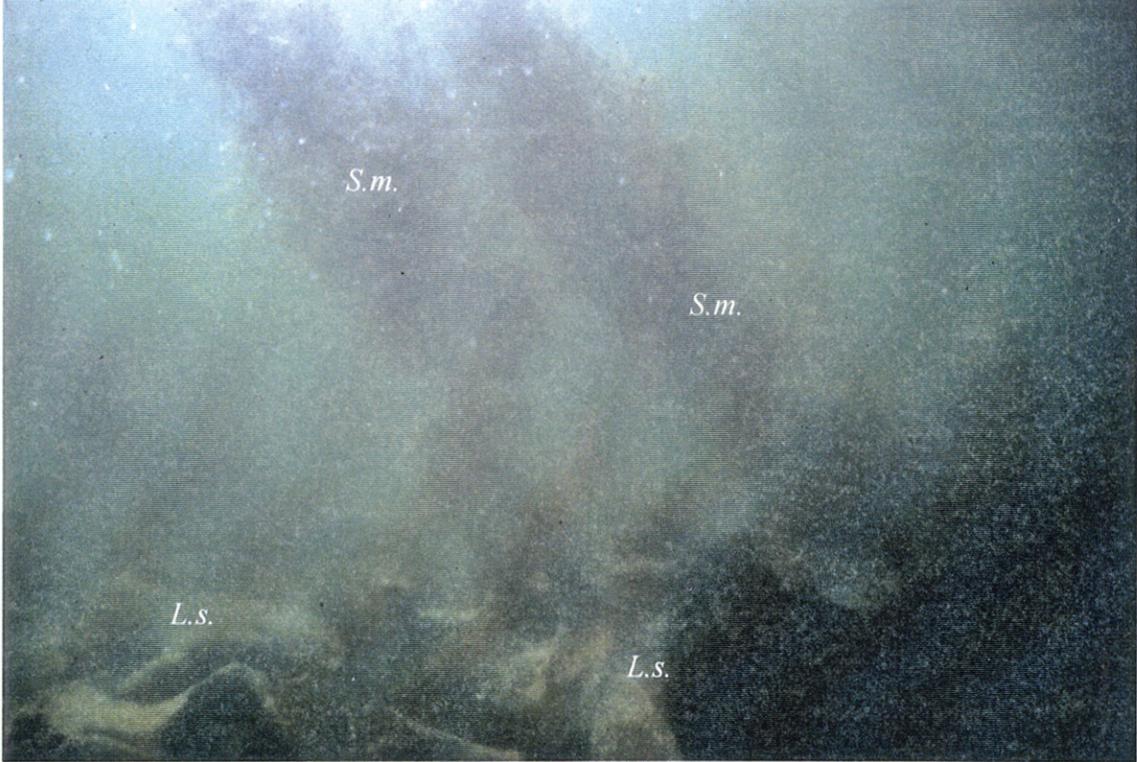
## INTRODUCTION

The lower intertidal to subtidal alga *Sargassum muticum* (Yendo) Fensholt 1955 (Phylum Phaeophyta, Order Fucales) was introduced to the West coast of North America with Japanese oyster spat in the 1940s (Abbott and Hollenberg, 1992: 275). Since then it has established itself as a persistent member of coastal communities from British Columbia to Mexico, competing for space with other benthic macroalgae such as: *Laminaria* spp., *Cystoseira* spp., *Scytosiphon lomentaria*, *Gracilaria verrucosa*, and *Macrocystis integrifolia* (Ribera and Boudouresque, 1995). In Puget Sound, *S. muticum* is said to out-compete and replace *Zostera marina* (Mumford, 1990: 5-9) and *Nereocystis luetkeana* (Thom and Hallum, 1990). *S. muticum* replaced *Macrocystis pyrifera* near Catalina Island (Ambrose and Nelson, 1982) and excluded *Neorhodomela larix* and *Lithothrix aspergillum* in British Columbia (DeWreede and Vandermeulen, 1988). Large, dense stands of *S. muticum* are reported from Great Britain (Critchley *et al.*, 1986; Farnham *et al.*, 1981).

*S. muticum* is documented to thrive in several habitats. Critchley (1983) reports its presence on rocky shores, mud flats, attached to man-made structures, in sand and small cobble, and free floating at the surface. *S. muticum* grows in protected to moderately exposed areas and has low tolerance for wave stress (Viejo *et al.*, 1995).

A single *S. muticum* plant can reach up to three meters in length with numerous thickly branched axes, forming a veritable underwater tree (Figure 1). The three-dimensional structure is due to the numerous air bladders along each axis that maintain the plant erect resulting in a streamlined, vertically fusiform shape in the





**Figure 1.** Underwater seascape showing two *Sargassum muticum* (*S.m.*) plants in the water column. The understory alga *Laminaria saccharina* (*L.s.*) covers the substrate. The *S. muticum* plants are approximately 2 m in length.



water column. Exposure determines the shape of individual *S. muticum* plants (DeWreede, 1978). Plants in areas with the most exposure to waves and current tend to be shorter and bushier (more lateral branches) than plants in more protected areas (Viejo *et al.*, 1995). Also, irradiance level influences growth of secondary and tertiary laterals (Lewey and Gorham, 1984) thus affecting the bushiness of individual plants. Age also affects plant shape. A second or third year plant has more primary laterals than a first year plant (Critchley *et al.*, 1986). Maximum *S. muticum* length varies widely with region due to differences in irradiance and temperature patterns (Critchley *et al.*, 1986; Farnham *et al.*, 1981; DeWreede, 1978; Ambrose and Nelson, 1982). In the native habitat of Japan, *S. muticum* reaches a maximum size of just over 1 m (Critchley, 1983). Plants attain a length of up to 6 m in Europe (Critchley, 1983), 4 m in California (Ambrose and Nelson, 1982) and 2 m in British Columbia (DeWreede, 1978).

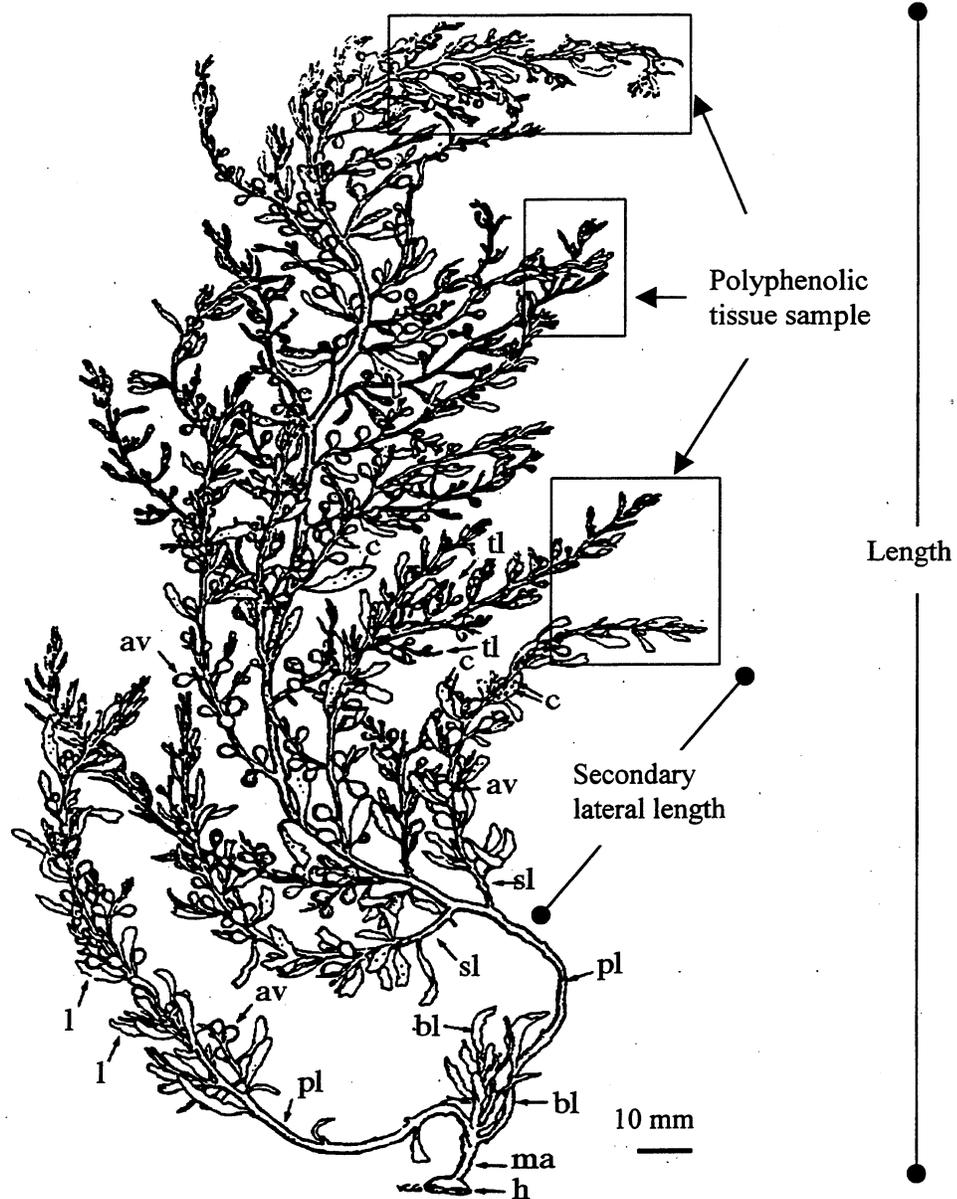
*S. muticum* is a perennial alga that dies back to the holdfast and basal leaves each year and over winters in that state. In Puget Sound, *S. muticum* grows from approximately May to September. Plants grow very rapidly in spring reaching maximum size in summer and then deteriorate in the fall. When *S. muticum* becomes reproductive, growth slows, reproductive structures are cast off, and annual leaves and air vesicles are lost (Norton, 1981; Farnham *et al.*, 1981). During the reproductive period, energy is transferred from growth to reproductive output and plants are less able to deal with herbivore pressure.

The large upright structure of *S. muticum* is likely to affect water flow, light penetration, and space available to other algae. These effects are likely to become

more pronounced if the abundance of *S. muticum* increases (Ambrose and Nelson, 1982). If *S. muticum* has negative impacts on benthic communities, management of the species will be difficult because all prior attempts to eradicate *S. muticum* in Great Britain have failed (Critchley *et al.*, 1986). However, annual removal of *S. muticum* could reduce effects of shading and reduced water movement on native algae.

Although previous studies have focused on its negative impacts (Ribera and Boudouresque, 1995; Mumford, 1990: 5-9; Thom and Hallum, 1990; Ambrose and Nelson, 1982; DeWreede and Vandermeulen, 1988; Critchley *et al.*, 1986; Farnham *et al.*, 1981) *S. muticum* may have a positive influence by providing habitat for members of the coastal community. *S. muticum* exhibits a variety of structural forms within a single plant (Figure 2): a felty, fibrous holdfast, cylindrical and moderately branched axes, mature leaflets that are flattened and relatively narrow, basal leaves that are large and obovate, and air vesicles (Scagel, 1972). These features provide a structurally complex habitat for epibionts. Edgar (1983a) found that algae with variation in the width of axes and branches typically support diverse faunal communities. The large three-dimensional structure of this alga may also provide protection from predators for larval and juvenile fish and invertebrates. *S. muticum* supports an extensive community of micro- and macro-fauna (Norton and Benson, 1983) and may serve as a rich food source, a nursery, and a refuge for members of the surrounding community.

In further support of the idea that *S. muticum* may not be negatively impacting native communities, Viejo (1997) found that a 50% increase in *S. muticum* cover on the coast of Spain caused a significant decline in only one alga, the leathery alga



**Figure 2.** *Sargassum muticum* plant with processing procedures indicated. Length was measured from the base of the holdfast to the distal tip of the longest primary lateral branch. Secondary length was measured as the length of the longest secondary lateral branch. The number of primary lateral branches was determined. Tissue samples were combined from distal tips of secondary lateral and tertiary lateral branches, as indicated by the boxes, to equal 1.5 g from each plant. The morphology of a first year plant is taken from Critchley (1983): holdfast (h); main axis (ma); basal leaf (bl); primary lateral branch (pl); secondary lateral branch (sl); air vesicle (av); cryptostomata (c); tertiary lateral branch (tl); leaf (l).

*Bifurcaria bifurcata*. Also, removal of *S. muticum* from sites on Catalina Island previously occupied by *M. pyrifera* did not always lead to the re-establishment of *M. pyrifera* (Ambrose and Nelson, 1982). These findings suggest that *S. muticum* may be utilizing an unoccupied niche (Viejo, 1997; Critchley *et al.*, 1986; Farnham *et al.*, 1981). This may be the case in northern Puget Sound where *S. muticum* seems to occur only at relatively low densities compared to elsewhere; 57 per square meter at Catalina Island (Ambrose and Nelson, 1982) and 18 per square meter in Great Britain (Critchley *et al.*, 1986).

When considering algae as habitat the impact of polyphenolics compounds must be considered. Polyphenolics are plant secondary metabolites that may deter settlement and grazing on the tissues where they are sequestered. Both the diversity and abundance of associated organisms may be related to secondary metabolite concentrations in algae (Duffy and Hay, 1990), and *Sargassum* species are known to produce tannins (Sieberth and Conover, 1965). Hay and Steinberg (1992: 371-413) found a range of 0 to 18% dry weight was common for furoid and laminiaran algae, with more than 50% of the algae surveyed containing less than 2% polyphenolics by dry weight and an overall mean of 1.3%. The role of polyphenolics in preventing fouling and herbivory is controversial. Many authors point out that polyphenolics do not deter all herbivores or completely prevent settlement on algae (Duffy and Hay, 1990; Hay and Steinberg, 1992: 371-413; Steinberg and Van Altena, 1992). Some invertebrates even select algae that produce polyphenolics over those that do not (Hay and Steinberg, 1992: 371-413). Polyphenolics are most effective in deterring

herbivores such as fish and urchins and they stimulate feeding or have no effect on mesograzers such as amphipods, polychaetes, and isopods (Hay and Steinberg, 1992: 371-413). Because of the contradictory evidence in the literature, the effect of polyphenolics on epibionts is of interest to ecologists.

*S. muticum* is ideal for investigation into the relationship between polyphenolic concentration and epibionts because of the numerous species that live in close association with the alga (Norton and Benson, 1983; Withers *et al.*, 1975; Gray, 1978) and the suggested seasonal variability in polyphenolic production (Gorham and Lewey, 1984). This research investigates if natural polyphenolic concentrations in *S. muticum* affect the abundance and composition of the epibiont community.

*S. muticum* is of particular concern to environmental managers because it has particularly effective dispersal strategies (Kendrick and Walker, 1995), enabling it to take quick advantage of available substrate (DeWreede, 1983; DeWreede and Vandermeulen, 1988). Given this advantage, one important question is, how does the presence of *S. muticum* affect the ecology of local coastal communities? If *S. muticum* has a negative impact on the diversity of the benthic community as has been suggested (Ribera and Bouderesque, 1995), the loss of species may go unnoticed due to lack of baseline information on the community which is critical to any management plan (Winston, 1992: 156-158). Accordingly, this study focuses on: 1) establishing baseline information useful when making decisions about control of this invasive alga by characterizing the animal communities utilizing *S. muticum* as a habitat; 2) comparing the composition of these epibiont communities with those on the native alga *Laminaria saccharina*, and 3) briefly investigating *S. muticum* growth,

particulate load, and polyphenolic content, all of which may impact epibiont communities.

## METHODS

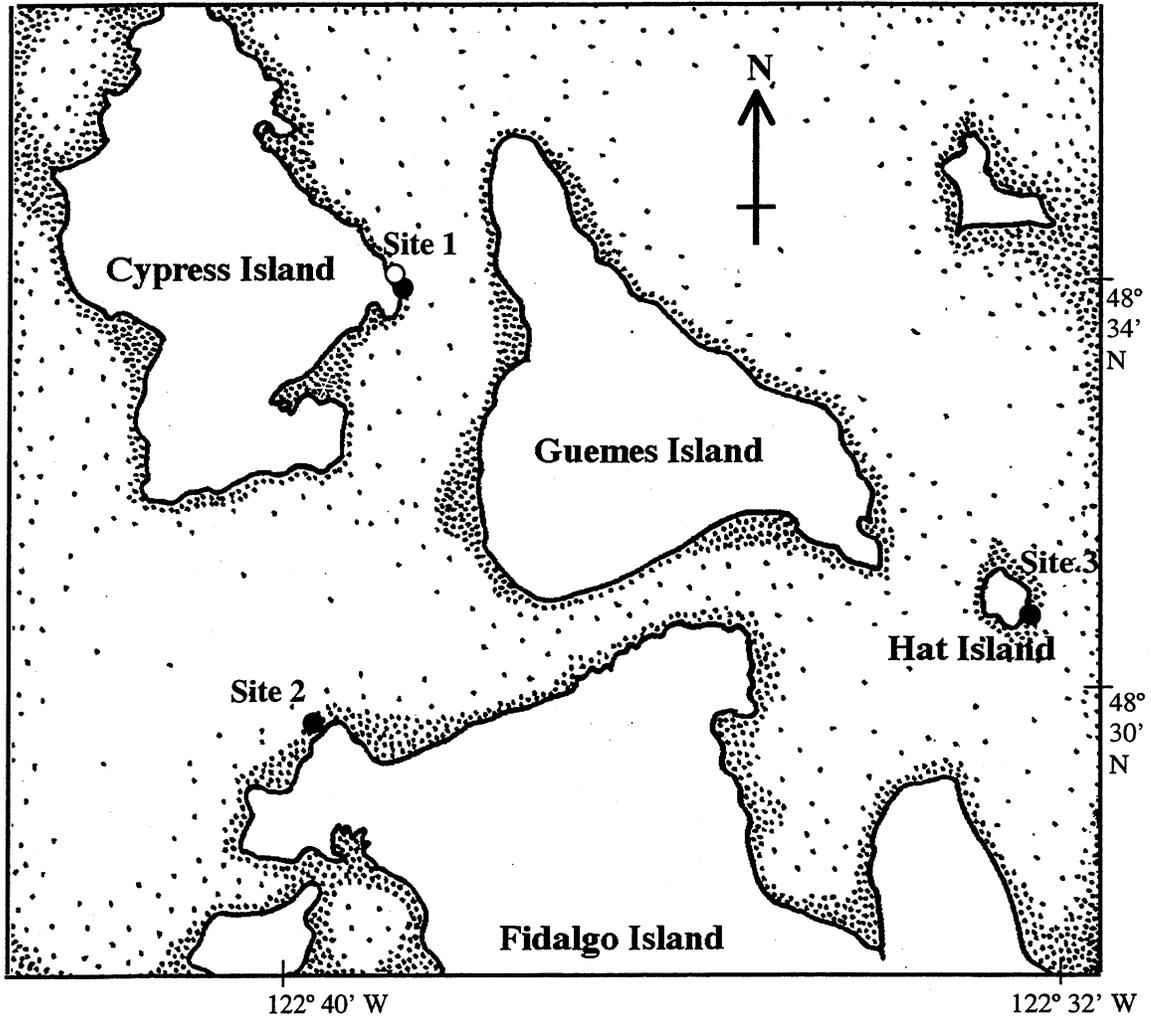
### Study Sites

Three nearshore subtidal sites in north Puget Sound (Figure 3) were chosen based on the abundance of *Sargassum muticum* and boat accessibility to the site. The depth range for *S. muticum* at all sites was approximately 2 to 6 m below MLLW. Maximum currents at sites were estimated for each month using Nautical Software's Currents program data for each site.

Site 1 was located on the east side of the north bay at Cypress Head (48° 34.163' N, 122° 40.236' W; Table 1). The area surrounding *S. muticum* was dominated by *Laminaria saccharina*, a *Nereocystis luetkeana* bed bordered the site to the north, and foliose and highly branched algae, which were found just above the *S. muticum*. Sampling occurred approximately 5 m offshore.

Site 2 was located at Shannon Point Marine Center beach (SPMC) on Guemes Channel (48° 30.583' N, 122° 40.977' W; Table 1). This site was also dominated by *L. saccharina* as well as harboring a wide variety of red algal species. Sampling occurred approximately 10 m offshore, east of the beacon.

Site 3 was on the east side of Hat Island (48° 31.439' N, 122° 32.582' W), at the mouth of Padilla Bay National Estuarine Research Reserve. The island rises steeply from the mud bottom resulting in an abrupt rock-mud interface and narrow intertidal zone (Table 1). *S. muticum* formed a narrow band (< 2 m) at the interface. Abundant foliose algae such as *Ulva* spp. dominated the area just above the *S. muticum* band. Below the *S. muticum* band, there was an approximately 3 m wide area of bare mud before the eelgrass (*Zostera marina*) beds began. Plants were



**Figure 3.** Study sites in the San Juan Islands, North Puget Sound, Washington. Solid circles indicate the locations of the three main study sites: Cypress Island (Site 1), Shannon Point Marine Center (SPMC, Site 2), and Hat Island (Site 3). The open circle indicates the location of the site of the Cypress West collection in August.

