Herbivory and the Seasonal Abundance of Algae on a High Intertidal Rocky Shore
Author(s): John D. Cubit
Source: *Ecology*, Vol. 65, No. 6 (Dec., 1984), pp. 1904-1917
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1937788
Accessed: 06/08/2014 17:44

*Ecology*, 65(6), 1984, pp. 1904–1917

# HERBIVORY AND THE SEASONAL ABUNDANCE OF ALGAE ON A HIGH INTERTIDAL ROCKY SHORE[1]

JOHN D. CUBIT
*Smithsonian Tropical Research Institute, Apartado 2072,*
*Balboa, Republic of Panama*

*Abstract.* This paper examines the contribution of herbivory to seasonal variations in algal coverage at the uppermost intertidal levels of a rocky shore on the outer coast of Oregon, USA. In this habitat, simple, fast-growing algae are abundant during the wetter, less sun-exposed, and cooler weather of the winter months, but disappear in the drier, sunnier, and warmer conditions of the summer. Acmaeid limpets, the predominant herbivores in the habitat, are present throughout the year. Previous studies of the high intertidal zone have suggested that physical stresses alone prevent the survivial of algae through the summer months, and that grazing affects algal abundance when physical conditions are more benign.

To test these hypotheses, cageless methods were used to exclude the limpets from plots on the uppermost intertidal rocks. The experiments were repeated at 3–4 mo intervals over a period of several years. This partial reduction in herbivory resulted in the development and persistence of dense covers of algae through the summer months, as well as increasing algal abundance during the other times of year. Apparently the primary cause of the seasonal fluctuations in algal abundance is variation in rates of algal production rather than change in absolute rates of algal loss to herbivory or physical stresses. Evidence from this study and the literature indicates that the limpets in this habitat are probably consuming more, not less, algae in the winter months. However, higher rates of algal production in winter more than compensate for the increased herbivory, and the algae become more abundant. During the summer, drier conditions cause rates of production by the algae to fall below rates of consumption by limpets, and the limpets remove most of the standing crop of algae. Thus, increased grazing pressure coincides with increased physical stress. To be a perennial or summer annual in this habitat, an alga not only must be resistant to desiccation, insolation, and high temperatures, but also must be inaccessible to herbivores or be resistant to herbivory. In the uppermost intertidal zone, the abundance of algae in winter evidently depends on the pattern of changes in primary production over the entire year. Scarcity of forage in the summer months reduces populations of the resident limpets, and the favorable conditions for primary production in winter months allow the transient species of algae to establish rapidly, grow, and reproduce before the populations of limpets recover. If even the most favorable physical conditions for algal growth remained constant through the year, the transient algae would probably disappear.

It is speculated that under present conditions the establishment of perennial algae in this habitat is limited by the intensity of herbivory in the summer and by competition with transient algae in the winter. If this is correct, less fluctuating physical conditions, even if severe, would change the species composition of this high intertidal community by favoring the establishment of perennial algae.

*Key words: algal blooms;* Bangia; Blidingia; Collisella; *diatoms; ephemeral algae; herbivory; intertidal zonation; limpets; marine algae; physical stress;* Porphyra; *seasonality;* Ulva; Urospora.

## INTRODUCTION

The importance of biotic factors in controlling the distribution and abundance of marine organisms is generally thought to decrease with increasing height in the intertidal zones of rocky shores. Consistent with this perspective, algal abundance has been shown to be influenced by competition and herbivory at lower intertidal levels, while at upper intertidal levels algal abundance appears governed principally by physical stresses (Aleem 1950, Lawson 1957, Castenholz 1961, Lewis 1964, Chapman 1973, Haven 1973, Underwood 1980, 1981). However, herbivores are abundant even at the uppermost intertidal levels of most rocky shores (Stephenson and Stephenson 1972); in this paper I examine the effects of herbivory and its seasonal variation on algal abundance in a high intertidal community.

In the uppermost intertidal zones of certain rocky shores pronounced seasonal fluctuations in the abundance of algae are inversely correlated with the extent of the habitats' exposure to the physical stresses of desiccation, solar radiation, and high temperatures during low tides. In seasons (usually winter) when these habitats are relatively wet, cool, and protected from intense sunlight, "blooms" of morphologically simple, fast-growing algae (blue-green algae, diatoms, and filamentous and membranous species of red and green algae) cover portions of the high intertidal rocks. During conditions that are hotter, drier, and more sun-exposed (usually in the summer months), these algae disappear, leaving the uppermost intertidal rocks nearly devoid of visible algal cover. Such patterns have been observed on a range of high intertidal shores

---

[1] Manuscript received 30 July 1982; revised 15 July 1983; accepted 23 July 1983.