**Table 1.** Location, substrate, and dominant flora at study sites in northern Puget Sound during 1997 (Current data from Nautical Software).

Site Number	Location and Coordinates	Substrate	Maximum Current	Dominant Flora
Site 1	Cypress Island, North bay at Cypress Head, East side 48° 34.163' N 122° 40.236' W	Variable sized cobble and rock, interspersed large grain sand and mud	2.1 m/s	<i>Laminaria saccharina</i> , <i>Nereocystis luetkeana</i> bed nearby
Cypress West	Cypress Island 48° 34.163' N 122° 40.236' W North bay at Cypress Head, West side	Variable sized cobble and rock, interspersed large grain sand and mud	2.1 m/s ?	<i>Laminaria saccharina</i> , small <i>Z. marina</i> bed nearby
Site 2	Shannon Point Marine Center 48° 30.583' N 122° 40.977' W	Large rock and cobble with interspersed sand and mud	1.8 m/s	<i>L. saccharina</i> and other foliose and branched macroalgae, small <i>Zostera marina</i> beds nearby
Site 3	Hat Island 48° 31.439' N 122° 32.582' W	Interface of solid rock and large rock with mud	0.9 m/s	<i>L. saccharina</i> , large <i>Z. marina</i> bed nearby

collected approximately 1.5 m offshore.

An additional collection occurred near Site 1 in August. Plants were sampled from the west side of the north bay at Cypress Head (referred to as Cypress West, Figure 3) on the same date as plants collected from the east side of the bay (Table 2). Samples were taken from this area because the *S. muticum* population on the east side of the bay had dramatically decreased and the few plants that remained were severely damaged. Most of the plants on the east side consisted of little more than holdfasts and thus did not represent an adequate comparison to plants from the other two study sites in August. Plant condition was documented for *S. muticum* on both sides of the bay. The Cypress West site was more protected from currents and supported an extensive population of *S. muticum* that, in August 1997, was practically a monoculture of this species. The plants were large, close together, and tangled into a dense mass. *L. saccharina* was found above and below the *S. muticum* band. The site was found by swimming around the small bay at normal sampling depth. The currents to the north of Site 1 are very strong because the area is located on the leading edge of the peninsula that forms Cypress Head. However, the west side of the bay (Cypress West) experiences weaker currents because it is on the more distant and protected side of the bay. Thus currents are likely to be much lower at Cypress West than at Site 1.

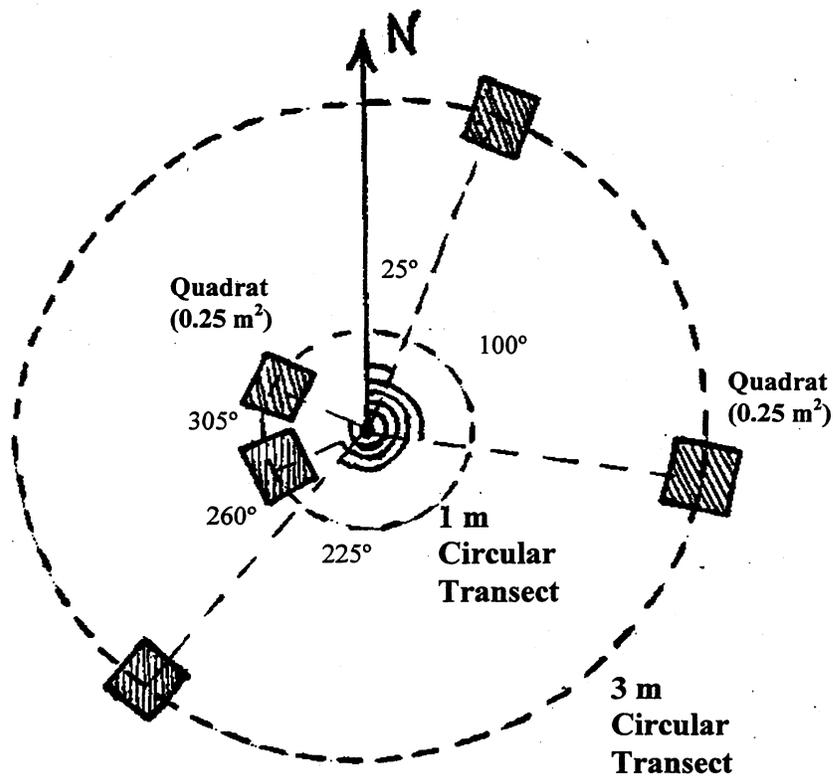
**Table 2.** The number of *Sargassum muticum* (*S.m.*) and *Laminaria saccharina* (*L.s.*) plants collected at each site each month of 1997. Dates shown are the actual collection dates in each month.

	May		June		July		August		September		Total	
Dates:	5/22 - 5/26		6/17 - 6/18		7/14 - 7/17		8/8 - 8/12		9/9 - 9/10			
Study Site	<i>S.m.</i>	<i>L.s.</i>										
Site 1	3		3		3		3	3	3	3	15	6
Site 2	3		3		3		3	3	3	3	15	6
Site 3	3		3		3		3	3	3	3	15	6
Site 3 (evening)					3						3	0
Cypress West							3	3			3	3
<b>Total</b>	12	0	9	0	12	0	12	12	9	9	51	21

## Field Surveys

Algal species at the three main sites were surveyed during July 24 to 28, 1997 at high slack tide using SCUBA. A diver, holding a line marked in one meter intervals, was positioned next to a haphazardly selected *S. muticum*. The line was used to define the circular transect system used to survey the subtidal algal communities (Figure 4). Surveys were taken of five 0.25 m<sup>2</sup> quadrats at 1 and 3 m distances from the selected *S. muticum* plant (Figure 4). The positions of the quadrats were selected as compass bearings using a random numbers table. The survey design was conducted twice at each site, resulting in 10 quadrats surveyed per site. Within each quadrat, all macroalgae were identified to the lowest possible taxon, their percent cover estimated by line-of-sight from less than 1 m directly above the substrate, and the number of holdfasts of each species counted. Encrusting algae were counted as the number of discrete patches (approximating number of individuals) instead of number of holdfasts. The circular transects were designed to diminish depth-related zonation effects and provide a reasonable assessment of the benthic algal communities within three meters of *S. muticum* plants. Surveys covered a vertical depth range of no more than two meters at 2 - 6 m below MLLW.

During surveys and plant collections, fish and other large mobile macrofauna often observed on *S. muticum* plants were not collected with samples. Therefore, surveys were conducted during August 8 -12 during slack high tide to quantify the presence of these larger, highly mobile fauna. From the point of water entry, two divers swam parallel to each other approximately 1.5 m apart, following a compass heading that led through the middle of the *S. muticum* community. Care was taken to



**Figure 4.** Schematic of algal community survey design. The center is the location of a haphazardly chosen *Sargassum muticum* plant. One meter and 3 m radii circles are indicated as well as the positions of all five 0.25 m<sup>2</sup> quadrats surrounding one *S. muticum*. The positions of quadrats used for all surveys at all sites are indicated by compass bearings. The degrees from North were randomly chosen using a random number table.

not disturb plants while inspecting them for macrofauna. The total number of each animal taxon observed and the total number of plants surveyed at each site by the two divers were recorded.

To document the condition of *S. muticum* plants when algae were severely damaged on the east side of the bay at Site 1, surveys of *S. muticum* plant condition were conducted from August 8 through 12, 1997. Surveys were conducted at Site 3 and both the east (Site 1) and west (Cypress West) sides of the bay at Site 1. Site 3 was included in the plant condition surveys as a reference because it did not appear to have an abnormally large snail population and plants at that site were similar in condition to plants at Site 2. Prior to the dives, criteria were established (Table 3) to characterize a range of plant conditions. Two divers swam through the sites parallel to each other, stopping at each *S. muticum* plant encountered to rank it according to the predetermined criteria. Divers recorded the total number of plants each observed and ranked.

### **Plant Collections and Processing**

Three *S. muticum* plants were collected from each study site on a monthly basis from May to September 1997 (Table 2). May collections were carried out at slack low tide with snorkel and dry suit. Plants were fully submerged at the time. All other collections occurred during slack high tide using SCUBA. Due to variation in tidal cycles over time, actual collection times ranged from 1000 h to 1500 h. Plants to be sampled were haphazardly chosen by taking the first one encountered at each study site. The second and third plants were haphazardly selected from the most

**Table 3.** Visual criteria used to assess plant condition of *Sargassum muticum* in field surveys in August 1997.

<b>Condition</b>	<b>Description</b>
1	Only damaged holdfast remains
2	Damaged holdfast, some leaflets present
3	Primary and some tertiary branches present
4	Healthy plant with some deterioration evident
5	Healthy plant

densely populated area of the *S. muticum* stand. Each plant was surrounded by a 100 × 60 cm, 200 μm mesh bag, the drawstring closed around the holdfast, and the holdfast detached from the substrate. Each bag containing a plant was then emptied into a labeled 5 gallon bucket with enough seawater to cover the sample during transportation to the marine lab. Buckets with plants were held for 1-12 hours at ambient seawater temperature until the samples were processed.

The length and number of primary lateral branches, and the length of the longest secondary lateral branch of each plant was recorded (Figure 2). The plant was then inspected for evidence of herbivore damage and reproductive state. The plant was then cut into portions (from 4 to 20) small enough to fit into a 1 L jar and seawater from the holding bucket was added. Lidded jars were shaken twenty times to dislodge epifauna. Each plant portion was then transferred to a second jar with additional seawater from the bucket. The second jar was again shaken 20 times. The seawater from all jars (two per plant portion; up to 40 jars total) was combined and filtered through a 1 mm sieve to collect the dislodged fauna. These fauna were removed from the sieve and placed in a labeled jar. The filtrate (< 1 mm) from all portions of the plant was retained in a graduated 10 L bucket for particulate load processing (see below). All portions of the plant were then visually inspected for organisms remaining attached to the surface. Remaining epibionts were removed; fauna were added to the labeled jar and algae were identified and discarded. All nudibranchs, jellies, and most hermit crabs were identified immediately due to the degradation of color and/or structure that occurs during fixation. All other organisms collected in the May and June samples were immersed directly in 70% ethanol for

fixation and storage. The July, August and September fauna were immersed in 10% formalin which is a better fixative for samples kept long term. After three days the formalin was replaced with 70% ethanol for storage.

Each plant was weighed after removal of epibionts. All portions of each plant were placed in a mesh bag and the bag was spun by hand 20 times to remove water. The plant portions were then spread out on blotter paper and allowed to air dry for 30 minutes before weighing each portion to the nearest gram. Whole plants from the August and September collections were placed in an oven at 60 °C and dried to constant weight. An average ratio of dry to wet weight was obtained from the twenty-one *S. muticum* plants collected during that period. This value was used to estimate dry weight from wet weight values of the May through July plants.

*Laminaria saccharina* was chosen for the comparison of epibiont communities on *S. muticum* and native algae because it is a large phaeophyte with identical habitat requirements to *S. muticum* and was the dominant alga in the habitats *S. muticum* utilized. Three *L. saccharina* were collected from each of the study sites during the August and September collections and processed in the same manner as described above for *S. muticum*. Dry weight of each *L. saccharina* was obtained by drying whole plants at 60 °C to constant weight.

Since the *S. muticum* population at Site 1 was severely diminished by the middle of August, three *S. muticum* and three *L. saccharina* were collected from the west side of the north bay at Cypress Head (Cypress West). These samples were processed as described above for all other collections and included in comparisons of plants from the other two sites in August. This additional collection also provided the

opportunity to compare herbivore communities between east and west sides of the bay.

To determine if the mobile epifaunal communities vary on a diel basis, an evening collection was taken from Site 3 for comparison to mid-day samples. *Idotea resecata* and *Caprella californica*, two herbivores prevalent on eel grass, exhibit diel migrations (Shaw, 1994). Populations of the two mobile herbivores peak in July and dense populations of *C. californica* are required for diel migrations to occur at detectable levels (Shaw, 1994). Since collections from Site 3 revealed the presence of several caprellid and idotoid species on *S. muticum*, three *S. muticum* plants were taken from Site 3 at dusk (approximately 1930 h) on July 15, 1997 and were processed as above.

#### **Particulate Load Associated with Algae**

Samples of the seawater used to process plants were used to estimate the weight of total and organic particulates associated with plants. The filtrate (less than 1 mm particle size) obtained from sieving the seawater used to hold and shake each plant was measured to the nearest 100 ml. The filtrate was stirred vigorously to re-suspend particles and a known volume was filtered under gentle vacuum through a pre-weighed 47 mm GF/F filter to retain particles greater than 0.7  $\mu\text{m}$  in size. The filters were folded over and kept frozen in labeled foil packets until all filter samples were processed.

Thawed filters were weighed, dried to constant weight in a 60 °C oven, cooled in a desiccator, and re-weighed. They were then placed in a muffle furnace at 550 °C

for one hour, removed to cool in a desiccator, and re-weighed. Initial filter weight, loaded wet filter weight, dry weight, and ash-free dry weight were measured to the nearest 0.001 g for each filter and for six control filters. Control filters were treated in the same manner as sample filters but had filtered seawater passed through them instead of the < 1 mm filtrate. The changes in weight of control filters at each step of the process were used to adjust all sample filter weights. The total particulates (0.7  $\mu\text{m}$  – 1000  $\mu\text{m}$ ) are expressed as percent dry weight of the sample plants. The percent organic matter of the particulate fraction was also determined for each sample.

### **Polyphenolic Concentration of *Sargassum muticum***

Distal portions of plants were used to monitor polyphenolic levels within *S. muticum* throughout the study. In a preliminary study with *S. muticum* collected in May, the distal portions were found to have the least variable concentrations of polyphenolics when compared with holdfast/basal leaves, primary lateral branches, and air vesicles. Thus, after removal of epiphytes, 1.5 g of distal tissue was taken from each plant (Figure 2) and frozen.

One gram of thawed wet tissue was ground in 15 ml of 80% methanol for 1.5 minutes using a Virtis "45" homogenizer to break up cells and release the polyphenolics into the solvent. The sample was then gravity-filtered through a GF/A filter and the filtrate containing the extracted polyphenolics stored in a labeled vial at 0 °C until all samples were analyzed in December 1997.

The Folin-Ciocalteu analysis for total polyphenolics (Van Alstyne, 1988; Van Alstyne, personal communication) was carried out on each extracted tissue sample. Microfuge tubes (1.5 ml) were labeled and arranged in sets of 15. Two 80% methanol blanks were prepared for each run. Distilled water (0.5 ml) was added to each tube as well as 50  $\mu$ l of filtered extract and 0.5 ml fresh 40% Folin-Ciocalteu reagent. This mixture was allowed to sit for five minutes after which 0.5 ml 2N  $\text{Na}_2\text{CO}_3$  was added to each tube. The tubes were then capped, shaken, and placed in a 50  $^\circ\text{C}$  water bath for 30 minutes. At the end of this incubation, tubes were removed and the samples poured into disposable 1.5 ml cuvettes. The absorbencies of the samples were read at 765 nm using a Hewlett-Packard 845A Diode Array Spectrophotometer. Methanol blanks were used to zero the spectrophotometer before each set was run and also midway through the set of 13 samples. Five sub-samples of each tissue sample were run in separate sets and the resulting absorbencies averaged. Polyphenolic content was expressed as percent dry weight after converting absorbencies to concentration of polyphenolics using a standard curve. The standard curve was produced using concentrations of phloroglucinol ranging from 0.8 to 6.0  $\mu\text{g}/\text{ml}$ .

### **Data Analysis and Statistics**

The numbers of individuals of each species occurring on *S. muticum* and *L. saccharina* were used to calculate the percentage of plants that bore at least one of each species, the number of individuals of each species occurring per plant at each site, and the number of individuals occurring per plant each month. The number of

individuals was summed for either site or month and this number was divided by the appropriate number of plants. Division by number of plants was necessary to enable direct comparison between sites and between months where unequal numbers of plants were sampled (Table 2). This method assumes that plant size does not affect number of individuals or number of species per plant. The Renkonen index (Krebs, 1989: 304-305) was used to estimate the degree of similarity of faunal communities on *S. muticum* between sites and between months.

$$\% \text{ similarity} = \sum \min(X_1, X_2)$$

Where  $X = n_i/N$  and  $n_i$  equals the number of individuals of a species and  $N$  equals the total number of individuals in the sample. Similarity comparisons aid identification of patterns in the faunal community data and utilize all species and abundance data. The number of variables that can be included limits other analytical methods such as principle component analysis.

Because plants changed in size as the season progressed, plant biomass used to obtain epibionts varied from month to month and from site to site. As a result, diversity indices could not be used to compare epibiont diversity between sites and between months (Ludwig and Reynolds, 1988: 86-89). This variability in plant biomass causes the richness index in all diversity indexes to change in an unknown manner, making it impossible to interpret the diversity index (Ludwig and Reynolds, 1988: 86-89). Therefore, rarefaction was used to eliminate differences in size of epibiont communities among plants.

$$E(S_n) = \sum_{i=1}^S \left\{ 1 - \left[ \frac{\binom{N-n_i}{n}}{\binom{N}{n}} \right] \right\}$$

Rarefaction uses the number of species ( $S$ ), the number of individuals of each species ( $n_i$ ), and the total number of individuals in a sample ( $N$ ) to predict how many species would be found in that community if only a certain number of individuals were included in the analysis (Ludwig and Reynolds, 1981: 86-89). This analysis accounts for differences in sampling effort and, in this case, differences in size of sampled plants. Also, the steepness of a rarefaction curve describes the relative evenness of the communities (James and Rathbun, 1981).

Rarefaction was used to compare *S. muticum* epibiont communities throughout the study and to compare *S. muticum* and *L. saccharina* communities sampled in August and September. *S. muticum* species richness at a sampling effort of 1000 epibiont individuals was analyzed with a two-way ANOVA for the variables of site and month. Mean number of species per plant and mean number of species per gram wet weight of plant tissue were used to compare *S. muticum* and *L. saccharina* epibiont communities.

Polyphenolic concentrations, particulate load, percent organic matter of particulate load, and plant size (both length and wet weight) were analyzed with a two-way ANOVA for the variables of site and month. For polyphenolic data, a post-hoc Tukeys HSD was used to determine significance within each variable at a confidence level of 99%. All ANOVA assumptions were met for each data set with the exception of normal distributions in the particulate load, percent organic matter of particulate matter, and polyphenolic concentration data sets. However, ANOVA has been shown to be robust enough to accommodate non-normal distributions caused by constrained data (Sokal and Rohlf, 1995) expressed as percentages. *S. muticum* and

*L. saccharina* data from August and September collections were compared using three-way ANOVA tests for the variables of month, site and species. Size of plant (both length and wet weight), particulate load, and percent organic matter of particulate load were compared for these samples. Level of significance for all statistical tests (except the post hoc test discussed above) was  $\alpha = 0.05$ .

Surveys of benthic algal communities (algal density and percent cover) were compared using Kendall's rank correlation (Sokal and Rohlf, 1995: 593-600). Plant conditions in August were analyzed with a chi-square contingency table.

Principle component analysis (PCA) was run on the log base 10 transformed total numbers of each of the 15 most commonly occurring species associated with *S. muticum*. PCA was carried out using a variance-covariance matrix. The high total species richness and complexity of species abundances between sites and months made this multivariate analysis necessary for general pattern identification.

Component scores by site were then analyzed for statistical significance using a one-way ANOVA and Tukey HSD test.

## RESULTS

### Benthic Algal Communities

All sites had high total algal cover, ranging from 78 to 96% (Table 4). The total algal density (indicated by number of holdfasts) varied little from site to site (Table 4). The mean algal density for all sites was 63 plants per square meter. The benthic algal community around *S. muticum* was dominated by *Laminaria saccharina* (Table 4). *Ulva* spp., *Mazzaella* spp., and *Odonthalia floccosa* were also common, followed by a wide variety of red algae (Table 4). Site 2 was the most species rich with 14 algal species. Sites 1 and 3 supported 9 and 10 species, respectively. There were no significant correlations in algal density at the three study sites (Table 5). There was a significant correlations in percent algal cover at Sites 1 and 2 (Table 5).

### Monthly Changes in *Sargassum muticum*

#### Plant Size and Condition

*S. muticum* is present year round in northern Puget Sound but is most conspicuous from May to September. Monthly trends in wet weight and length of collected plants are presented in Figure 5. Length of *S. muticum* increased at all sites from May to July and at Sites 2 and 3 until August. Length then decreased until the end of the study in September (Figure 5). Wet weight follows approximately the same pattern as length, with variability at Site 2 where individual plants were highly branched. There was a significant interaction between the variables of site and month in the ANOVA of wet weight (Table 6). Thus wet weight and length displayed different temporal variation among sites.