(Aleem 1950, Lawson 1957, Castenholz 1961, Lewis 1964, Haven 1973, Underwood 1981).

Although there is evidence that herbivory can affect the abundance of algae at high tidal levels, most investigators have concluded that the summer disappearance of algae is a direct result of mortality caused by physical stresses. For example, on the coast of Oregon, Castenholz (1961) produced blooms of algae in the summer months by excluding acmaeid limpets and littorinid snails from plots in the high intertidal zone, but concluded that at higher intertidal levels (the levels considered in this paper) mortality from physical stresses probably prevented the year-round survivial of these algae. On the coast of California, Haven (1973) increased the abundance of algae through midsummer by excluding acmaeid limpets from a plot in the high intertidal-supratidal zone. He suggested that although littorinid snails invaded the study plot, the disappearance of algae in the late summer was probably independent of grazing pressure. Underwood (1981) suggested that similar patterns in the seasonality of algal abundance in New South Wales, Australia, may result from cycles of algal reproduction and growth, or from the effects of seasonal weather patterns on the activities of herbivores. From herbivore exclusion experiments he concluded that above the low intertidal zone, grazing prevented the colonization of foliose algae, but harshness of the physical environment prevented the growth of these algae past the sporeling stage (Underwood 1980).

Other investigators have attributed the overall seasonal periodicity of algal standing crop solely to the direct effects of physical stresses. Lawson (1957), working on the coast of Ghana, and Lewis (1964), referring to the coast of Britain, have interpreted such changes in algal cover as part of the "physiologically critical limits" theory of zonation. These limits are exceeded in summer on the uppermost levels of the shore and the algae there die. The more benign conditions of winter permit the reestablishment of algae at higher intertidal levels. The results of related experiments have been consistent with this theory; algal cover was increased in the high intertidal zone by increasing the wetness of the rock substrate (Frank 1965, Dayton 1970, Connell 1974).

It is unlikely, however, that algal abundance in the uppermost intertidal zones is unaffected by biotic factors: there are substantial populations of benthic-feeding, herbivorous gastropods and arthropods at these levels of most rocky shores (Ricketts et al. 1968, Stephenson and Stephenson 1972, Newell 1979). If the preceding explanations for the seasonal changes in algal covers are correct, the effects of herbivory should be confined to the parts of the year that are more physically benign, and should be pre-empted by the lethal effects of physical stresses when conditions are more harsh. Such a relationship could be regarded as a temporal corollary of the theory of spatial zonation, which holds that predominantly biotic factors limit the distribution of marine organisms at the lower, more physically benign, levels of the shore, while tolerance of physical stresses controls the upper limits of zonation (Connell 1972, Newell 1979, Underwood 1979, Lubchenco 1980). This relationship would also be consistent with the theory that the intensity of predation is negatively correlated with the harshness of the environment (Connell 1975, Menge and Sutherland 1976, Menge 1978).

In the following study I have attempted to define further the influence of herbivory on the abundance of algae in several high intertidal communities, and to assess the seasonal effects of herbivory on algal abundance.

## Sites and Species Studied

The study sites were on the outer coast of Oregon at South Cove of Cape Arago (latitude 43°18′N, longitude 124°25′W), and Sunset Bay, ≈3 km to the north. During low tides the Sunset Bay site is somewhat more protected from wave action by several low rocks and a shelf extending seaward from the study area, but both sites are exposed to moderate wave action.

The rock substrate in this area is sandstone. The surfaces of the study plots at South Cove were primarily horizontal. At Sunset Bay the surfaces ranged from horizontal to nearly vertical; the inclined surfaces were on the more sun-exposed south, southwest, and west faces of the rock outcropping.

The study plots were between 1.8 and 2.8 m above mean lower low water (MLLW). Mean high water is 1.8 m above MLLW, and mean higher high tides reach to 2.1 m. All study plots were on portions of the rock projecting above the high water shelf, an erosional feature of most sandstone shores at mean high tide level (Bartrum 1926). This is the uppermost level of the intertidal shore and corresponds to Zone 1 in the scheme of Ricketts et al. (1969).

As described earlier, algal abundance in the high intertidal zone is inversely correlated with exposure to desiccation, insolation, and high temperatures (Lawson 1957, Castenholz 1961). The severity of these stresses varies seasonally as a result of changing atmospheric conditions, daylengths, and annual cycles of the tides. On the Oregon coast in the late autumn, winter, and early spring, day lengths are shorter, skies are more overcast, precipitation is greater, temperatures are cooler, and the rocks above tidal level receive more wash and spray from storm-generated waves. (Since this habitat is so often above the level of the tide, the length of time it is wetted by seawater is largely dependent on the amount of wash and spray it receives from the waves.) In addition, tidal levels are higher during the daylight hours of winter, and lower in summer. In summer the high rocks can be exposed on the average for periods of >8 h/d to the drier, warmer, sunnier weather (Fig. 1, see also Frank [1982: Fig. 2]).

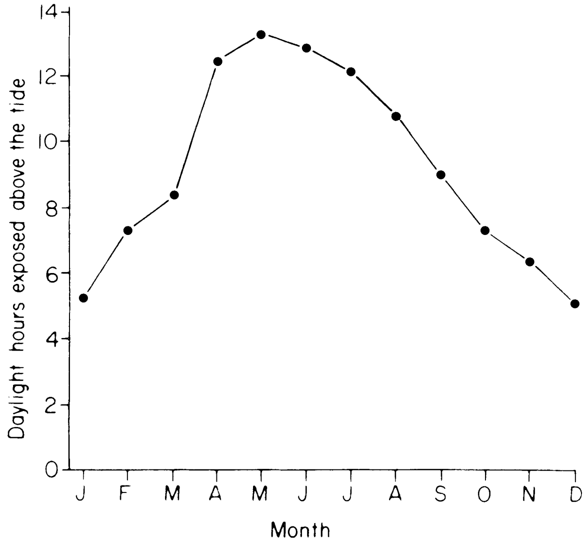

FIG. 1. The number of daylight hours per day that the shore above the 1.5 m tidal level is exposed above water level throughout the year. The 0 level (datum) is mean lower low water. The high intertidal study areas described in this paper are above the 1.8 m tidal level; thus, for those days with wave heights of <30 cm these areas remain unwetted by the sea for an average of eight or more daylight hours per day during the period of March through September. Daylight hours are defined as 0.5 h before sunrise to 0.5 h after sunset.

These data are derived from a listing of the predicted hourly to tidal heights for Coos Bay, Oregon for the period of 1 October 1972 to 31 October 1973, provided through the courtesy of D. C. Simpson of the United States National Oceanic and Atmospheric Administration, National Ocean Survey.

In some years weather during the late spring and early summer may be ameliorated by cool, wet coastal fogs. For convenience, in the following parts of this paper the wetter, cooler, and less insolated part of the year (November through April) will be referred to as "winter" and the warmer, drier, and more insolated months (May through October) will be referred to as "summer." Similar annual patterns of weather and tides have been described for other coastal habitats (Lawson 1957, Sutherland 1970, Dayton 1975).

The algae of the winter blooms were simple, fast-growing species including the following: filamentous diatoms (primarily *Melosira nummuloides* [Dillw.] Ag.), simple filamentous green and red algae (Chlorophyta: *Urospora penicilliformis* [Roth] Aresch. and Rhodophyta: *Bangia fuscopurpurea* [Dillw.] Lyngb.), and membranous greens and reds (Chlorophyta: *Ulva* sp., *Blidingia minima* var. *vexata* [Setch. et Gardn.] J. Norris, and three species of *Porphyra* (Rhodophyta): *P. perforata* j. Ag., *P. pseudolanceolata Krishnamurthy,* and *P. schizophylla* Hollen.). *Dermocarpa*-like and *Oscillatoria*-like blue-green algae sometimes formed a thin film over the surface of the rock or appeared only as a color variation or stain on the rock. Perennial algae usually constituted <1% of the total areal coverage in the study areas; in order of relative abundance those present were *Endocladia muricata* (Post. et Rupr.) J. Ag., *Ralfsia* sp., *Iridaea flaccida* (Setch. et Gardn.) Silva and *Gigartina papillata* (C. Ag.) J. Ag.