**Table 4.** Results of the benthic algal community surveys conducted July 24 - 28, 1997, showing species, percent cover, and algal density (number of holdfasts per square meter) for each species. Mean values are given for individual sites ( $n = 10$ ) as well as for all sites combined (in bold;  $n = 30$ ).

Algal Species	Mean Percent Cover				Mean Algal Density			
	Site 1	Site 2	Site 3	All Sites	Site 1	Site 2	Site 3	All Sites
<b>Phylum Chlorophyta</b>								
<i>Enteromorpha</i> spp.	-	-	2.0	<b>0.7</b>	-	-	1.2	<b>0.4</b>
<i>Ulva</i> spp.	16.5	0.6	33.0	<b>16.7</b>	24.8	3.2	28.8	<b>18.9</b>
<b>Phylum Phaeophyta</b>								
<i>Alaria marginata</i>	2.5	-	-	<b>0.8</b>	7.6	-	-	<b>2.5</b>
<i>Laminaria saccharina</i>	52.0	66.5	40.0	<b>52.8</b>	8.8	10.0	6.4	<b>8.4</b>
<i>Fucus gardneri</i>	-	-	2.2	<b>0.7</b>	-	-	2.8	<b>0.9</b>
<i>Sargassum muticum</i>	0.2	5.5	3.7	<b>3.1</b>	10.8	1.2	1.6	<b>4.5</b>
<b>Phylum Rhodophyta</b>								
Pink crust	0.2	-	-	<b>0.1</b>	2.4	-	-	<b>0.8</b>
<i>Constantinea</i> spp.	-	-	-	-	-	1.2	-	<b>0.4</b>
<i>Gigartina</i> spp.	0.5	7.2	-	<b>2.6</b>	1.2	6.8	-	<b>2.7</b>
<i>Mazzaella</i> spp.	5.0	7.3	0.5	<b>4.3</b>	2.8	14.0	0.4	<b>5.7</b>
<i>Prionitis lanceolata</i>	-	-	-	-	1.2	-	-	<b>0.4</b>
<i>Callophyllis edentata</i>	0.2	1.0	-	<b>0.4</b>	2.0	2.4	-	<b>1.5</b>
<i>Schizymenia pacifica</i>	-	-	-	-	-	2.0	-	<b>0.7</b>
<i>Mastocarpus papillatus</i>	-	-	2.5	<b>0.8</b>	-	3.2	3.6	<b>2.3</b>
<i>Plocamium pacificum</i>	-	-	-	-	-	4.0	-	<b>1.3</b>
<i>Sarcodiotheca gaudichaudii</i>	-	-	-	-	-	0.4	-	<b>0.1</b>
<i>Cryptopleura ruprechtiana</i>	-	2.2	1.0	<b>1.1</b>	-	8.4	0.4	<b>2.9</b>
<i>Laurencia spectabilis</i>	-	-	-	-	-	0.4	-	<b>0.1</b>
<i>Odonthalia floccosa</i>	0.7	5.8	2.5	<b>3.0</b>	4.4	7.2	14.8	<b>8.8</b>
<b>Total</b>	<b>77.8</b>	<b>96.1</b>	<b>87.4</b>	<b>87.1</b>	<b>66.0</b>	<b>64.4</b>	<b>60.0</b>	<b>63.5</b>

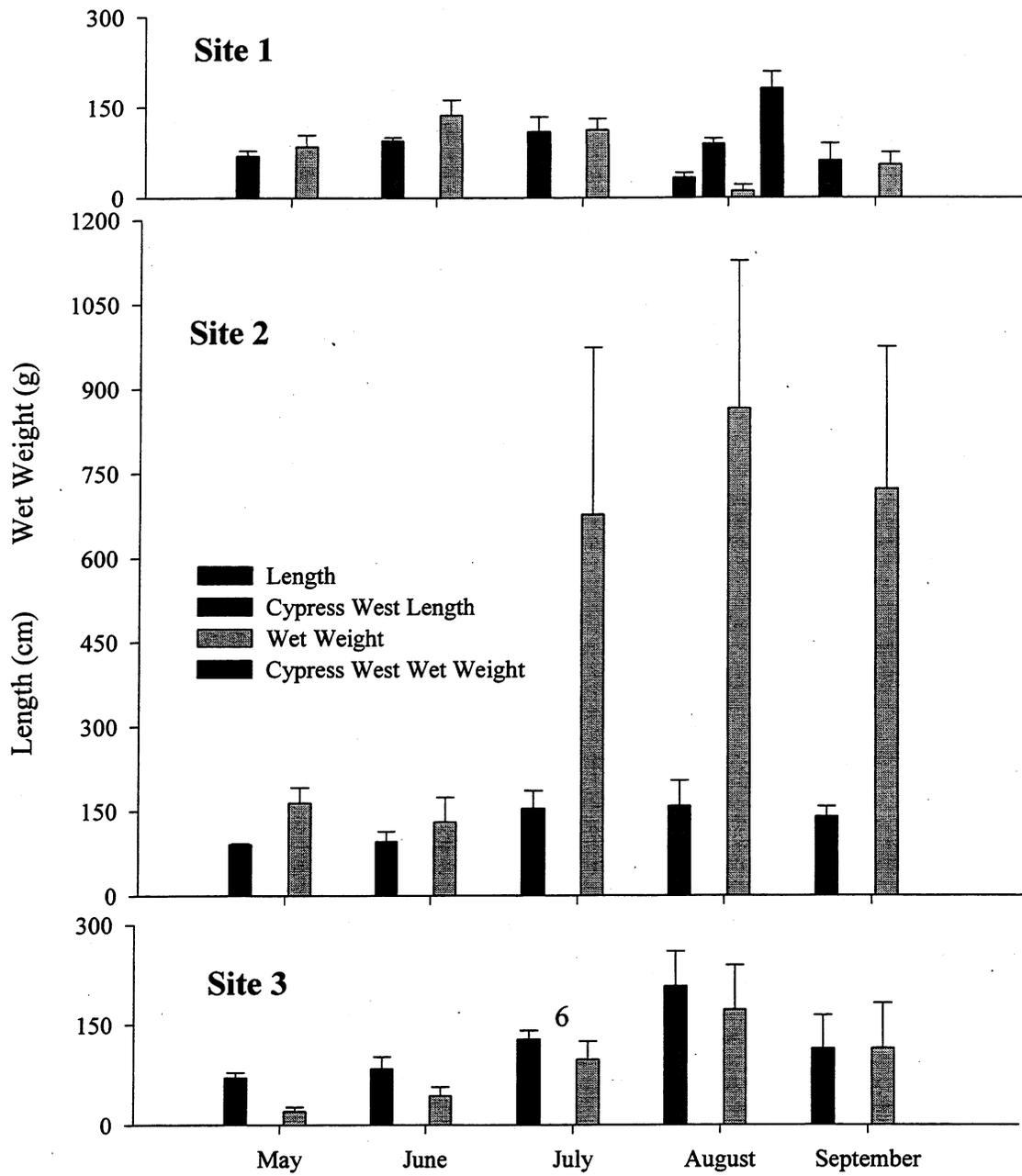
**Table 5.** Benthic algal community comparisons using Kendall's rank correlations for (A) percent cover and (B) algal density (# holdfasts/m<sup>2</sup>) within each algal species at each study site. Correlation values are provided ( $n = 13$  and  $19$  respectively for each test). An asterisk indicates significance at the 0.05 level.

**A) Percent cover**

**B) Algal density**

	Site 1	Site 2		Site 1	Site 2
Site 2	0.58*		Site 2	0.22	
Site 3	0.19	0.23	Site 3	0.38	0.37

\*  $p < 0.05$



**Figure 5.** Size (length and wet weight) of *Sargassum muticum* plants collected from May to September 1997 at each site. There are two additional bars for Cypress West in the Site 1 graph. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above pairs of bars).

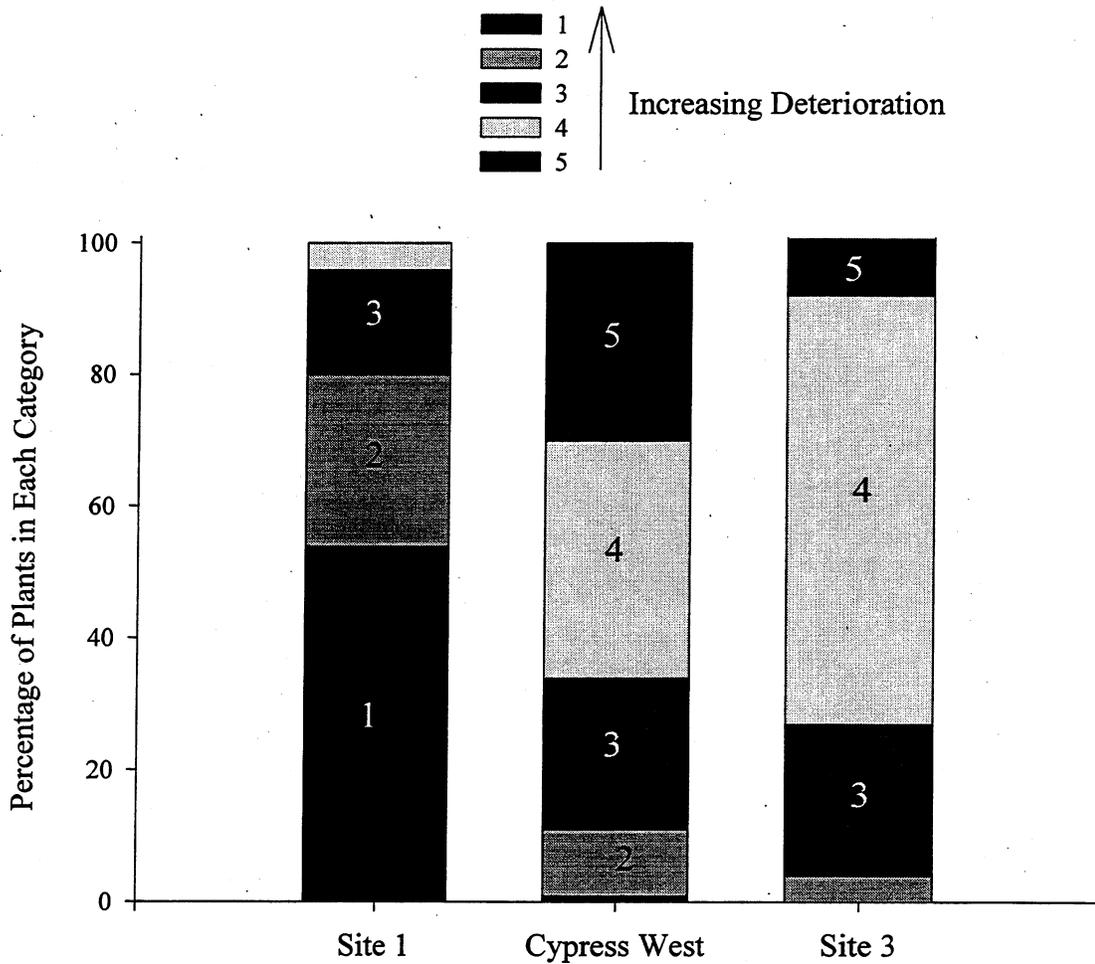
**Table 6.** Results of six two-way ANOVA tests of *Sargassum muticum* data from summer 1997 collections: plant length (length), plant wet weight (weight), polyphenolic concentrations of plant tissue (polyphenolics), particulate load, percent organic matter of particulate load (% organic matter), and species richness values obtained from rarefaction analysis with a sample size of 1000 epibiont individuals (species richness). *F* test values are given with significance at the 0.05 level indicated by an asterisk.

<b>Factor</b>	<b>Month</b>	<b>Site</b>	<b>Month × Site</b>
Length	3.4*	5.4*	1.9*
Weight	3.8*	21.3*	2.6*
Polyphenolics	20.5*	7.2*	3.3*
Particulate load	1.8	0.8	3.1*
% Organic matter	1.3	0.5	0.6
Species richness	1.0	0.1	2.6*

\*  $p < 0.05$

Plants at Site 1 were generally short and sparsely branched and plants at Site 2 were long and thickly branched. Plants at Site 3 were long and sparsely branched. Plants at all sites began producing reproductive cryptostomata in late July and continued to produce these throughout August. In August, plant tissue was fragile and broke easily when handled. By September, few annual leaflets remained on plants and air vesicles were generally missing or damaged, causing plants to be less buoyant. Deterioration of *S. muticum* was particularly evident at Site 1, where plants began to deteriorate in July. However, plants from the west side of the bay (Cypress West) did not display the same degree of deterioration as plants collected from the east side of the site (Figure 6). Plant condition at Site 1 was significantly different (contingency table,  $df = 8$ ,  $p < 0.01$ ) from that of plants at Cypress West and at Site 3 (Figure 6). Plants at Site 1 were essentially stripped of all tissue produced that year, reduced to holdfasts, a few basal leaves, and a few primary lateral branches (Figure 6). At Site 3 and Cypress West, the plants retained much of the tissue produced that year (Figure 6) with only moderate deterioration evident.

*S. muticum* growth rate was calculated by plotting all length data from each site for each month and fitting two regression lines to the data (one from May to August and one from August to September). *S. muticum* increased in length at a rate of 23.5 cm per month ( $r^2 = 0.39$ ,  $n = 45$ ) from May to August and decreased in length at a rate of 37.5 cm per month ( $r^2 = 0.13$ ,  $n = 21$ ) from August to September.



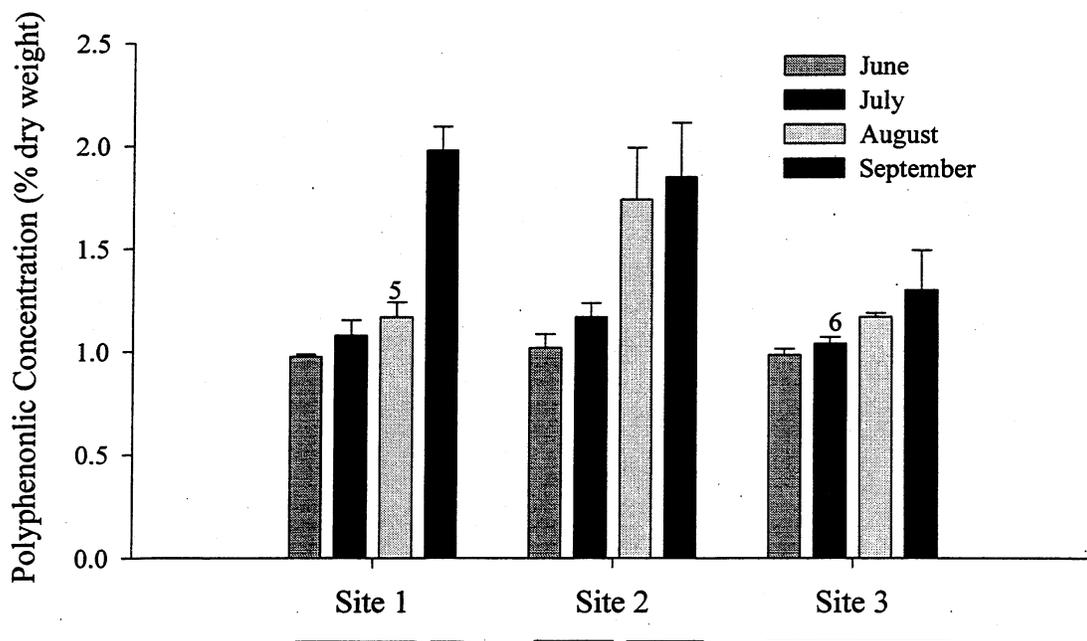
**Figure 6.** *Sargassum muticum* plant condition at three sites surveyed in August 1997. The percentage of plants occurring in each condition category (Table 3) is shown with its category number. Category 1 describes a severely deteriorated plant while category 5 describes a healthy plant that shows little or no deterioration.

## **Polyphenolic Concentrations**

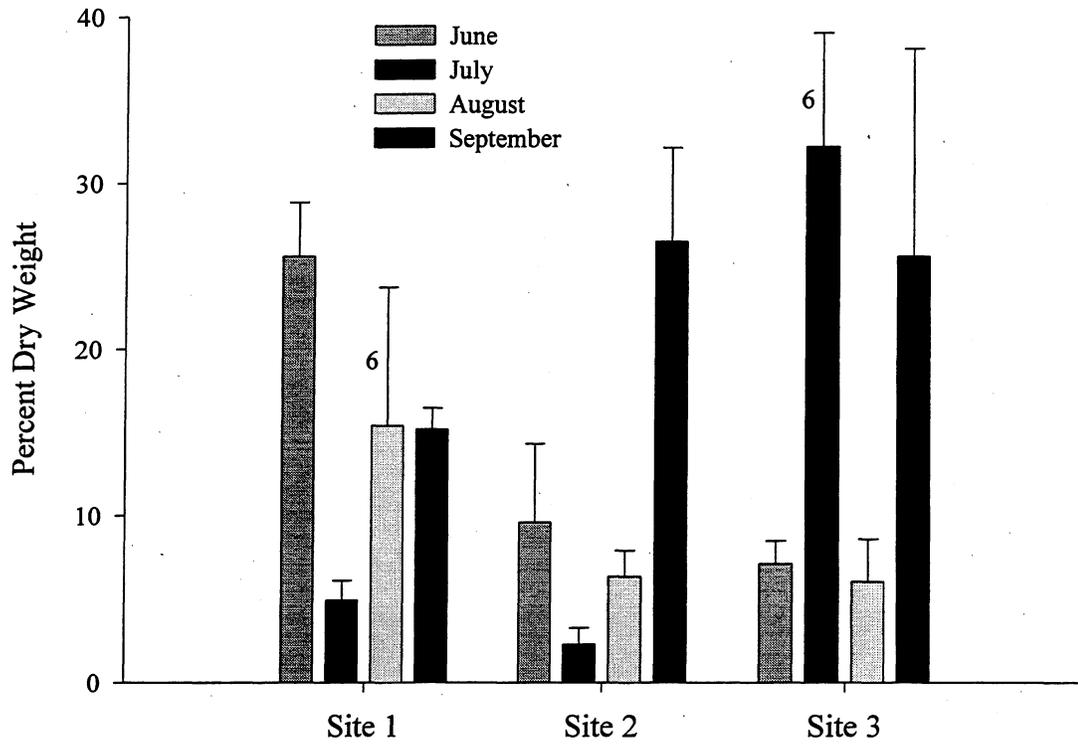
The dry to wet weight ratio for *S. muticum* was  $0.176 \pm 0.005$  ( $n = 21$ ). Polyphenolic concentrations in distal tip tissue of *S. muticum* ranged from 1 to 2% dry weight (Figure 7). A significant interaction in polyphenolic concentrations occurred between month and site (Table 6). Polyphenolic concentration increased in all plants from June to September. The increase was significant for plants at Sites 1 and 2 but not for plants at Site 3 (Figure 7).