The most abundant herbivore (measured as biomass) was the acmaeid limpet *Collisella* (=*Acmaea*) *digitalis* (Rathke). The littorinid snails *Littorina scutulata* Gould and *L. sitkana* Philippi and gammarid amphipods were common only near crevices in the rock, clumps of barnacles, and other shelter. The herbivorous chironomid flies *Parclunio alaskensis* (Coquillett) and *Saunderia marinus* (Saunders), and a tipulid fly *Limonia* sp. were also abundant at times. Two other herbivorous arthropods, *Ligia pallasi* Brandt and *Hemigrapsus nudus* (Dana), were common in nearby areas but were not found in these particular study sites. The two barnacles *Chthamalus dalli* Pilsbry and *Balanus glandula* Darwin were present in low overall abundance.

## METHODS

### *Limpet exclosures*

To measure the effect of herbivory by limpets (the predominant grazers in this system) on algal abundance, I periodically excluded these animals from experimental plots using cageless methods. I then compared algal cover between these and control plots. Preliminary experiments demonstrated that cages and fences made of wire and plastic mesh were inappropriate for comparing the relative effects of naturally occurring herbivory and physical stress. The shading effect of both experimental and control treatments provided protection from desiccation, insolation, and high temperatures. The cages and fences also reduced the mechanical stress of wave action, trapped bits of water-retaining debris, and attracted smaller herbivores such as littorinid snails and amphipods, which were rarely found on exposed rock surfaces. Boosting the densities of these smaller herbivores would have at least partially negated the effect of excluding the limpets in the experimental treatments and possibly would have created unnaturally high levels of herbivory in the control treatments (with partial cages or fences). To avoid these problems a painted barrier of copper lacquer was used to exclude limpets (Shining Armor Brand copper paint Number 606, Illinois Bronze Powder and Paint Company, Lake Zurich, Illinois). The copper content (15% by mass) of each 59-mL (2-ounce) jar of paint was increased by adding 29 g of copper powder (Luco Brand copper lining bronze, Leo Uhlfelder Company, Mount Vernon, New York). A scraper, wire brush, and propane torch were used to clean and dry the surface of the rock when necessary, and the paint was brushed on to the clean, dry surface. To avoid possible toxic effects of copper compounds on the organisms within the study plots, painted strips were located so that water did not drain into the plots. Exclosure plots were surrounded by a continuous strip of copper paint 3 to 4

Table 1. Dates of establishment for exclosure and control plots.

| Date | Number of plots | |
|---|---|---|
| | Exclosures | Controls |
| Sunset Bay | | |
| 16 July 1971 | 4 | 4 |
| 30 November 1971 | 4 | 4 |
| 25 February 1972 | 4 | 4 |
| 13 May 1972 | 5 | 5 |
| South Cove | | |
| 23 August 1971 | 5 | 4 |
| 7 May 1972 | 5 | 5 |
| 14 August 1972 | 5 | 5 |
| 4 November 1972 | 4 | 5 |
| 2 February 1973 | 4 | 2 |

cm wide. Control plots were constructed in the same manner as exclosure plots, but were bounded by patches, rather than continuous lines, of the copper paint.

The property of the copper paint that makes it repellent to limpets is not known. In preliminary experiments, strips of copper foil glued to the rock had the same effect, suggesting that the limpets are repelled by some effect of the copper and not by some other material in the paint. The response may be to a chemical or galvanic property of the paint. Admixtures of other Shining Armor Brand metallic paints (such as chromium) seemed to enhance the repellent effect.

This paint effectively excluded only the limpets: it did not prevent littorinid snails and arthropod herbivores from entering the exclosure plots. In a separate series of experiments the latter herbivores were excluded by using Tanglefoot barriers (see Robles and Cubit 1981). Limpets inside an exclosure at the time of establishment were killed or removed, not placed outside the exclosure. Any limpets that subsequently invaded an exclosure were replaced outside the exclosure.

A few individual experimental and control treatments were deleted when the paint did not develop an exposed copper layer or flaked off the rock and could not be repaired.

A sequence of random numbers (Fisher and Yates 1963) was used to select each study plot from an initial array of potential plots, and to designate them as exclosures or controls.

Seventeen exclosures and 17 controls plots were set up at Sunset Bay; 23 exclosures and 21 controls were established at South Cove. To avoid confounding seasonal with successional effects, the establishment of study plots was staggered over time: four or five sets of exclosures and controls were constructed at 3–4 mo intervals over ≈18 mo (Table 1).

Shapes and areas of the plots varied with the topography. Study plots at Sunset Bay were significantly (*t* test $P < .001$) larger ($\bar{x} = 2599$ cm$^2$) than those at South Cove ($\bar{x} = 1500$ cm$^2$), but there was no significant difference between the sizes of the exclosure and control plots within each location (*t* tests: $P > .4$ in both cases).

The first set of study plots, established 16 July 1971 at Sunset Bay, differed from the others in the following respects: (1) locations of the study plots were not determined by the random procedure, but were placed only on the higher, drier portions of the study area that are more exposed to the sun, (2) the controls consisted of areas of equal size immediately adjacent to the exclosures, and (3) at ≈2-wk intervals during the first 3 mo after the establishment of the exclosure plots, any littorinid snails found within the plots were removed by hand. In the following analyses of results the data from this set of exclosures are only considered with respect to seasonal variations in algal cover.

Particularly during the winter months, high waves limited access to the study areas even during low tides. To maximize data collected 35-mm color transparencies were made of each exclosure and control plot at intervals of ≈1 mo. Small samples (<1 cm$^2$) were occasionally scraped from the surface of the rock to establish identities of the organisms, but the study plots were disturbed as little as possible.

To estimate the percent cover of organisms within the study plots I slightly modified Connell's (1970) method of superimposing an array of sampling points on a projection of each transparency (see also Dayton 1971). Large-scale clumping of the sample points was prevented by using a stratified-random, rather than a fully random, array.

The same array of points was used to census each control and exclosure. To increase the independence between each census of a given plot, each color transparency was projected with a different orientation: upside down, reversed, etc. In addition, because the camera was hand-held when the photographs were taken, the orientation of the image of a plot on the transparency varied; this also helped to assure that the points would not fall on the same places of each plot at each census.

The size of the projected transparency was adjusted until ≈100 points fell within the area to be censused. The following categories were used in scoring algal coverage under the dots: (1) microalgae (blue-green algae, diatoms, sporelings), (2) *Bangia,* (3) *Urospora,* (4) *Bangia-Urospora* mixed stand, (5) *Porphyra,* (6) *Ulva,* (7) *Blidingia,* and (8) perennial macroalgae (*Endocladia, Gigartina, Iridaea, Ralfsia*).

### *Size-specific body masses and grazing areas*

Inferences regarding the productivity of the habitat and temporal variations in the availability of food can be made from measurements of size-specific body masses of the limpets and the areas grazed per limpet. The term size-specific body mass, as used here, refers to the mass of organic material (i.e., ash-free dry mass) of the limpet body per unit volume of its shell. This was measured as follows: limpets were collected from