## **Particulate Load**

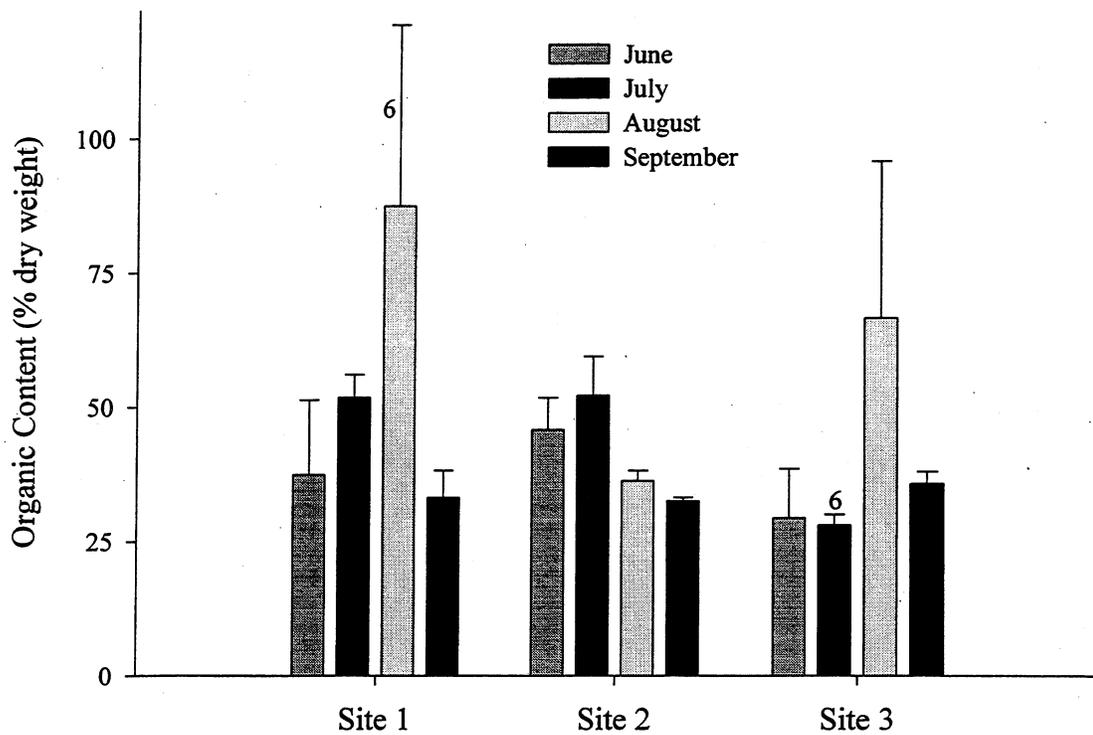
All *S. muticum* plants retained particulates consisting of both live and dead organisms and inorganic particles. The material was easily removed from the plant by agitating the water surrounding the plant. The amount of particulates ranged from 5 to nearly 40% of plant dry weight, with an overall mean of 16.3% for *S. muticum* (Figure 8). A significant interaction was found between site and month for plant particulate load (Table 6). Further analysis into patterns in individual variables was not pursued because the patterns seen were haphazard, did not relate to tidal height at time of collection, and because of the large variability in amount of seawater used to process plants (3 – 10 L). Particulate load on plants from Sites 1 and 3 varied between months between highest and lowest particulate load values while Site 2 plants maintained a consistent particulate load close to the average for the study. There was no significant difference in organic content of the particulate load for site or month (Table 6). Organic content ranged from 25 to 80% of the particulate load dry weight with a mean of 46% (Figure 9).



**Figure 7.** Polyphenolic concentration in *Sargassum muticum* distal tip tissues from each site and month. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above bar). Horizontal bars below the x-axis indicate significant differences at  $p < 0.05$  as determined by a two-way ANOVA and a Tukey HSD test of each site's data.



**Figure 8.** Particulate load on *S. muticum* plants at each site during the study. Values are shown as a percentage of plant dry weight. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above bar). Differences in particulate load were not significant for month or site (two-way ANOVA).



**Figure 9.** Organic content of the particulate load on *S. muticum* plants at each site from June to September 1997. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above bar). The organic content was not significantly different for site or month (two-way ANOVA).

## Community Associated with *Sargassum muticum*

### *Sargassum muticum* Epibiont Community Members

One hundred and fifteen taxa were identified on the 51 *S. muticum* plants collected at the three study sites (Table 7). The following algal taxa were found growing epiphytically on *S. muticum*: *Antithamnion* spp., *Polyneura latissima*, *Callophyllis* spp., *Odonthalia* spp., *Costaria costata*, *Enteromorpha* spp., an unidentified brown blade, and the colonial diatom *Navicula*. The animals consisted of 10 phyla from at least 53 families. Thirty-five of the 107 animal taxa occurred on greater than 10% of the plants (Table 7). Polychaetes, gastropods, amphipods, and decapods were the most abundant and species-rich groups, constituting 64% of the identified species. Species occurring on more than 10% of the plants are referred to as "common" species and are indicated in Table 7 with an asterisk.

*Lacuna variegata* and *L. vincta* were the most abundant and common members of the epifaunal community. These two snail species occurred with an overall mean density of 98 and 466 individuals per plant, respectively. The snails *Margarites pupillus*, *Onoba carpenteri*, and *Alia gausapata* were also common, each occurring on greater than 28% of plants (Table 7). The polychaete *Platynereis bicanaliculata* occurred on 39% of all plants. Polychaetes listed as "unidentified nereids" may have been *P. bicanaliculata* but were too small to manipulate for species-level identification.

*Idotea rufescens* was the most common isopod in the *S. muticum* community, occurring on 39% of the 51 plants (Table 7). The gammarid amphipods *Pontogenia rostrata*, *Ischyrocerus anguipes*, and *Aoroides intermedius* each occurred on more

**Table 7.** Frequency and abundance of epifauna on *Sargassum muticum* expressed as the percentage of plants that bore at least one of each species (column 1) and as the total number of individuals occurring on the 51 *S. muticum* plants collected from May to September 1997 (column 2). One hundred and seven epifaunal taxa were identified. Asterisks indicate common species (found on > 10% of plants).

	% Plants with each Species	Total # Individuals
<b>Phylum Cnidaria</b>		
<i>Eperetmus typus</i> Bigelow, 1915	1.9	1
<i>Aurelia aurita</i> (Linnaeus, 1758)	3.7	2
<i>Halichystus stejnegeri</i> Kishinouye, 1899	1.9	3
<i>Epiactis prolifera</i> Verrill, 1869	1.9	1
<b>Phylum Ctenophora</b>		
<i>Pleurobrachia bachia</i> A. Agassiz, 1860	1.9	1
<b>Phylum Nemertea</b>		
*Unidentified species	11.1	7
<b>Phylum Nematoda</b>		
Unidentified species	2.0	1
<b>Phylum Annelida</b>		
<i>Gyptis brevipalpa</i> (Hartmann-Shroder)	3.7	2
<i>Nereis (Nereis) procera</i> Ehlers, 1868	2.0	1
* <i>Platynereis bicanaliculata</i> (Baird, 1863)	38.9	95
*Unidentified nereids	20.4	24
* <i>Harmothoe imbricata</i> (Linnaeus, 1766)	11.1	13
Unidentified terebellid	4.0	6
Unidentified spirorbid	4.0	2
<b>Phylum Mollusca</b>		
<b>Class Gastropoda</b>		
* <i>Margarites (Valvatella) pupillus</i> (Gould, 1841)	27.8	37
<i>Margarites (Margarites) marginatus</i> Dall, 1919	9.3	10
<i>Lirularia lirulata</i> (Carpenter, 1864)	4.0	5
<i>Tectura scutum</i> (Rathke, 1833)	2.0	1
<i>Lottia</i> spp.	2.0	1
* <i>Lacuna (Epheria) variegata</i> Carpenter, 1864	87.0	5,274
* <i>Lacuna (Epheria) vincta</i> (Montagu, 1803)	90.7	25,171
<i>Littorina sitkana</i> Philippi, 1845	7.4	6
<i>Littorina scutulata</i> (Gould, 1849)	2.0	1
* <i>Onoba (Onoba) carpenteri</i> (Weinkauff, 1885)	44.4	143
* <i>Alia gausapata</i> (Carpenter, 1864)	31.5	117
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	2.0	1
<i>Haminoea vesicula</i> (Gould, 1855)	2.0	2

	% Plants with each Species	Total # Individuals
Unidentified dorida	2.0	1
<i>Flabellina verrucosa</i> (M. Sars, 1829)	2.0	1
<b>Class Bivalvia</b>		
* <i>Mytilus</i> spp.	25.9	26
<i>Chlamys (Chlamys) hastata</i> (Sowerby, 1843)	2.0	1
<b>Phylum Arthropoda</b>		
<b>Class Pycnogonid</b>		
Unidentified pycnogonid (juvenile)	2.0	1
<i>Phoxichilidium femoratum</i> (Rathke, 1799)	2.0	1
<b>Order Mysidacea</b>		
<i>Mysis litoralis</i> (Banner, 1948)	9.3	99
<i>Neomysis mercedis</i> Holmes, 1897	2.0	1
<b>Order Tanaidacea</b>		
<i>Leptochelia savignyi</i> (Kroyer, 1842)	2.0	1
<b>Order Isopoda</b>		
<i>Gnorimosphaeroma oregonense</i> Dana, 1854-55	2.0	2
Unidentified isopod juveniles	4.0	4
* <i>Idotea (Idotea) fewkesi</i> Richardson, 1905	14.8	55
* <i>Idotea (Idotea) ochotensis</i> Brandt, 1851	13.0	32
* <i>Idotea (Idotea) rufescens</i> Fee, 1926	38.9	104
<i>Idotea (Idotea) urotoma</i> Stimpson, 1864	2.0	1
<i>Idotea (Pentidotea) resecata</i> Stimpson, 1857	5.6	17
<i>Idotea (Pentidotea) vosnesenskii</i> (Brandt, 1851)	2.0	1
<b>Order Amphipoda</b>		
<i>Accedomoera vagor</i> Barnard, 1969	4.0	2
* <i>Pontogeneia cf. rostrata</i> Gurjanova, 1938	51.9	359
<i>Paracalliopiella pratti</i> (Barnard, 1954)	5.6	5
* <i>Pleustes depressa</i> Alderman, 1936	20.4	26
<i>Hyale frequens</i> Stout, 1913 (group)	2.0	2
<i>Parallorchestes</i> spp.	4.0	9
<i>Eobrolgus spinosus</i> (Holmes, 1905)	2.0	1
* <i>Ampithoe</i> spp.	42.6	103
* <i>Ampithoe lacertosa</i> Bate, 1858	33.3	83
<i>Ampithoe simulans</i> Alderman, 1936	4.0	2
* <i>Peramphithoe</i> spp.	14.8	18
* <i>Peramphithoe humeralis</i> (Stimpson, 1864)	20.4	39
* <i>Peramphithoe lindbergi</i> (Gurjanova, 1938)	29.6	57
* <i>Peramphithoe mea</i> (Gurjanova, 1938)	40.7	109
<i>Peramphithoe plea</i> (Barnard, 1965)	2.0	2
<i>Photis</i> spp.	4.0	6
* <i>Ischyrocerus anguipes</i> (Kroyer, 1838)	66.7	265
<i>Jassa</i> spp.	7.4	4
* <i>Aoroides</i> spp.	25.9	58

	% Plants with each Species	Total # Individuals
* <i>Aoroides inermis</i> Conlan and Bousfield, 1982	11.1	12
* <i>Aoroides intermedius</i> Conlan & Bousfield, 1982	66.7	197
<i>Corophium</i> spp.	4.0	3
<i>Corophium salmonis</i> Stimpson, 1857	2.0	1
Unidentified amphipod sp.1	2.0	1
* <i>Caprella incisa</i> Mayer, 1903	20.4	39
* <i>Caprella laeviuscula</i> Mayer, 1903	70.4	1,323
* <i>Caprella verrucosa</i> Boeck, 1872	24.1	53
* <i>Metacaprella kenneerlyi</i> (Stimpson, 1864)	29.6	56
<b>Order Decapoda</b>		
Unidentified shrimp zoea	6.0	23
<i>Pandalus tridens</i> Rathbun, 1902	4.0	3
* <i>Hippolyte clarki</i> Chace, 1951	11.1	7
<i>Hippolyte californiensis</i>	6.0	3
* <i>Heptacarpus brevirostris</i> (Dana, 1852)	29.6	56
<i>Heptacarpus stylus</i> (Stimpson, 1864)	2.0	1
<i>Heptacarpus tenuissimus</i> Holmes, 1900	2.0	2
<i>Eualus suckleyi</i> (Stimpson, 1864)	2.0	1
<i>Eualus herdmani</i> (Walker, 1898)	2.0	1
<i>Spirontocaris</i> spp.	2.0	1
* <i>Pagurus</i> spp.	16.7	18
<i>Pagurus armatus</i> (Dana, 1851)	4.0	3
<i>Pagurus granosimanus</i> (Stimpson, 1858)	6.0	4
<i>Pagurus beringanus</i> (Benedict, 1892)	2.0	1
<i>Pagurus caurinus</i> Hart, 1971	4.0	2
<i>Pagurus hirsutiusculus</i> (Dana, 1851)	9.3	8
Unidentified porcellanid (zoea)	2.0	1
Unidentified crab megalopa	2.0	1
<i>Oregonia gracilis</i> Dana, 1851	7.4	13
<i>Pugettia producta</i> (Randall, 1839)	4.0	2
* <i>Pugettia gracilis</i> Dana, 1851	59.3	143
<i>Telmessus cheiragonus</i> (Tilesius, 1815)	9.3	6
Unidentified Cancer zoea	6.0	47
<i>Cancer oregonensis</i> (Dana, 1852)	7.4	5
<i>Cancer magister</i> Dana, 1852	4.0	2
Unidentified pinixid (megalopa and zoea)	4.0	2
<b>Phylum Bryozoa</b>		
cheilostome sp. 1	9.3	5
cheilostome sp. 2	2.0	1
cheilostome sp. 3	2.0	1
cheilostome sp. 4	4.0	2
cheilostome sp. 5	6.0	3
cheilostome sp. 6	2.0	1
cheilostome sp. 7	2.0	1

	% Plants with each Species	Total # Individuals
cheilostome sp. 8	2.0	1
cheilostome sp. 9	2.0	1
<i>Tubulipora</i> spp. (cyclostome sp. 1)	2.0	1
cyclostome sp. 2	2.0	1
<b>Phylum Echinodermata</b>		
* <i>Leptasterias hexactis</i> (Stimpson, 1862)	18.5	29
Unidentified ophiuroid (juvenile)	4.0	2
<i>Strongylocentrotus droebachiensis</i> (O. F. Muller, 1776)	2.0	1
<b>Phylum Vertebrata, Class Osteichthyes</b>		
<i>Pholis laeta</i> (Cope, 1873)	7.0	8
<i>Pholis ornata</i> (Girard, 1854)	2.0	1
* <i>Apodichthyes flavidus</i> Girard, 1854	22.2	22

than 50% of plants. *Peramphithoe* and *Ampithoe* species were also common, with a total occurrence on 69 and 57% of plants, respectively (Table 7). Each of the four species of caprellid amphipods associated with *S. muticum* were abundant and occurred on over 20% of plants. *Caprella laeviuscula* was the third most abundant animal on *S. muticum*. The two most common shrimp, *Heptacarpus brevirostris* and *Hippolyte clarki*, occurred on 30 and 11% of plants, respectively (Table 7). Hermit crabs were common members of the epifaunal community. Species-level identification was not possible for several individuals because they were preserved in alcohol, which leaches the color from the exoskeleton. Coloration is a key characteristic in hermit crab identification. In total, hermit crabs occurred on 30% of plants. The crab *Pugettia gracilis* occurred on 59% of plants (Table 7) and was the only common species of majid crab. Crabs of this species ranged in carapace width from 4 mm to approximately 500 mm, but most were between 8 and 20 mm.

The six-armed sea star *Leptasterias hexactis* occurred on 18% of plants (Table 7). These were usually small individuals, ranging from 8 to 80 mm from the tip of one arm across to the tip of the opposite arm.

Three species of bony fish were collected with *S. muticum*. *Apodichthyes flavidus*, the pen-point gunnel, was the most common, occurring on 22% of plants (Table 7). Other fish were often observed closely associated with *S. muticum* plants but were not collected due to their ability to escape during plant collection. Three species of fish observed during the macrofauna surveys (Table 8) were not collected with sample plants (Table 7). The silver-spotted sculpin *Blepsias cirrhosus* occurred on 16% of surveyed plants. These fish were typically seen resting in the outer

**Table 8.** Number (#) and density (%; measured as number of individuals per total number plants surveyed  $\times$  100) of macrofauna on *S. muticum* during visual surveys August 8 - 12, 1997 using SCUBA.

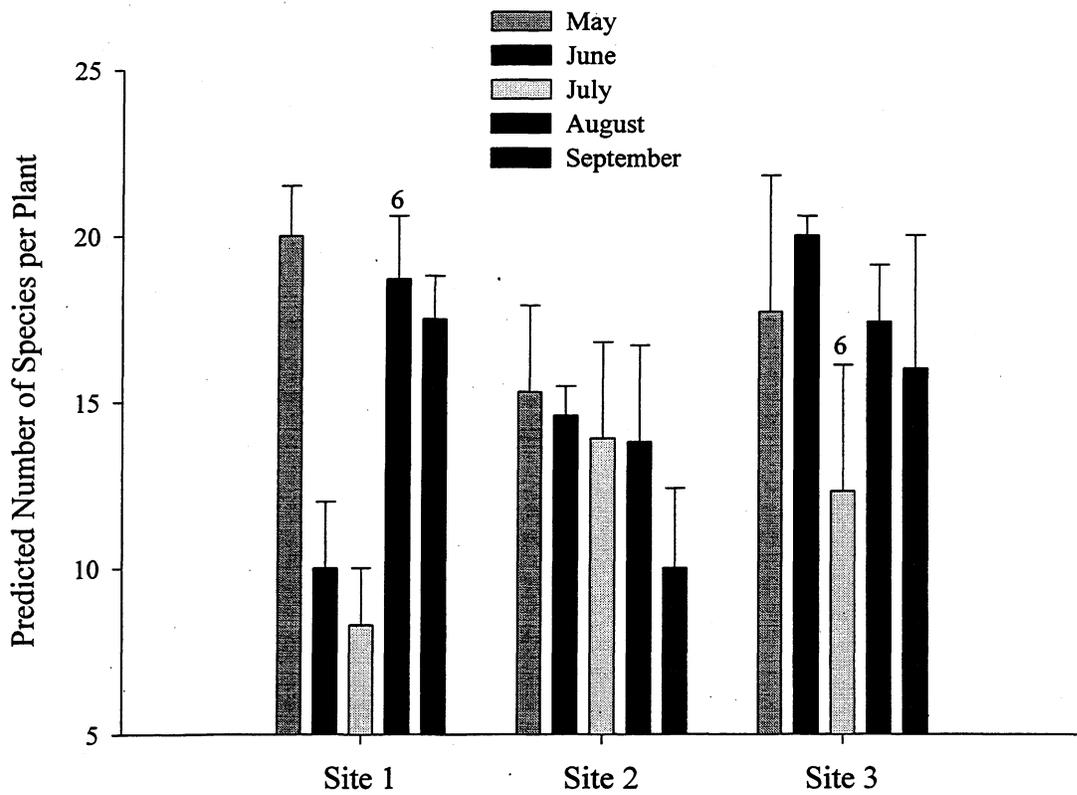
	Site 1		Site 2		Site 3		All Sites	
	#	%	#	%	#	%	#	%
<b># <i>S. muticum</i> Plants Surveyed</b>	13		18		43		74	
<b>Cnidaria</b>								
<i>Epiactis productus</i>	-	-	-	-	3	7	3	4
<b>Mollusca</b>								
<i>Haminoea</i> spp.	-	-	-	-	1	2	1	1
<b>Arthropoda</b>								
<i>Pagurus</i> spp.	-	-	-	-	2	5	2	2.7
Kelp crabs	18	138	16	89	7	16	41	55
<b>Echinodermata</b>								
<i>Leptasterias hexactis</i>	-	-	6	33	-	-	6	8
<b>Chordata</b>								
<i>Blepsias cirrhosus</i>	6	46	6	33	-	-	12	16
Pholidae spp.	9	69	3	17	22	51	34	46
<i>Aulorhynchus flavidus</i>	1	8	-	-	5	12	6	8
Unidentified fish	-	-	2	11	-	-	2	3

branches of *S. muticum*. When disturbed they first swam to another part of the same plant and, if pressed, left the plant to swim to another *S. muticum*. On two occasions this species was observed on a sample plant during the collection process but the fish escaped before the bag was closed. Forty-six percent of surveyed plants (Table 8) had a resident gunnel (family Pholidae). It was not possible to identify these fish to species level during the underwater observations. Pholids occurred on 27% of all collected plants (Table 7), indicating that about half the pholids escaped collection.

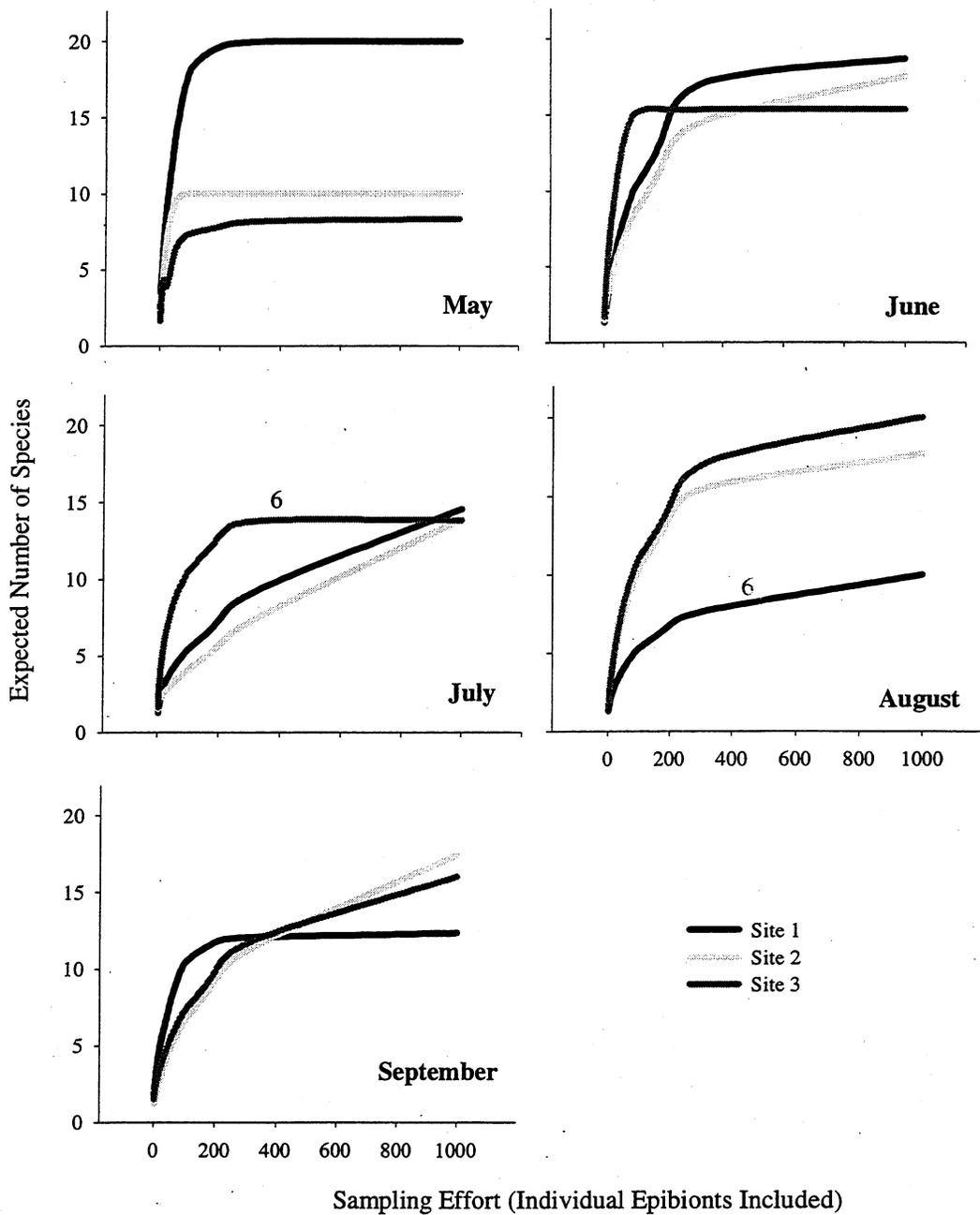
#### **Diversity of Epibiont Community Associated with *Sargassum muticum***

Diversity (measured by rarefaction) changed differently over time at each site (Figure 10), resulting in a significant interaction (two-way ANOVA, Table 6) between month and site. The highest mean number of expected species with a sample size ranging from 5 to 1000 individuals per plant was 20 species per plant (Figure 11). Nineteen percent of the plants supported more than 1000 individuals with a mean of 21 species per plant. Both number of species and abundance of individuals were positively correlated with plant size (both wet weight and length; Table 9).

Interesting patterns in species abundance and diversity occurred at the three study sites. The Renkonen similarity index revealed highest overall similarity between Sites 1 and 2 (Table 10). Plants from Site 1 supported unusually high abundances of the snail *Margarites pupillus*, the gammarid amphipod *Pontogenia rostrata*, and decapod crabs (Table 11). Plants from this site also supported the highest diversity of nudibranchs, gammarid amphipods, and shrimp. All decapod megalopae and zoea were collected on plants at Site 1, except for one. Site 2



**Figure 10.** Number of species predicted to occur on *S. muticum* if each plant hosted 1000 individuals. The mean number of species was calculated by rarefaction based on data collected each month from May to September 1997. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above bar).



**Figure 11.** Rarefaction curves showing predicted epibiont diversity on *Sargassum muticum* at all sites each month of the study ( $n = 3$  except where indicated above curve). Individuals sampled represents sampling effort and thus normalizes for differences in size of individual plants.

**Table 9.** Pearson correlations of both epibiont species richness (Species) and total number of epibiont individuals (Individuals) found on *S. muticum* with size of plants measured as both wet weight and length ( $n = 51$ ). All correlations are positive and significant.

<b>Variables</b>	<b>Correlation</b>	<b><i>p</i> value</b>
Species × Wet weight	0.59	< 0.01
Species × Length	0.61	< 0.01
Individuals × Wet weight	0.64	< 0.01
Individuals × Length	0.39	0.04

**Table 10.** Renkonen index showing percent similarity of epibiont samples for each study site based on total number of individuals of each epibiont species ( $n = 18, 15,$  and  $18$  plants for Sites 1, 2, and 3 respectively). Data (total individuals of each epibiont species) from May through September were pooled for each site.

	Site 1	Site 2	Site 3
Site 3	62	68	-
Site 2	86	-	■
Site 1	-	■	■

- High similarity
- Intermediate similarity
- Low similarity

**Table 11.** The mean number of individuals of each species present on each *Sargassum muticum* plant at each site. Monthly data for each site were pooled and divided by the total number of plants sampled at each site.

	Site 1	Site 2	Site 3
<b>Total Number <i>S. muticum</i> Plants (<i>n</i>)</b>	18	15	18
<b>Phylum Cnidaria</b>			
<i>Eperetmus typus</i> Bigelow, 1915	-	-	0.1
<i>Aurelia aurita</i> (Linnaeus, 1758)	0.1	-	0.1
<i>Halichystus stejnegeri</i> Kishinouye, 1899	-	-	-
<i>Epiactis prolifera</i> Verrill, 1869	-	-	0.1
<b>Phylum Nemertea</b>			
Unidentified species	0.1	0.1	0.2
<b>Phylum Nematoda</b>			
Unidentified species	-	-	0.1
<b>Phylum Annelida</b>			
<i>Gyptis brevipalpa</i> (Hartmann-Shroder)	-	-	0.1
<i>Nereis (Nereis) procera</i> Ehlers, 1868	-	0.1	-
<i>Platynereis bicanaliculata</i> (Baird, 1863)	1.7	0.9	2.8
Unidentified nereids	0.6	0.4	0.4
<i>Harmothoe imbricata</i> (Linnaeus, 1766)	0.2	0.1	0.3
Unidentified terebellid	-	0.1	0.3
Unidentified spirorbid	0.1	-	0.1
<b>Phylum Mollusca</b>			
<b>Class Gastropoda</b>			
<i>Margarites (Valvatella) pupillus</i> (Gould, 1841)	1.4	0.3	0.4
<i>Margarites (Margarites) marginatus</i> Dall, 1919	-	0.1	0.4
<i>Lirularia lirulata</i> (Carpenter, 1864)	-	0.1	0.2
<i>Tectura scutum</i> (Rathke, 1833)	0.1	-	-
<i>Lottia</i> spp.	-	-	0.1
<i>Lacuna (Epheria) variegata</i> Carpenter, 1864	38.4	248.9	47.2
<i>Lacuna (Epheria) vincta</i> (Montagu, 1803)	417.4	995.5	151.3
<i>Littorina sitkana</i> Philippi, 1845	0.1	0.3	0.1
<i>Littorina scutulata</i> (Gould, 1849)	-	-	0.1
<i>Onoba (Onoba) carpenteri</i> (Weinkauff, 1885)	3.4	0.3	4.3
<i>Alia gausapata</i> (Carpenter, 1864)	0.1	7.1	0.5
<i>Haminoea vesicula</i> (Gould, 1855)	-	-	0.1
Unidentified dorid	0.1	-	-
<i>Flabellina verrucosa</i> (M. Sars, 1829)	0.1	-	-
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	0.1	-	-

	Site 1	Site 2	Site 3
<b>Class Bivalvia</b>			
<i>Mytilus</i> spp.	0.4	0.4	0.7
<i>Chlamys (Chlamys) hastata</i> (Sowerby, 1843)	0.1	-	-
<b>Phylum Arthropoda</b>			
<b>Class Pycnogonid</b>			
Unidentified pycnogonid (juvenile)	-	-	0.1
<i>Phoxichilidium femoratum</i> (Rathke, 1799)	-	0.1	-
<b>Order Mysidacea</b>			
<i>Mysis litoralis</i> (Banner, 1948)	5.5	-	-
<i>Neomysis mercedis</i> Holmes, 1897	-	0.1	-
<b>Order Tanaidacea</b>			
<i>Leptochelia savignyi</i> (Kroyer, 1842)	-	0.1	-
<b>Order Isopoda</b>			
Unidentified idotoid juveniles	-	0.3	-
<i>Idotea (Idotea) fewkesi</i> Richardson, 1905	-	0.4	2.7
<i>Idotea (Idotea) ochotensis</i> Brandt, 1851	-	-	1.7
<i>Idotea (Idotea) rufescens</i> Fee, 1926	0.3	0.9	4.7
<i>Idotea (Idotea) urotoma</i> Stimpson, 1864	-	0.1	-
<i>Idotea (Pentidotea) resecata</i> Stimpson, 1857	-	-	0.9
<i>Idotea (Pentidotea) wosnesenskii</i> (Brandt, 1851)	-	0.1	-
<b>Order Amphipoda</b>			
<i>Accedomoera vagor</i> Barnard, 1969	0.1	0.1	-
<i>Pontogeneia cf. rostrata</i> Gurjanova, 1938	13.6	3.3	2.9
<i>Paracalliopiella pratti</i> (Barnard, 1954)	-	0.1	-
<i>Pleustes depressa</i> Alderman, 1936	0.7	0.9	-
<i>Hyale frequens</i> Stout, 1913 (group)	0.1	-	-
<i>Parallorchestes</i> spp.	-	0.6	-
<i>Eobrolgus spinosus</i> (Holmes, 1905)	0.1	-	-
<i>Ampithoe</i> spp.	0.6	4.7	1.0
<i>Ampithoe lacertosa</i> Bate, 1858	0.7	3.8	0.4
<i>Ampithoe simulans</i> Alderman, 1936	-	0.1	0.1
<i>Peramphithoe</i> spp.	0.1	-	0.9
<i>Peramphithoe humeralis</i> (Stimpson, 1864)	0.7	1.3	0.2
<i>Peramphithoe lindbergi</i> (Gurjanova, 1938)	0.3	2.7	0.6
<i>Peramphithoe mea</i> (Gurjanova, 1938)	1.2	2.1	3.1
<i>Peramphithoe plea</i> (Barnard, 1965)	0.1	-	-
<i>Photis</i> spp.	-	0.4	-
<i>Ischyrocerus anguipes</i> (Kroyer, 1838)	4.7	6.9	4.3
<i>Jassa</i> spp.	0.1	0.1	-
<i>Aoroides</i> spp.	1.8	0.5	0.9
<i>Aoroides inermis</i> Conlan and Bousfield, 1982	0.1	0.1	0.5
<i>Aoroides intermedius</i> Conlan & Bousfield, 1982	5.2	4.3	2.1

	Site 1	Site 2	Site 3
<i>Corophium</i> spp.	0.1	-	0.1
<i>Corophium salmonis</i> Stimpson, 1857	-	-	0.1
Unidentified amphipod sp. 1	0.1	-	-
<i>Caprella incisa</i> Mayer, 1903	-	0.1	2.1
<i>Caprella laeviuscula</i> Mayer, 1903	1.1	10.3	63.6
<i>Caprella verrucosa</i> Boeck, 1872	0.1	0.1	2.8
<i>Metacaprella kennerlyi</i> (Stimpson, 1864)	0.6	1.2	1.5
<b>Order Decapoda</b>			
Unidentified shrimp zoea	1.3	-	-
<i>Pandalus tridens</i> Rathbun, 1902	0.2	-	-
<i>Hippolyte clarki</i> Chace, 1951	0.3	0.1	-
<i>Hippolyte californiensis</i>	0.2	-	-
<i>Heptacarpus brevisrostris</i> (Dana, 1852)	1.2	2.2	0.1
<i>Heptacarpus stylus</i> (Stimpson, 1864)	-	0.1	-
<i>Heptacarpus tenuissimus</i> Holmes, 1900	0.1	-	-
<i>Eualus suckleyi</i> (Stimpson, 1864)	0.1	-	-
<i>Eualus herdmani</i> (Walker, 1898)	0.1	-	-
<i>Spirontocaris</i> spp.	-	0.1	-
<i>Pagurus</i> spp.	0.4	0.5	-
<i>Pagurus armatus</i> (Dana, 1851)	-	0.2	-
<i>Pagurus granosimanus</i> (Stimpson, 1858)	-	0.3	-
<i>Pagurus beringanus</i> (Benedict, 1892)	-	-	0.1
<i>Pagurus caurinus</i> Hart, 1971	-	0.1	-
<i>Pagurus hirsutiusculus</i> (Dana, 1851)	0.1	0.3	0.1
Unidentified porcellanid (zoea)	0.1	-	-
Unidentified crab (megalopa)	-	0.1	-
<i>Oregonia gracilis</i> Dana, 1851	0.7	-	0.1
<i>Pugettia producta</i> (Randall, 1839)	-	-	0.1
<i>Pugettia gracilis</i> Dana, 1851	3.2	4.6	0.4
<i>Telmessus cheiragonus</i> (Tilesius, 1815)	0.1	0.2	0.1
Unidentified Cancer zoea	2.6	-	-
<i>Cancer oregonensis</i> (Dana, 1852)	0.2	-	0.1
<i>Cancer magister</i> Dana, 1852	0.1	-	0.1
Unidentified pinixid (megalopa and zoea)	0.1	-	-
<b>Phylum Bryozoa</b>			
cheilostome sp. 1	-	-	0.3
cheilostome sp. 2	-	0.1	-
cheilostome sp. 3	-	-	0.1
cheilostome sp. 4	-	0.1	-
cheilostome sp. 5	0.1	0.1	-
cheilostome sp. 6	-	0.1	0.1
cheilostome sp. 7	-	-	0.1
cheilostome sp. 8	-	0.1	-

	Site 1	Site 2	Site 3
<i>Tubulipora</i> spp. (cyclostome sp. 1)	-	0.1	-
cyclostome sp. 2	-	0.1	-
<b>Phylum Echinodermata</b>			
<i>Leptasterias hexactis</i> (Stimpson, 1862)	0.1	1.8	-
Unidentified ophiuroid (juvenile)	0.1	-	0.1
<i>Strongylocentrotus droebachiensis</i> (O. F. Muller, 1776)	0.1	-	-
<b>Phylum Vertebrata, Class Osteichthyes</b>			
<i>Pholis laeta</i> (Cope, 1873)	0.1	0.4	0.1
<i>Pholis ornata</i> (Girard, 1854)	-	-	-
<i>Apodichthyes flavidus</i> Girard, 1854	0.4	0.3	0.4
<b>Total Number Taxa</b>	<b>66</b>	<b>65</b>	<b>62</b>

- indicates absence of species

supported the highest abundances of the snails *L. vincta*, *L. variegata*, and *Alia gausapata* and the lowest abundance of the snail *Onoba carpenteri* (Table 11). Site 2 also supported the largest populations of: amphipods of the family Ampithoidae, the gammarid amphipod *Ischyrocerus anguipes*, hermit crabs, the shrimp *Heptacarpus brevirostris*, the kelp crab *Pugettia gracilis*, and the sea star *Leptasterias hexactis*. Bryozoans were most diverse at this site also. Site 3 supported the highest diversity of gastropods as well as the highest diversity and largest populations of polychaetes, isopods, and caprellid amphipods (Table 11).

Several patterns emerge from the mean number of epifauna on plants collected each month (Table 12). Megalopae and zoea occurred only on plants collected in May. The population of the gammarid amphipod *Pontogeneia rostrata* was large from May to July then declined to almost zero, whereas the amphipod *Pleustes depressa* was present only from July to September (Table 12). Isopod populations peaked in July and August. Mysids were most abundant on *S. muticum* in August. *Caprella laeviuscula* populations increased from May to July. Both *Lacuna* species were most abundant from July to September as were the snail *Alia gausapata*, the mussel *Mytilus spp.*, the shrimp *Heptacarpus brevirostris*, and the sea star *Leptasterias hexactis* (Table 12). Total snail density on *S. muticum* for each site (Figure 12) increases at Sites 1 and 3 over time. Renkonen's index revealed that May samples were unique with respect to the abundance of epibionts from all other months' samples (Table 13).

Principle component analysis revealed that 62% of variation was due to components 1 (37%) and 2 (25%). Component 3 accounted for only 13% of the

**Table 12.** The mean number of individuals of each species present on each *S. muticum* plant for each month from May to September 1997. Site data for each month were pooled and divided by the number of plants sampled each month.

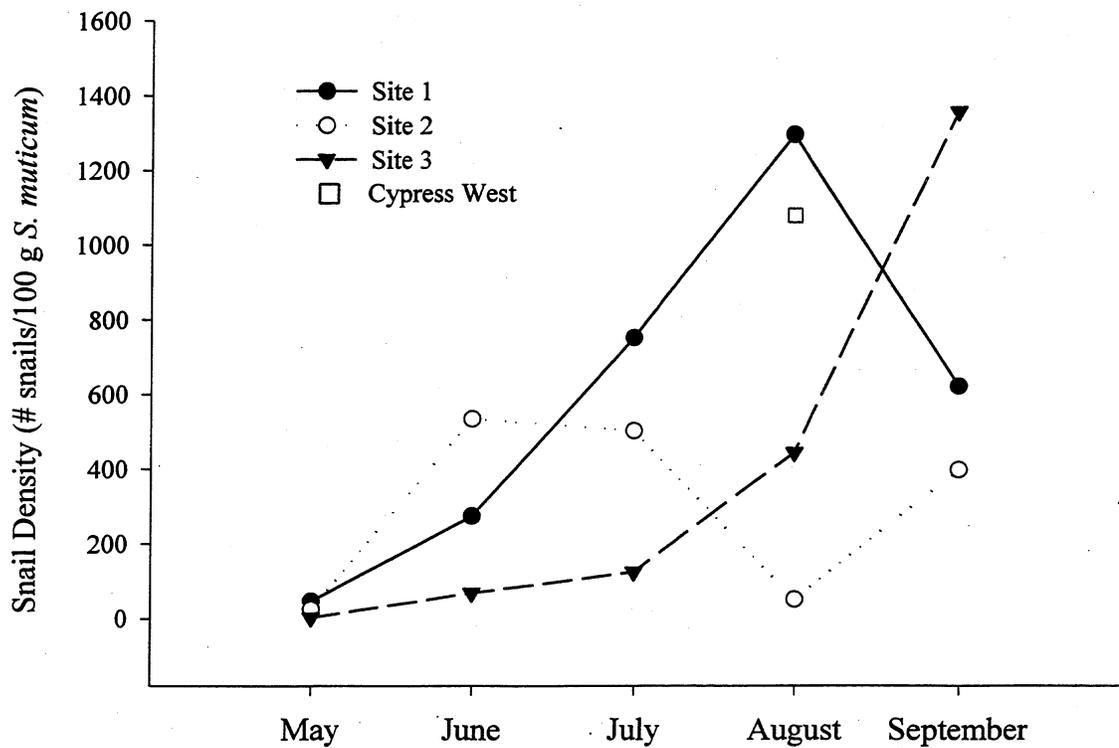
	May	June	July	August	September
<b>Total Number <i>S. muticum</i> Plants (<i>n</i>)</b>	9	9	12	12	9
<b>Phylum Cnidaria</b>					
<i>Eperetmus typus</i> Bigelow, 1915	-	-	0.1	-	-
<i>Aurelia aurita</i> (Linnaeus, 1758)	0.2	-	-	-	-
<i>Halicyclstus stejnegeri</i> Kishinouye, 1899	-	0.3	-	-	-
<i>Epiactis prolifera</i> Verrill, 1869	-	-	-	-	0.1
<b>Phylum Ctenophora</b>					
<i>Pleurobrachia bachia</i> A. Agassiz, 1860	0.1	-	-	-	-
<b>Phylum Nemertea</b>					
Unidentified species	-	0.2	0.2	0.1	0.2
<b>Phylum Nematoda</b>					
Unidentified species	-	-	0.1	-	-
<b>Phylum Annelida</b>					
<i>Gyptis brevipalpa</i> (Hartmann-Shroder)	-	0.1	0.1	-	-
<i>Nereis (Nereis) procera</i> Ehlers, 1868	-	-	-	0.1	-
<i>Platynereis bicanaliculata</i> (Baird, 1863)	-	3.4	0.6	3.8	1.6
Unidentified nereids	0.8	0.6	0.3	0.3	0.3
<i>Harmothoe imbricata</i> (Linnaeus, 1766)	0.1	0.8	0.1	-	0.4
Unidentified terebellid	-	-	0.5	-	-
Unidentified spirorbid	-	-	0.1	0.1	-
<b>Phylum Mollusca</b>					
<b>Class Gastropoda</b>					
<i>Margarites (Valvatella) pupillus</i> (Gould, 1841)	-	0.2	0.3	0.3	3.0
<i>Margarites (Margarites) marginatus</i> Dall, 1919	-	-	-	0.4	0.6
<i>Lirularia lirulata</i> (Carpenter, 1864)	-	-	-	-	0.6
<i>Tectura scutum</i> (Rathke, 1833)	-	-	-	-	0.1
<i>Lottia</i> spp.	-	-	-	0.1	-
<i>Lacuna (Epheria) variegata</i> Carpenter, 1864	5.0	43.6	243.8	57.5	134.1
<i>Lacuna (Epheria) vincta</i> (Montagu, 1803)	16.1	362.7	499.3	469.0	1121.7
<i>Littorina sitkana</i> Philippi, 1845	-	-	-	0.5	-
<i>Littorina scutulata</i> (Gould, 1849)	-	-	-	0.1	-
<i>Onoba (Onoba) carpenteri</i> (Weinkauff, 1885)	2.7	1.1	1.8	1.3	7.2
<i>Alia gausapata</i> (Carpenter, 1864)	0.1	0.6	4.6	0.9	5.0
<i>Haminoea vesicula</i> (Gould, 1855)	-	-	0.1	-	-
Unidentified dorid	-	0.2	-	-	-
<i>Flabellina verrucosa</i> (M. Sars, 1829)	-	0.1	-	-	-