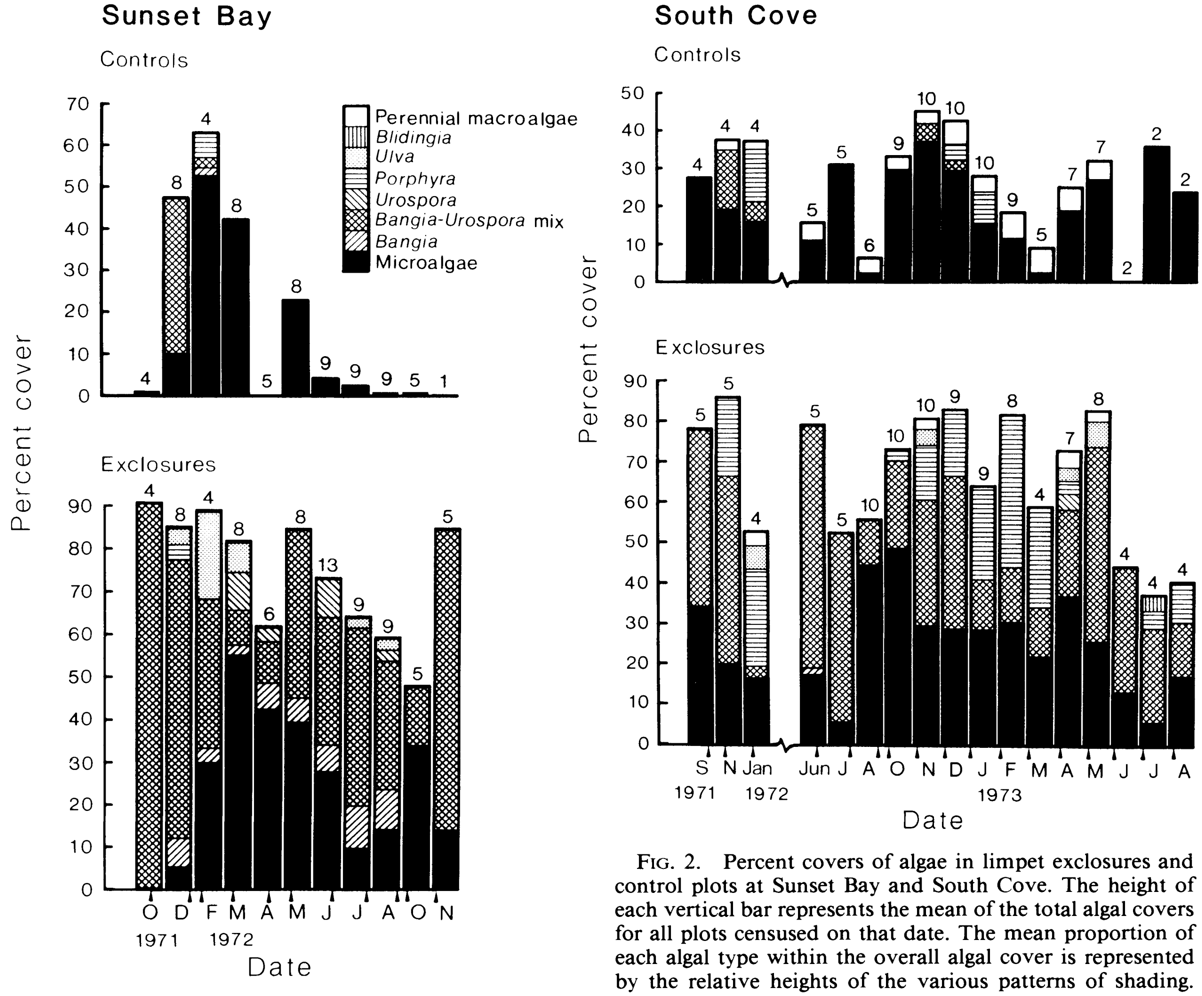

FIG. 2. Percent covers of algae in limpet exclosures and control plots at Sunset Bay and South Cove. The height of each vertical bar represents the mean of the total algal covers for all plots censused on that date. The mean proportion of each algal type within the overall algal cover is represented by the relative heights of the various patterns of shading. Categories with <2% coverage are not shown. The position of the mark below each bar indicates the day of sampling for that month. The number of plots censused on each date is shown above each bar.

the study areas and preserved by freezing within 4 h of collection. (For sources of the limpets see Results.) All collections were processed simultaneously and identically so that any effects of the drying and ashing procedures might apply to all samples. "Size" refers to the internal volume of the limpet's shell, which was measured by filling with a 1:1 water-ethanol mixture (which has less of a meniscus than pure water). The ash-free dry masses of the limpet bodies were obtained by removing the bodies from the shell, drying them at 90°–100°C for 24 h, cooling them in a desiccator, and weighing them. The bodies were then ashed at 450°–500°, cooled in a desiccator, weighed again, and this mass was substracted from the dry mass of the bodies.

Grazing areas of the limpets were measured on a nearly vertical, natural rock wall at South Cove near the limpet exclosure plots. Here various sized patches of the thin (<1 mm thick), continuous mats of algae had been cleared by *C. digitalis*. These mats comprised mainly the felt-like holdfasts of the green alga *Blidingia minima* var. *vexata*. Measurements of the density of limpets within the grazed patches provided additional information regarding seasonal variation in area grazed per limpet. Measurements were made, once in winter and once in summer, only of grazed areas bounded on all sides by the algal mat, rather than by crevices, clumps of larger perennial algae, or by other features that could be inedible or act as barriers to the limpets. The sizes of individual limpets within the grazed areas were determined from color transparencies.