	May	June	July	August	September
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	-	-	-	-	0.1
<b>Class Bivalvia</b>					
<i>Mytilus</i> spp.	-	1.0	0.3	0.5	0.9
<i>Chlamys (Chlamys) hastata</i> (Sowerby, 1843)	-	-	0.1	-	-
<b>Phylum Arthropoda</b>					
<b>Class Pycnogonid</b>					
Unidentified pycnogonid (juvenile)	-	-	-	0.1	-
<i>Phoxichilidium femoratum</i> (Rathke, 1799)	-	0.1	-	-	-
<b>Order Mysidacea</b>					
<i>Mysis litoralis</i> (Banner, 1948)	-	0.2	0.1	8.0	-
<i>Neomysis mercedis</i> Holmes, 1897	0.1	-	-	-	-
<b>Order Tanaidacea</b>					
<i>Leptocheilia savignyi</i> (Kroyer, 1842)	0.1	-	-	-	-
<b>Order Isopoda</b>					
<i>Gnorimosphaeroma oregonense</i> Dana, 1854-55	0.2	-	-	-	-
Unidentified idotoid juveniles	-	0.1	-	-	0.3
<i>Idotea (Idotea) fewkesi</i> Richardson, 1905	-	0.7	-	4.1	-
<i>Idotea (Idotea) ochotensis</i> Brandt, 1851	0.1	0.2	2.0	0.4	-
<i>Idotea (Idotea) rufescens</i> Fee, 1926	0.1	0.7	3.2	4.2	1.0
<i>Idotea (Idotea) urotoma</i> Stimpson, 1864	-	-	-	-	0.1
<i>Idotea (Pentidotea) resecata</i> Stimpson, 1857	-	-	1.1	0.3	-
<i>Idotea (Pentidotea) vosnesenskii</i> (Brandt, 1851)	-	-	-	-	0.1
<b>Order Amphipoda</b>					
<i>Accedomoera vagor</i> Barnard, 1969	-	0.1	-	0.1	-
<i>Pontogeneia cf. rostrata</i> Gurjanova, 1938	9.8	13.2	9.5	0.3	0.7
<i>Paracalliopiella pratti</i> (Barnard, 1954)	0.3	-	0.1	-	-
<i>Pleustes depressa</i> Alderman, 1936	-	-	0.3	0.9	1.3
<i>Hyale frequens</i> Stout, 1913 (group)	-	-	-	0.2	-
<i>Parallorchestes</i> spp.	-	-	0.8	-	-
<i>Eobrolgus spinosus</i> (Holmes, 1905)	0.1	-	-	-	-
<i>Ampithoe</i> spp.	0.7	0.7	0.9	1.5	7.0
<i>Ampithoe lacertosa</i> Bate, 1858	0.8	2.3	0.1	1.8	3.3
<i>Ampithoe simulans</i> Alderman, 1936	-	-	0.1	-	0.1
<i>Peramphithoe</i> spp.	0.1	0.2	0.4	0.5	0.4
<i>Peramphithoe humeralis</i> (Stimpson, 1864)	0.8	0.9	0.1	0.4	1.8
<i>Peramphithoe lindbergi</i> (Gurjanova, 1938)	0.7	0.4	1.0	-	3.7
<i>Peramphithoe mea</i> (Gurjanova, 1938)	1.7	4.4	1.7	2.2	0.3
<i>Peramphithoe plea</i> (Barnard, 1965)	0.2	-	-	-	-
<i>Photis</i> spp.	-	-	0.3	-	0.2
<i>Ischyrocerus anguipes</i> (Kroyer, 1838)	5.5	4.4	4.8	2.3	8.2
<i>Jassa</i> spp.	0.2	-	0.1	-	0.1
<i>Aoroides</i> spp.	1.3	1.8	1.6	0.1	0.8
<i>Aoroides inermis</i> Conlan and Bousfield, 1982	-	0.3	0.5	0.1	0.2
<i>Aoroides intermedius</i> Conlan & Bousfield, 1982	2.9	6.7	3.4	3.6	2.0

	May	June	July	August	September
<i>Corophium</i> spp.	0.1	-	0.2	-	-
<i>Corophium salmonis</i> Stimpson, 1857	-	0.1	-	-	-
Unidentified amphipod sp. 1	-	-	0.1	-	-
<i>Caprella incisa</i> Mayer, 1903	0.3	0.8	0.9	1.3	0.2
<i>Caprella laeviuscula</i> Mayer, 1903	32.1	12.3	46.6	12.2	13.6
<i>Caprella verrucosa</i> Boeck, 1872	-	0.4	1.5	2.4	0.2
<i>Metacaprella kennealyi</i> (Stimpson, 1864)	0.8	0.1	2.1	-	2.3
<b>Order Decapoda</b>					
Unidentified shrimp zoea	1.9	-	-	-	-
<i>Pandalus tridens</i> Rathbun, 1902	-	0.3	-	-	-
<i>Hippolyte clarki</i> Chace, 1951	0.1	0.6	0.1	-	-
<i>Hippolyte californiensis</i>	-	0.2	0.1	-	-
<i>Heptacarpus brevirostris</i> (Dana, 1852)	0.2	0.1	1.5	1.9	1.3
<i>Heptacarpus stylus</i> (Stimpson, 1864)	-	-	-	0.1	-
<i>Heptacarpus tenuissimus</i> Holmes, 1900	-	-	-	-	0.2
<i>Eualus suckleyi</i> (Stimpson, 1864)	-	0.1	-	-	-
<i>Eualus herdmani</i> (Walker, 1898)	0.1	-	-	-	-
<i>Spirontocaris</i> spp.	-	-	-	-	0.1
<i>Pagurus</i> spp.	0.9	0.1	-	0.3	0.2
<i>Pagurus armatus</i> (Dana, 1851)	-	-	-	-	0.3
<i>Pagurus granosimanus</i> (Stimpson, 1858)	-	0.1	-	0.1	0.2
<i>Pagurus beringanus</i> (Benedict, 1892)	-	0.1	-	-	-
<i>Pagurus caurinus</i> Hart, 1971	-	-	0.1	0.1	-
<i>Pagurus hirsutiusculus</i> (Dana, 1851)	-	0.2	-	0.5	-
Unidentified porcellanid (zoea)	0.1	-	-	-	-
Unidentified crab megalopa	-	-	-	-	0.1
<i>Oregonia gracilis</i> Dana, 1851	0.1	-	-	0.3	1.0
<i>Pugettia producta</i> (Randall, 1839)	-	-	0.1	0.1	-
<i>Pugettia gracilis</i> Dana, 1851	1.5	4.4	0.8	4.3	2.8
<i>Telmessus cheiragonus</i> (Tilesius, 1815)	0.1	0.2	-	0.1	0.2
Unidentified Cancer zoea	3.9	-	-	-	-
<i>Cancer oregonensis</i> (Dana, 1852)	-	-	0.2	0.1	0.2
<i>Cancer magister</i> Dana, 1852	-	-	0.2	-	-
Unidentified pinixid (megalopa and zoea)	0.1	0.1	-	-	-
<b>Phylum Bryozoa</b>					
cheilostome sp. 1	-	0.2	0.1	0.1	0.1
cheilostome sp. 2	-	-	-	-	0.1
cheilostome sp. 3	-	-	0.1	-	-
cheilostome sp. 4	-	-	0.1	-	0.1
cheilostome sp. 5	-	0.1	-	0.2	-
cheilostome sp. 6	-	0.1	-	-	-
cheilostome sp. 7	0.1	-	-	-	-
cheilostome sp. 8	-	0.1	-	-	-
cheilostome sp. 9	0.1	-	-	-	-
<i>Tubulipora</i> spp. (cyclostome sp. 1)	0.1	-	-	-	-

	May	June	July	August	September
cyclostome sp. 2	-	-	-	0.1-	-
<b>Phylum Echinodermata</b>					
<i>Leptasterias hexactis</i> (Stimpson, 1862)	-	0.8	0.3	0.6	1.3
Unidentified ophiuroid (juvenile)	-	-	-	-	0.2
<i>Strongylocentrotus droebachiensis</i> (O. F. Muller, 1776)	-	-	-	-	0.1
<b>Phylum Vertebrata, Class Osteichthyes</b>					
<i>Pholis laeta</i> (Cope, 1873)	-	0.1	-	0.1	0.7
<i>Pholis ornata</i> (Girard, 1854)	-	-	-	0.1	-
<i>Apodichthyes flavidus</i> Girard, 1854	0.6	0.6	0.6	0.2	0.1
<b>Total Number Taxa</b>	<b>46</b>	<b>56</b>	<b>57</b>	<b>55</b>	<b>57</b>

- indicates absence of species



**Figure 12.** Average total snail density (*Margarites pupillus*, *Lacuna vincta*, *L. variegata*, *Alia gausapata*, *Onuba carpenteri*) on *S. muticum* each month at each site. The average densities are given as number of individuals per 100 grams wet weight of *S. muticum* tissue ( $n = 3$ ). Data is only available for one month of sampling at Cypress West.

**Table 13.** Renkonen index showing percent similarity of samples from each month based on total number of individuals of each epibiont species ( $n = 9, 9, 12, 12,$  and  $9$  plants for May through September respectively). Data (total number of individuals of each species) from each month were pooled for all sites ( $n = 18, 15,$  and  $18$  plants for Sites 1, 2, and 3 respectively).

	May	June	July	August	September
September	27	89	73	93	-
August	28	92	93	-	■
July	32	75	-	■	■
June	35	-	■	■	■
May	-	■	■	■	■

High similarity

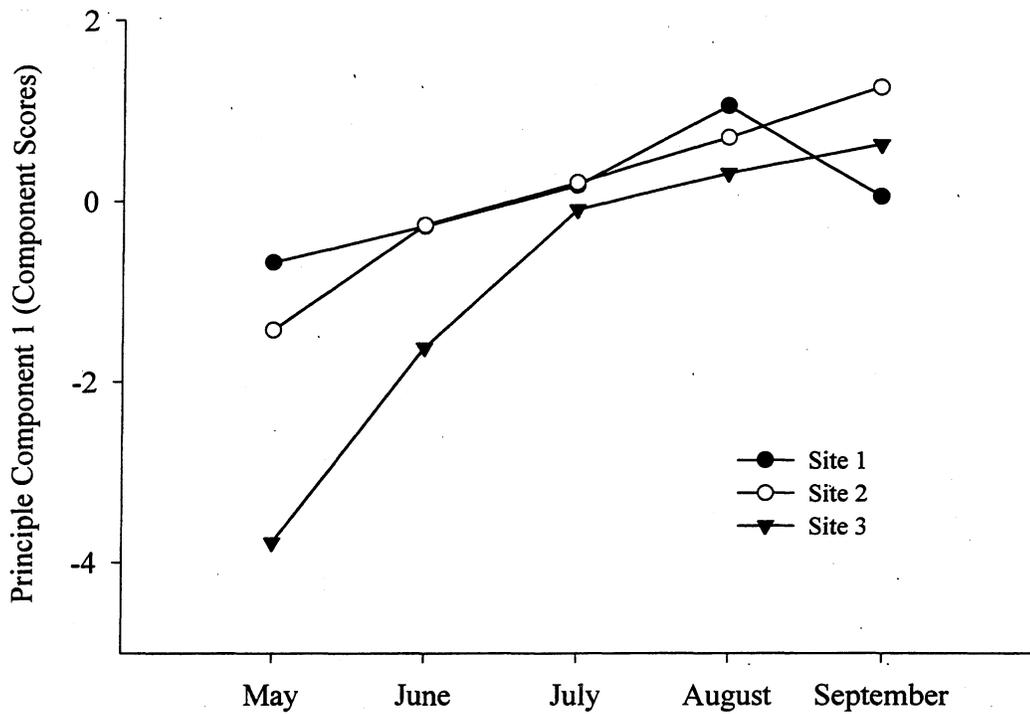
Intermediate similarity

Low similarity

variation and therefore is not discussed further. Component 1 showed a strong monthly trend (Figure 13) primarily due to the density of: *Lacuna vineta*, *L. variegata*, *Alia gausapata*, *Ampithoe* spp., and *Pugettia gracilis*. The pattern is less distinct in August and September samples (Figure 13). Component 2 showed a significant difference between Sites 1 and 3, but not between Site 2 and either Site 1 or 3, according to a one-way ANOVA of component scores (Table 14;  $F = 8.04$ ,  $p < 0.01$ ) and a Tukey HSD test. This difference between sites (component 2) is primarily due to differences in the densities of *Peramphithoe* spp., idotoid isopods, and caprellid amphipods.

#### **Evening Collection at Hat Island**

Of the two species reported to migrate daily on eelgrass, *Caprella californica* was never found on *S. muticum* and *Idotea ressecata* was found on only three plants during the study (collected at Site 3 in July and August). A total of 17 individuals on those three plants made this species only the fourth most common idotoid isopod of six species. *C. californica* and *I. ressecata* were not found on plants from the evening collection. Since these are the two known migrators and their abundance was low, time of collection is not an important factor in characterizing *S. muticum* communities.



**Figure 13.** Relationship between principle component 1 (component scores) and month of collection for *S. muticum* epifauna at each site. Principle component analysis was run on the densities (total number of individuals per site per month) of the 15 most abundant taxa on *S. muticum*.

**Table 14.** Results of principle component analysis. Total numbers of individuals in each of the fifteen most commonly occurring taxa associated with *S. muticum* were used in the analysis. Bold characters indicate high variable loadings.

	PC1	PC2
Eigenvalue	2.026	1.346
Percent of Total Variation	37.3	24.8
Chi-square	100	62.9
<i>df</i>	104	90
<b>Variable Loadings</b>		
Nereidae	0.046	-0.098
<i>Margarites pupillus</i>	0.107	0.080
<i>Lacuna variegata</i>	<b>0.518</b>	-0.111
<i>Lacuna vincta</i>	<b>0.661</b>	0.061
<i>Onuba carpenteri</i>	0.014	0.205
<i>Alia gausapata</i>	<b>0.271</b>	-0.182
<i>Idotea</i> spp.	0.132	<b>-0.470</b>
<i>Pontogenia rostrata</i>	-0.168	0.210
<i>Ampithoe</i> spp.	<b>0.239</b>	-0.106
<i>Peramphithoe</i> spp.	-0.045	<b>-0.232</b>
<i>Ichyrocerus anguipes</i>	-0.055	-0.133
<i>Aoroides</i> spp.	0.022	0.100
Caprellidea	-0.144	<b>-0.698</b>
<i>Pugettia gracilis</i>	<b>0.213</b>	0.161
Hippolytidae	0.183	0.150

## Comparison of *Sargassum muticum* and *Laminaria saccharina*

### Plants and Communities

This section compares data from the 21 *S. muticum* and 21 *L. saccharina* plants collected in August and September, 1997.

*S. muticum* and *L. saccharina* were similar in length and wet weight (Table 5). The dry to wet weight ratio for *L. saccharina* was  $0.214 \pm 0.007$ . The particulate load sustained by *S. muticum* and *L. saccharina* differs significantly by month with *S. muticum* supporting higher loads than *L. saccharina* according to a three-way ANOVA (Table 15). Percent organic matter of the particulate load does not differ for the two species but does differ significantly between August and September samples (Table 15).

*S. muticum* and *L. saccharina* differed in species composition and epifauna abundance. Seventy-six species occurred on *S. muticum* and 65 on *L. saccharina* (Table 16). The mean number of species per plant was higher on *S. muticum* (20) than on *L. saccharina* (10) at Sites 2 and 3 but was the same at Site 1 (11, Figure 14). *S. muticum* supported over twice as many species on the basis of plant wet weight than *L. saccharina* at Sites 1 and 3 but not at Site 2 (Figure 14). *S. muticum* also consistently supported many more individuals than did *L. saccharina* (Figure 15). The rarefaction curves are different for the epibiont communities associated with the two algae (Figure 16). For small epibiont communities, the curves predict higher species richness for *L. saccharina*. However, at sample sizes of 200 or more epibiont individuals, *S. muticum* harbors a more diverse epibiont community. *L. saccharina* supports a stable level of at approximately 10 species per plant while *S.*

**Table 15.** Results of four three-way ANOVA tests of *Sargassum muticum* and *Laminaria saccharina* data from August and September 1997 collections: plant length (length), plant wet weight (weight), particulate load, and percent organic matter of particulate load (% organic matter). The three variables used to calculate each ANOVA were month, site, and algal species. *F* test values are given with significance at the 0.05 level indicated by an asterisk. Interaction terms are as follows: M, month; S, site; Sp, species.

<b>Factor</b>	<b>Month</b>	<b>Site</b>	<b>Species</b>	<b>M×S</b>	<b>M×Sp</b>	<b>S×Sp</b>	<b>M×S×Sp</b>
Length	0.1	6.5*	0.2	1.3*	5.2	1.2	0.9
Weight	1.1	15.8*	0.1	0.5	5.2*	10.0*	1.3
Particulate load	10.9*	0.5	5.1*	0.4	0.1	0.8	2.7
% Organic matter	4.8*	0.4	0.5	1.4	0.1	0.7	0.1

\*  $p < 0.05$

**Table 16.** Number of *S. muticum* and *L. saccharina* plants containing at least one individual of the following epifaunal species and the total number of individuals on the 21 *S. muticum* (*S.m.*) and 21 *L. saccharina* (*L.s.*) plants collected in August and September 1997 (- indicates absence of the species).

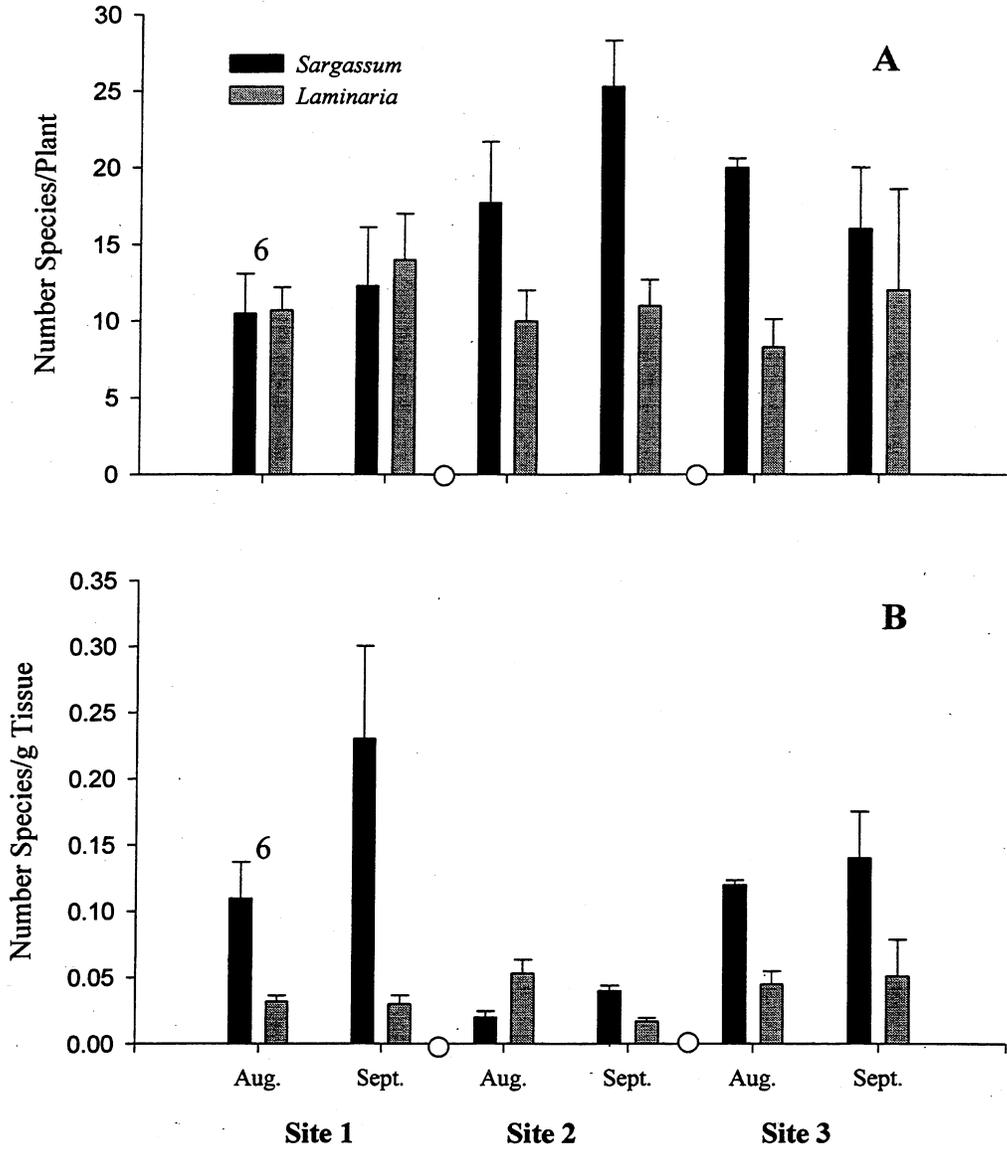
Plant Species	# Plants with ≥ 1 individual		Total # Individuals on 21 Plants	
	<i>S. m.</i>	<i>L. s.</i>	<i>S. m.</i>	<i>L. s.</i>
<b>Phylum Cnidaria</b>				
<b>Class Hydrozoa</b>				
<i>Obelia geniculata</i> (Linnaeus, 1758)	-	1	-	8
<b>Class Anthozoa</b>				
<i>Epiactis prolifera</i> Verrill, 1869	1	1	1	2
<b>Phylum Nemertea</b>				
Unidentified species	2	2	3	3
<b>Phylum Annelida, Class Polychaeta</b>				
<i>Nereis (Nereis) vexillosa</i> Grube, 1851	-	1	-	1
<i>Nereis (Nereis) eakini</i> Hartman, 1936	-	1	-	2
<i>Nereis (Nereis) procera</i> Ehlers, 1868	1	-	1	-
<i>Platynereis bicanaliculata</i> (Baird, 1863)	12	9	59	31
Unidentified nereids	2	-	6	-
<i>Harmothoe imbricata</i> (Linnaeus, 1766)	2	6	4	7
<i>Chrysopetalum occidentale</i> (Johnson, 1897)	-	1	-	1
<i>Lumbrineris zonata</i> (Johnson, 1901)	-	1	-	1
Unidentified terebellid	-	4	-	4
Unidentified sabellid	-	1	-	1
Unidentified spirorbid	1	2	1	4
Unidentified polychaete sp. 1	-	1	-	1
Unidentified polychaete sp. 2	-	1	-	1
<b>Phylum Mollusca</b>				
<b>Class Polyplacophora</b>				
<i>Tonicella lineata</i> (Woods, 1815)	-	1	-	1
<b>Class Gastropoda</b>				
<i>Margarites (Valvatella) pupillus</i> (Gould, 1841)	9	11	31	49
<i>Margarites (Margarites) marginatus</i> Dall, 1919	5	3	10	3
<i>Lirularia lirulata</i> (Carpenter, 1864)	2	3	5	4
<i>Tectura scutum</i> (Rathke, 1833)	1	-	1	-
<i>Lottia</i> spp.	1	-	1	-
<i>Lacuna (Epheria) variegata</i> Carpenter, 1864	20	21	1,897	231
<i>Lacuna (Epheria) vincta</i> (Montagu, 1803)	21	21	15,723	3,927
<i>Littorina sitkana</i> Philippi, 1845	4	-	6	-
<i>Littorina scutulata</i> (Gould, 1849)	1	2	1	3
<i>Onoba (Onoba) carpenteri</i> (Weinkauff, 1885)	5	11	80	59
<i>Alia gausapata</i> (Carpenter, 1864)	10	4	56	16

Plant Species	# Plants with ≥ 1 individual		Total # Individuals on 21 Plants	
	S. m.	L.s.	S. m.	L.s.
<i>Granulina margaritula</i> (Carpenter, 1857)	-	1	-	2
<i>Turbonilla</i> spp.	-	1	-	1
<i>Doridella steinbergae</i> (Lance, 1962)	-	1	-	1
<i>Archidoris montereyensis</i> (Cooper, 1862)	-	2	-	3
<i>Melibe leonina</i> (Gould, 1853)	-	1	-	1
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	1	1	1	1
<b>Class Bivalvia</b>				
<i>Mytilus</i> spp.	8	2	14	2
<b>Phylum Arthropoda</b>				
<b>Class Pycnogonida</b>				
Unidentified pycnogonid (juvenile)	1	-	1	-
<b>Class Cirripedia</b>				
<i>Balanus crenatus</i> Bruguire, 1789	-	2	-	3
<b>Class Malacostraca</b>				
<i>Mysis litoralis</i> (Banner, 1948)	3	2	96	3
<i>Leptochelia savignyi</i> (Kroyer, 1842)	-	1	-	1
<i>Gnorimosphaeroma oregonense</i> Dana, 1854-55	-	5	-	9
Unidentified idotoid juveniles	1	-	3	-
<i>Idotea (Idotea) fewkesi</i> Richardson, 1905	5	3	49	3
<i>Idotea (Idotea) ochotensis</i> Brandt, 1851	1	-	5	-
<i>Idotea (Idotea) rufescens</i> Fee, 1926	9	-	59	-
<i>Idotea (Idotea) urotoma</i> Stimpson, 1864	1	-	1	-
<i>Idotea (Pentidotea) resecata</i> Stimpson, 1857	2	-	4	-
<i>Idotea (Pentidotea) vosnesenskii</i> (Brandt, 1851)	1	-	1	-
<i>Accedomoera vagor</i> Barnard, 1969	1	1	1	7
<i>Pontogeneia cf. rostrata</i> Gurjanova, 1938	6	3	9	5
<i>Pleustes depressa</i> Alderman, 1936	7	4	23	6
<i>Hyale frequens</i> Stout, 1913 (group)	1	-	1	-
<i>Melita dentata</i> (Kroyer, 1842)	-	1	-	1
<i>Ampithoe</i> spp.	9	-	78	-
<i>Ampithoe lacertosa</i> Bate, 1858	9	10	51	41
<i>Ampithoe simulans</i> Alderman, 1936	1	-	1	-
<i>Peramphithoe</i> spp.	4	-	10	-
<i>Peramphithoe humeralis</i> (Stimpson, 1864)	5	5	21	13
<i>Peramphithoe lindbergi</i> (Gurjanova, 1938)	4	-	33	-
<i>Peramphithoe mea</i> (Gurjanova, 1938)	6	-	29	-
<i>Photis</i> spp.	1	-	2	-
<i>Ischyrocerus anguipes</i> (Kroyer, 1838)	13	-	101	-
<i>Jassa</i> spp.	1	-	1	-
<i>Aoroides</i> spp.	5	8	8	26
<i>Aoroides inermis</i> Conlan and Bousfield, 1982	2	-	3	-
<i>Aoroides intermedius</i> Conlan & Bousfield, 1982	13	10	61	55
<i>Corophium</i> spp.	-	1	-	1

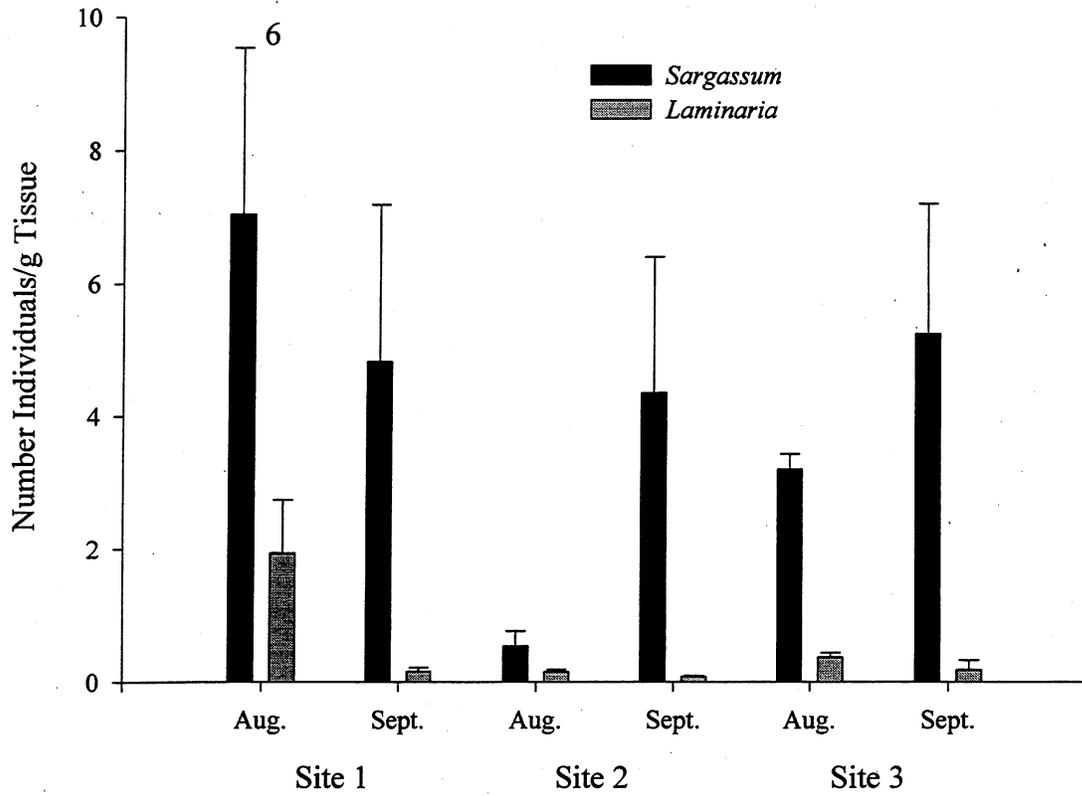
Plant Species	# Plants with ≥ 1 individual		Total # Individuals on 21 Plants	
	S. m.	L.s.	S. m.	L.s.
Unidentified gammarid amphipod sp. 2	-	1	-	-
<i>Caprella incisa</i> Mayer, 1903	5	-	17	-
<i>Caprella laeviuscula</i> Mayer, 1903	13	2	268	3
<i>Caprella verrucosa</i> Boeck, 1872	7	1	31	1
<i>Metacaprella kennerlyi</i> (Stimpson, 1864)	4	-	21	-
<i>Heptacarpus</i> spp.	-	2	-	2
<i>Heptacarpus brevirostris</i> (Dana, 1852)	8	6	35	14
<i>Heptacarpus stylus</i> (Stimpson, 1864)	1	1	1	1
<i>Heptacarpus tenuissimus</i> Holmes, 1900	1	-	2	-
<i>Spirontocaris</i> spp.	1	-	1	-
<i>Spirontocaris prionata</i> (Stimpson, 1864)	-	1	-	1
<i>Pagurus</i> spp.	3	-	6	-
<i>Pagurus armatus</i> (Dana, 1851)	3	1	3	4
<i>Pagurus granosimanus</i> (Stimpson, 1858)	2	-	3	-
<i>Pagurus caurinus</i> Hart, 1971	1	-	1	-
<i>Pagurus hirsutiusculus</i> (Dana, 1851)	1	-	6	-
Unidentified crab (megalopa)	1	-	1	-
<i>Oregonia gracilis</i> Dana, 1851	3	1	12	1
<i>Pugettia producta</i> (Randall, 1839)	1	-	1	-
<i>Pugettia gracilis</i> Dana, 1851	14	8	76	12
<i>Telmessus cheiragonus</i> (Tilesius, 1815)	3	-	3	-
<i>Cancer gracilis</i> Dana, 1852	-	1	-	1
<i>Cancer oregonensis</i> (Dana, 1852)	2	6	3	12
<b>Phylum Bryozoa</b>				
<b>Class Stenolaemata</b>				
cheilostome sp. 1	2	-	2	-
cheilostome sp. 2	1	1	1	1
cheilostome sp. 4	1	-	1	-
cheilostome sp. 5	2	-	2	-
cheilostome sp. 10	-	1	-	1
<i>Membranipora membranacea</i> (Linnaeus, 1767)	-	7	-	7
<i>Bugula pacifica</i> Robertson, 1905	-	2	-	4
<i>Cribrilina corbicula</i> (O'Donoghue, 1923)	-	1	-	1
<b>Class Gymnolaemata</b>				
cyclostome sp. 2	1	-	1	-
cyclostome sp. 3	-	1	-	1
<b>Phylum Echinodermata</b>				
<b>Class Asteroidea</b>				
<i>Leptasterias hexactis</i> (Stimpson, 1862)	6	6	19	19
<b>Class Ophiuroidea</b>				
Unidentified ophiuroid (juvenile)	2	-	2	-

Plant Species	# Plants with ≥ 1 individual		Total # Individuals on 21 Plants	
	<i>S. m.</i>	<i>L.s.</i>	<i>S. m.</i>	<i>L.s.</i>
<b>Class Echinoidea</b>				
<i>Strongylocentrotus droebachiensis</i> (O. F. Muller, 1776)	1	2	1	3
<b>Phylum Vertebrata, Class Osteichthyes</b>				
<i>Pholis laeta</i> (Cope, 1873)	3	-	7	-
<i>Pholis ornata</i> (Girard, 1854)	1	-	1	-
<i>Apodichthyes flavidus</i> Girard, 1854	2	-	3	-
<i>Globiesox meandricus</i> (Girard, 1858)	-	1	-	1
			19,084	4,635

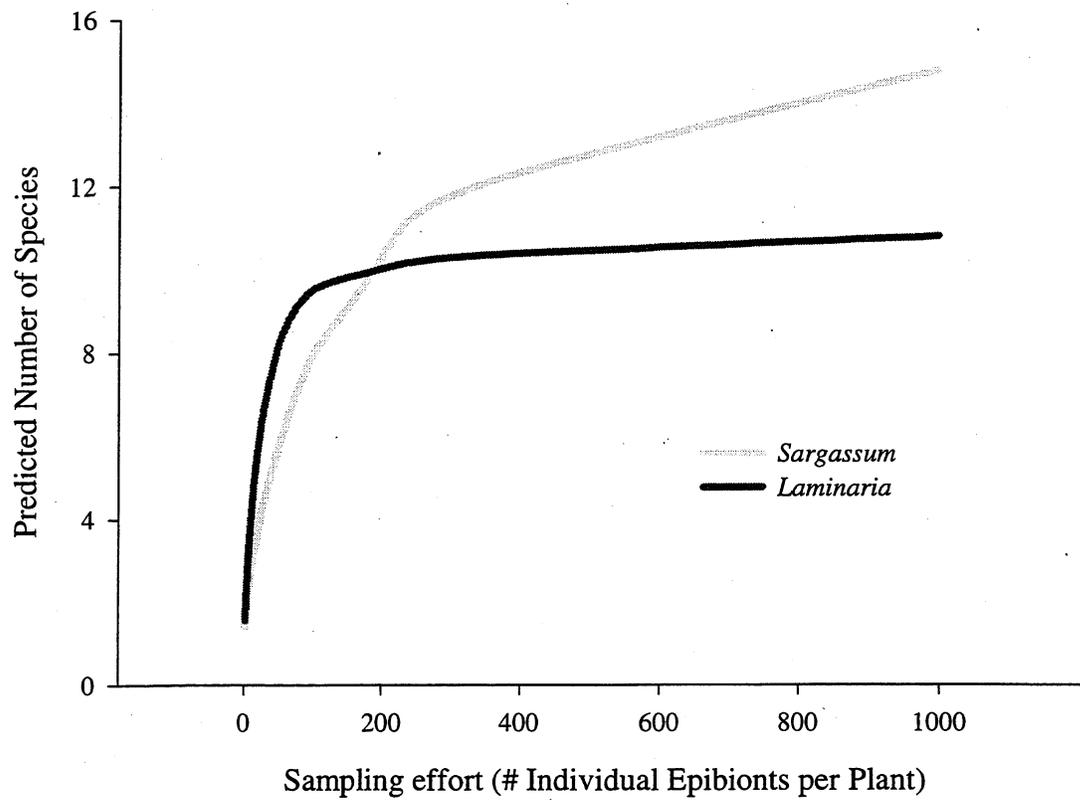
- indicates absence of species



**Figure 14.** A comparison of *S. muticum* and *L. saccharina* epibiont communities for August and September 1997 collections at the three sites: (A) number of epibiont species per plant and (B) number of species per gram wet weight. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above pair of bars).



**Figure 15.** A comparison of the number of epibiont individuals per gram plant wet weight of *S. muticum* and *L. saccharina* for August and September 1997 collections at the three sites. Error bars indicate standard error of each mean ( $n = 3$  except where indicated above pair of bars).



**Figure 16.** Rarefaction curves comparing the diversity of epibiont communities on *Sargassum muticum* and *Laminaria saccharina* collected in August and September 1997 ( $n = 21$ ). Data from all sites and both months were pooled.

*muticum* supports up to 20 or more species per plant (Figure 16). These derived numbers are comparable to the actual number of species observed on both algal species (mean species per plant in August and September: *S. muticum* = 18, *L. saccharina* = 11).

Thirty-seven species occurred exclusively on *S. muticum* and 30 species occurred exclusively on *L. saccharina* (Table 16). Of the species occurring exclusively on each alga, 15 were common (on > 10% of plants) on *S. muticum* and two were common on *L. saccharina*. *Mytilus* sp., *Caprella laeviuscula*, *C. verrucosa*, and the kelp crab *Oregonia gracilis* were common on *S. muticum* but rare (on ≤ 10% of plants) on *L. saccharina*. The scaleworm *Harmothoe imbricata* and the crab *Cancer oregonensis* were common on *L. saccharina* but rare on *S. muticum*. The polychaete *Platynereis bicanaliculata*, the snails *L. vineta*, *L. variegata*, *A. gausapata*, and shrimps, hermit crabs, and majid crabs were more abundant on *S. muticum* than on *L. saccharina*. Idotoid isopods, gammarid amphipods, caprellid amphipods, and fishes were more abundant and also more diverse on *S. muticum* than on *L. saccharina* (Table 16). The hydroid *Obelia geniculata* was found on *L. saccharina*, but no hydroids occurred on *S. muticum*. Although less abundant than on *S. muticum*, polychaetes were more diverse on *L. saccharina*. Eleven of the 13 polychaete taxa occurred on *L. saccharina* and five taxa on *S. muticum* (Table 16). All five nudibranch species identified occurred on *L. saccharina* whereas only 1 species occurred on *S. muticum*. The isopod *Gnorimosphaeroma oregonense*, a common member of the *L. saccharina* community, was not collected on *S. muticum*. Bryozoans also were more abundant and diverse on *L. saccharina* than on *S.*

*muticum*. A *S. muticum* plant had, at most, one bryozoan colony whereas a large percent (mean = 22%; ranged from 0 – 90%) of the dorsal surface area of *L. saccharina* was covered by bryozoans, making it impossible to determine the absolute number and size of colonies. The urchin, *Strongylocentrotus droebachiensis* was also found more often on *L. saccharina* (Table 16).

Two non-native epifaunal species found on *S. muticum* (*Harmothoe imbricata*, a scaleworm, and the mussel *Mytilus* sp.) also occurred on *L. saccharina*.

## DISCUSSION

### Benthic Algal Communities

The benthic algal community surrounding *S. muticum* is diverse (Table 4), and is composed of species typical of similar habitats in the region (Kozloff, 1993: 143-165). Although algal cover was high at each study site, the mean percent cover of *S. muticum* was low (3.1%; Table 4) in comparison to similar studies in Spain (Viejo, 1997), Southern California (Ambrose and Nelson, 1982), and Great Britain (Critchley *et al.*, 1986). In the San Juan Islands *S. muticum* may be utilizing an unoccupied niche when found at low densities (4.5 plants per square meter in this study).

At high density, *S. muticum* may have negative effects on invaded communities such as: shading, decreased water flow, and reduced light penetration. For example, a monoculture of *S. muticum* was observed at Cypress West, where more than ten square meters of substrate was utilized by *S. muticum* almost exclusively. *S. muticum* plants in the area were of moderate size (mean length = 89 cm, mean wet weight = 181 g), highly entangled, and found in slightly deeper water (3-7 m below MLLW) than plants at Site 1 on the east side of the bay. This single observation of a high-density *S. muticum* stand in northern Puget Sound contradicts all other observations and study results, yet is supported by literature from several other regions invaded by *S. muticum* (Ambrose and Nelson, 1982; DeWreede and Vandermeulen, 1988; Critchley *et al.*, 1986). Study of additional sites in Puget Sound is necessary for a complete evaluation of the impact of *S. muticum* at high densities on native communities.

The general shape and buoyancy of *S. muticum* minimize its impact on algal communities. This reduces the amount of shading of understory plants by individual *S. muticum* plants, especially at low plant densities. Buoyancy also minimizes the impact of *S. muticum* on the benthic community. Even when bent over by strong current, *S. muticum* does not lie on the substrate, thus avoiding abrasion of benthic organisms.

### ***Sargassum muticum* Growth Patterns**

Differences in morphology account for differences in the size of plants at the three sites (Figure 5, Table 6). Since currents were strongest at Site 1 and weakest at Site 3 (Table 1), plants were short and bushy at Site 1 and long, with few primary and secondary lateral branches, at Site 3. Most plants collected from Site 3 consisted of only one primary lateral branch, indicating that first year plants dominated the population at that site. Plants at Sites 1 and 2 were a mix of first year and older plants.

Peak growth of *S. muticum* varied with site (Figure 5). At Site 1, plants reached their maximum length in July and maximum wet weight in June (Figure 5). At Sites 2 and 3, plants reached their maximum length and wet weight in August (Figure 5). Maximum length measured during this study was 3 m. The differences in maximum size of plants between sites and months may be due to slight differences in water clarity, water movement, and herbivore activity (Lewey and Gorham, 1984; Viejo *et al.*, 1995; DeWreede, 1978; Critchley *et al.*, 1986; Farnham *et al.*, 1981; Ambrose and Nelson, 1982).

Growth rate of *S. muticum* (linear extension) averaged for all sites during the period of highest growth (Site 1, May to July; Sites 2 and 3, May to August) was 30.5 cm per month. This is comparable to the 25 cm per month measured by Viejo *et al.* (1995) for plants in Spain. Increase in weight was highest at Sites 2 and 3 with a mean of 30.4% per month from May to August, and 14.4% per month at Site 1. Norton and Benson (1983) report a mean growth rate of 9.6% per month for *S. muticum* near San Juan Island, Washington in August.

Reduction in growth at the onset of sexual reproduction, increased herbivore grazing (Figure 12), and faster currents at Site 1 (Table 1) contributed to the dramatic decline in plant condition seen at Site 1 in August 1997 (Figure 6). A dramatic increase in snails, particularly *L. vincta* and *L. variegata*, was measured at Site 1 (Figure 12) in July and August, corresponding to the deterioration of plants (Figure 6) and the reproductive period recorded for *S. muticum* in northern Puget Sound. Herbivory was evident: dark outer tissue was scraped away and the lighter colored (less photosynthetic) inner tissue exposed. *Lacuna* snails at lower densities than those reported here for July through September at Site 1, could remove more tissue than *S. muticum* produces through growth (Norton and Benson, 1983).

The increase in snail populations at Site 1 (Figure 12) had little effect on the plants growing at Cypress West (Figure 6) where snail populations were also high (Figure 12). There was more plant biomass at Cypress West than on the east side of the bay (Site 1) because Cypress West is more protected, experiencing slower tidal currents than Site 1. Because of the large standing stock of *S. muticum* at Cypress West, *S. muticum* grew faster than tissue was grazed. The dramatic decline in August

plant condition at Site 1 caused by slowed growth, fast current, and high herbivore abundance illustrates the importance of seasonal changes in abundance of epibionts to host algae (Gunnill, 1983).

### **Polyphenolic Concentrations**

Polyphenolic concentrations increased over time (Figure 7), reaching peak concentrations in September at Sites 1 and 2 with high concentrations also evident in August at Site 2 (Figure 7). This late summer peak in polyphenolic concentration is typical of furoid algae (Yates and Peckol, 1993; Hay and Steinberg, 1992: 371-413; Van Alstyne, 1988).

Abiotic factors that may influence polyphenolic concentration include: nutrient availability, irradiance level, and salinity (Yates and Peckol, 1993). Nutrient levels are high throughout the year in Puget Sound and are not likely to affect polyphenolic concentration patterns. Irradiance varies seasonally in northern Puget Sound and may be responsible for increased polyphenolic concentrations in late summer since moderate to high irradiance levels are related to higher polyphenolic concentrations (Sieburth, 1969). Also, growth may dilute polyphenolics causing plants sampled during periods of high growth rate to have lower polyphenolic levels (Norton and Benson, 1983). Growth of *S. muticum* is highest in spring and slows in late summer with the onset of reproductive effort. *S. muticum* reached peak reproductive activity in August and September, corresponding directly to peak polyphenolic concentration (Figure 7) and maximum plant size (Figure 5). However,

Ragan and Jensen (1978) found *Ascophyllum nodosum* and *Fucus vesiculosus*, two closely related species, have lowest polyphenolic levels during reproductive periods.

Polyphenolic concentrations ranged from 0.4 to 2.2% dry weight (Figure 7). These values are at the low end of the scale for fucoid and laminaran algae according to Hay and Steinberg (1992: 371-413) but are identical to the overall mean concentrations found by them. These values are also similar to polyphenolic concentrations found by Gorham and Lewey (1984) for *S. muticum* in Great Britain (3.3% dry weight).

Polyphenolic concentration had little effect on herbivores associated with *S. muticum*. There are few herbivorous fish (animals against which polyphenolics have been shown to be most effective) in northern Puget Sound (Kozloff, 1993: 95, 195-197) thus fish have little impact on *S. muticum*. The urchin *Strongylocentrotus droebachiensis* destroyed *S. muticum* stands at sites off British Columbia, Canada (DeWreede and Vandermeulen, 1988) but were rare on the *S. muticum* plants during this study (1 on 51 plants; Table 7) and few were seen on the substrate surrounding plants. Mesograzers (amphipods, isopods, polychaetes, and snails) were abundant on *S. muticum* (Table 7) indicating that at the concentrations measured, polyphenolics do not negatively impact mesograzer populations. The impact of these small organisms on large plants was seen at Site 1 in August when grazing on severely damaged plants (Figure 6) corresponded to increased abundances of snails (Figure 12).

Few sessile or attached animals (tunicates, bryozoans, entoprocts, or hydroids) were found on *S. muticum* (Table 7). The few attached species were located on the oldest plant portions where polyphenolic concentrations are low (Sieburth and

Conover, 1965). This lack of sessile fauna was also observed by Norton and Benson (1983) in northern Puget Sound but contrasts with *S. muticum* from Great Britain, where hydroids and bryozoans were the dominant members of the epifauna (Withers *et al.*, 1975; Gray, 1978). Differences in species composition and abundance between Great Britain and northern Puget Sound, not polyphenolic concentration, may explain the difference in dominant *S. muticum* epifauna of the two regions (Norton and Benson, 1983).

### **The *Sargassum muticum* Community**

*S. muticum* supports one of the most diverse communities associated with a macroalga. The community associated with *S. muticum* consisted of 107 animal and at least eight algal taxa (Table 7). Pelagic *Sargassum* supports from 67 (Fine, 1970) to 101 animal species (Morris and Mogelberg, 1973). *Sargassum serratifolium* has an equally diverse and abundant associated community in its native Japanese habitat (Mukai, 1971). Gray (1978) found 139 animal species on *S. muticum* in Great Britain and only 63 species on *Cystoseira nodicaulis*, an alga with similar morphology. In the present study, *S. muticum* supported more animal taxa than any other alga reported by Coleman in 1940. In contrast, Norton and Benson (1983) reported only 43 species on the *S. muticum* plants collected from San Juan Island, Washington. However, Norton and Benson (1983) collected partial plants instead of entire plants, which could account for the differences in richness obtained.

The community on *S. muticum* primarily consists of small mobile animals such as amphipods, isopods, decapods, gastropods, nereid polychaetes, and fish.

Norton and Benson (1983) also noted the predominance of mobile species over sessile species on *S. muticum* in northern Puget Sound. No hydroids or ascidians were found on *S. muticum* during this study and few were found by Norton and Benson (1983). The differences between abundant species on *S. muticum* in Great Britain and Puget Sound may be attributed to the different species pools of the two regions (Norton and Benson, 1983), environmental differences between regions (Norton, 1971; Edgar, 1983a), differences in longevity and density of the *S. muticum* communities in each region (Critchley *et al.*, 1983), or a combination of the above factors.

The monthly pattern obtained from the principle component analysis (Figure 13) was partially due to the increase in plant size over time (Figure 5, Table 9). Total number of individuals of each species for each variable (site and month) was used to derive the components. Mukai (1971) found that the abundance of small animals was positively correlated with plant size, but that of large, mobile animals was not. Most of the variability in the principle component analysis was due to five species, three of which were small snails. Mukai (1971) also found that peaks in animal abundance were due to only a few species. Abundance of several species varied monthly but not all increased through the summer (Table 12). For example, the abundance of the gammarid amphipods *Pontogeneia rostrata* and *Pleustes depressa* were inversely related (Table 12). This trend could be due to interspecific competition or differing life histories. As expected, there was little indication of trends through time for many of the species on *S. muticum*. Lack of monthly patterns in most epifaunal species may be attributed to small individual species abundances, many species arriving on

the alga by chance (Norton, 1971), and animals' responses to physical features of algae (Dean and Connell, 1987a).

It is important to consider if the sampling interval affects interpretations of abundance and diversity data. Is variation in epibiont communities due to short-term fluctuations or to actual monthly changes? This question is particularly important for cases where sample size is relatively small, as it was for this study (~ 9 plants each month; Table 2). When working on reefs off of Queensland, Australia, Martin-Smith (1994) found samples of *Sargassum fissifolium* collected less than two weeks apart were not significantly different in faunal abundance or species composition but samples collected more than two weeks apart showed distinct seasonal changes. Therefore, monthly collections taken during this study should have been far enough apart to detect monthly patterns if present.

There were distinct differences between May samples and those collected in later months (Table 13). Twice as many species occurring only once were found in May samples as were found in any other month's samples (Table 12). Species richness was lower in May with 46 species as opposed to 55 to 57 species in samples from each other month (Table 12). Abundance of epibionts was also low (Table 12, Figure 12 for abundance of the dominant epifauna). Norton and Benson (1983) suggest that the low epifaunal densities in spring are due to rapid growth of *S. muticum* during this season. However, Hacker and Steneck (1990) found that only 24 hours were needed for colonization of *Ceramium*, *Chondrus* and algal mimics (populations were similar to those on control algae within that time period). Martin-Smith (1994) found that within two weeks of complete fauna removal the

communities on the re-colonized *S. fissifolium* were indistinguishable from those on the plants prior to removal of epifauna. Both of these studies indicate that colonization by mobile species is rapid and should be able to keep pace with plant growth.

The die-back of *S. muticum* to the perennial holdfast is the most dramatic feature of its seasonal growth. The seasonal loss of habitat may restrict the diversity and abundance of *S. muticum* epibionts (Norton and Benson, 1983) if they live longer than six months and may limit the development of close species-specific relationships between fauna and host alga.

The differences in epibiont communities on *S. muticum* at Sites 1 and 3 were due differences in to the abundance and diversity of caprellids and isopods. The high abundance of caprellids and isopods at Site 3 may be due to input of individuals from the extensive nearby eelgrass beds. Although eelgrass beds were located near *S. muticum* plants at all sites, the bed at Site 3 is the largest eelgrass bed on Washington's coast. The high occurrence of species associated with *Z. marina* beds on *S. muticum* at Site 3 supports Norton and Benson's (1983) assertion that eelgrass is a source of fauna to the *S. muticum* community. There were few other notable differences in species composition or abundance on *S. muticum* at the three study sites. The slight differences between sites may be due to variation in abiotic factors such as water movement, turbidity, larval supply, and benthic substrate (Table 1). Norton (1971) noted the importance of habitat features in determining the abundance and species composition of fauna on the alga *Saccorhiza polyschides*.

Diversity measured by rarefaction did not differ significantly between sites (Table 6, Figures 10 and 11). The haphazard variability of the data may be due to individual variation between plants because the specific make-up of individual faunal communities varied widely, excluding dominant species. Site 1 *S. muticum* supported the most diverse community in May and the least diverse in August (Figure 11). The drop in diversity may be attributed to the rise in snail populations (Figure 12) and early deterioration of plants at that site (Figure 6).

A positive relationship between the abundance of associated fauna and epiphyte load prevails under certain environmental conditions (Lewis, 1987; Norton and Benson, 1983; Edgar, 1983b; Heck and Wetstone, 1977; Jennings and Steinberg, 1997) but does not always occur (Dean and Connell, 1987b). Although few macroalgae were attached to *S. muticum*, the particulate load was considerable throughout the summer (Figure 8) and of high organic content (Figure 9), consisting primarily of diatoms. This rich food source on the surface of *S. muticum* enables many species to survive on the plant. In summary, the community associated with *S. muticum* is large and diverse due to the habitat provided by the large, morphologically complex plant and its associated food sources (*S. muticum* tissue, particulate load, and small prey items).

#### **Comparison of *Sargassum muticum* and *Laminaria saccharina***

*Sargassum muticum* supports a more abundant and species rich biota than *Laminaria saccharina* (Figures 14 and 15). Mean rarefaction curves comparing *S. muticum* and *L. saccharina* epibiont communities (Figure 16) illustrate how *S.*

*muticum* harbored a more diverse assemblage of epibionts than *L. saccharina* in late summer 1997. However, when comparing two such morphologically distinct algae, the unit of sampling effort intrinsic to the calculation of rarefaction curves (the number of epibiont individuals) does not necessarily allow direct comparison of species richness of the two communities. Surface area might be a more appropriate unit of comparison. However, measuring surface area of an alga with the highly complex morphology of *S. muticum* is fraught with difficulty. Despite problems with the rarefaction comparison, useful information is obtained from the curves. The shape of rarefaction curves indicates the relative evenness of communities (James and Rathbun, 1981). The steepness of the *L. saccharina* curve from 1 to 100 epibiont individuals indicates high evenness (approximately equal numbers of individuals of each species) of the epibiont community and emphasizes the comparatively higher species richness of the *L. saccharina* community at small sample sizes. However, the mean size of a *L. saccharina* epibiont community was 220 individuals, well above the level at which rarefaction curves show diversity to be highest. As the number of epibiont community members included in the analysis increases, diversity of the *S. muticum* community quickly surpasses that of the *L. saccharina* community. The *L. saccharina* curve indicates that no matter how many individuals from the community are included, a single plant supports no more than ten species (Figure 16). Although no completely satisfactory method permitted direct comparison of *S. muticum* and *L. saccharina* epibiont diversity, changes in the benthic invertebrate community due to the presence of an introduced species and not the statistical or mathematical relevance

of a comparison of diversity, are of primary importance in determining the impact of this invasive species.

The differences in epibiont communities of *S. muticum* and *L. saccharina* are caused by differences in morphology of these algae. *S. muticum* is highly branched whereas *L. saccharina* is a broad, thick, slightly undulating blade. Because of these differences in shape, plants of equivalent length and weight do not have similar surface areas or the same degree of complexity. Dean and Connell (1987a) found algal structural features accounted for most of the variation in species richness and abundance of invertebrate communities on macroalgae. Adults of four invertebrate species (*Platynereis bicanaliculata*, *Lacuna marmorata*, *Hyale frequens*, and *Pugettia producta*) consistently selected clumps of algae with higher surface area over clumps with the same biomass but lower surface area (Dean and Connell, 1987b). These physical characteristics may be more important than chemical defenses (Dean and Connell, 1987b; Hacker and Steneck, 1990).

It is generally accepted that increased surface area creates more habitable space for organisms. Higher abundance of individuals correlates with higher species richness, a sampling artifact (Dean and Connell, 1987a; Russo, 1990). The *S. muticum* rarefaction curve (Figure 16) supports this idea; as the total number of epibiont individuals increases so does species richness. Mortality, water movement, food availability, and competition are a few factors that may increase the number of individuals and species richness in complex habitats (Dean and Connell, 1987a and b; Edgar, 1987a and b; Heck and Wetstone, 1977; Lewis, 1987). As several of these factors are likely to contribute to the structure of the epifaunal communities on *S.*

*muticum* and *L. saccharina*, each will be discussed in relationship to its possible contribution to the diversity of epibiont communities on these two algae.

Plants with high morphological complexity support greater diversity than plants with low morphological diversity (Edgar, 1983a). Morphological complexity of *S. muticum* is high because of the various widths of axes and leaflets and the differing shapes of cryptostomata and air vesicles (Figure 2; Critchley, 1983). Based on morphological complexity, *S. muticum* can support a wider range of species than the simpler, flat blade of *L. saccharina*. Small crustaceans (Table 7) are able to cling to *S. muticum*. In contrast, the wide flat thallus of *L. saccharina* is difficult for small grasping animals to hold on to. Also, Hacker and Steneck (1990) showed that the volume of spaces between folds or branches within an individual plant determines the size of individual animals able to utilize the algae as habitat. *S. muticum* is able to support a wide size range of individuals because of its high degree of spatial variability which *L. saccharina* lacks.

Complex habitats are known to provide a refuge against predation (Heck and Wetstone, 1977; Dean and Connell, 1987a). The highly branched *S. muticum* plant provides many more cryptic hiding places for prey organisms than does the wide, unbranched thallus of *L. saccharina*. Good size fit between hiding spaces in the macroalgae and the prey animals also decreases the rate of predation (Hacker and Steneck, 1990). With reduced predation the abundance of some small invertebrates will increase in the habitat given that other factors are not limiting growth.

*S. muticum* not only creates more refuges for animals but, on a larger scale, its buoyancy contributes to the complexity of the entire benthic community. *S. muticum*

is the only buoyant algal species at the study sites (Table 4). The native algae surrounding *S. muticum* essentially lie on or near the substrate. *S. muticum* extends into the water column in bushy masses (Figure 1). The addition of this third dimension to the subtidal benthic community vastly increases habitat for fauna and provides complexity in the benthic algal community.

Water movement is lower in areas of high algal biomass than in areas of low algal biomass and low structural complexity (Fretter and Manly, 1977; Dean and Connell, 1987b; Weiser, 1952). Low water flow also means there is less chance that an animal will be washed off its substrate. This is an important factor to animals with low mobility which remain in the area where they settle as larvae (Fretter and Manly, 1977) such as the numerous small gastropods on *S. muticum*. The increased structural complexity of benthic communities should increase larval settlement in the benthic community. The vertical three-dimensional structure of *S. muticum* in the water column serves as “fly paper” for larvae that settle using tactile cues (e.g. crab zoea; Sulkin, personal communication) as well as slows water movement through the area increasing passive import of larvae (Dean and Connell, 1987b).

Complexity and increased surface area logically lead to increased resources such as food. The high surface to volume ratio of *S. muticum* compared to that of *L. saccharina* provides increased access to tissue for herbivores. This is of great importance to small snails such as *Lacuna* spp. that feed on epidermal tissue of macroalgae (Fretter and Manly, 1977). The larger surface area of *S. muticum* also increases the amount of particulates (such as diatoms) accumulated by plants. Norton and Benson (1983) noted the importance of particulate food quantity and quality in

attraction of grazers. The significantly higher particulate load found on *S. muticum* (Table 15) suggests that *S. muticum* can support more grazer biomass than *L. saccharina*. In addition, the lamellar *L. saccharina* plants have a mucilaginous covering that sloughs off decreasing diatom growth (Fretter and Manly, 1977) as well as deterring animal settlement (Edgar, 1983b).

*S. muticum* and *L. saccharina* as habitat must be compared on an ecological time scale as well to determine effects on epibionts (Dean and Connell, 1987b; Edgar, 1983a). Since both algae exhibit seasonal growth, the habitat they both provide is available for only a few months of the year. Other than those animals able to survive on the perennial holdfast and basal portions, plants must be re-colonized every year. This annual renewal of the epibiont community may contribute to lack of species-specific interactions between epibionts and host algae. Lack of competition for resources between epifauna (Dean and Connell, 1987a and b; Heck and Wetstone, 1977; Coleman, 1940), planktonic dispersal of many epibionts (Fretter and Manly, 1977), and mobility of many of the animals (Hacker and Steneck, 1990) may also contribute to the lack of species specific interactions.

In summary, epibiont diversity and abundance increase in areas invaded by *S. muticum* because of the new habitat, which *S. muticum* provides. For this reason, management plans for the elimination of *S. muticum* are not recommended. However, high densities of *S. muticum* may change water movement, light penetration, sediment accumulation, and contribute to anoxia at night. Further research is needed before management decisions concerning its removal can be made.

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