## RESULTS

The exclosure experiments indicate that grazing by limpets reduces algal cover in the uppermost intertidal zone in all months of the year (Fig. 2). On a yearly average, overall algal covers in the control plots were 25%, while those in the limpet exclosure plots were 72% (Fig. 3). This pattern of differences is consistent among seasons and between the study sites (Fig. 2). The data presented in Figs. 2 and 3 are only for censuses taken in the first six months following the establish-

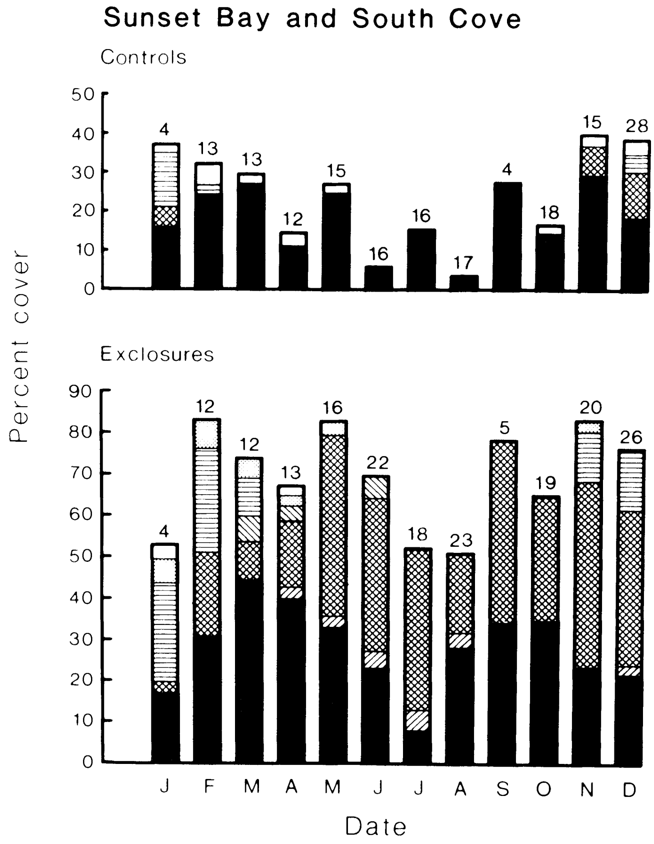

FIG. 3. The annual pattern of algal coverage in limpet exclosures and control plots in the uppermost intertidal zone. Data are combined by month from the Sunset Bay and South Cove study sites for all years. Numbers above each bar are total number of plots censused in that calendar month. Key to shading as in Fig. 2. (Data for *Bangia, Urospora,* and *Porphyra* were previously presented in Lubchenco and Cubit 1980, Table 1.)

ment of an exclosure or control plot. After this time successional changes involving the colonization by barnacles and small herbivores caused considerable divergence in the composition of plants and animals appearing in the exclosure plots, a process described later.

The limpet exclosures that were constructed in the late spring and the summer months (Table 1) tested the hypothesis that physical stresses such as desiccation, insolation, or high temperatures alone could prevent the growth of algae at that time. In all 24 exclosure plots constructed in the months between May and August (see Table 1) blue-green algae and sporelings of other algae formed thin, dark-colored mats within 2–3 wk following the exclusion of limpets. Diatoms (mostly *Fragilaria* and *Melosira* spp.), filamentous green and red algae (*Urospora* and *Bangia*), and membranous green and red algae (*Ulva, Blidingia,* and *Porphyra*) appeared approximately in that order within the 1st 3 mo; in the late summer and early fall, when algal covers are normally at their lowest, there were lush growths of algae in the limpet exclosure plots (Fig. 2, see also color photographs in Carefoot 1977). These particular algae were well able to tolerate summer conditions at the uppermost intertidal levels. On warm, dry, sunny days, the algae became dried and stiff, with no apparent mortality. Algal abundance did not decline after such weather, and the individual fronds did not show signs of bleaching or other damage. The only apparent loss of algae associated with changes in weather occurred in the spring when the thalli of some of *Porphyra* and *Ulva* disintegrated into spores.

Among the exclosure plots constructed in the late spring and summer months the median algal coverage at the first census (still within the summer) was 73% at Sunset Bay and 87% at South Cove, as compared with 2% and 9% in their respective controls (Table 2). The coverages of algae that developed in the exclosure plots in the summer months exceeded the highest values recorded from the control plots during the natural algal bloom in the winter months (Table 2).

Rates of algal development in the exclosure plots varied seasonally. After the removal of limpets, stands of macroalgae became established more rapidly in winter than in summer. In the following analysis these rates are compared between winter and summer for stands of *Bangia* and *Urospora,* the first macroalgae to appear within the exclosures. To provide the necessary resolution in time, these comparisons are restricted to 22

TABLE 2. Algal coverage in exclosure and control plots during the summer months, with comparison to the algal coverage in control plots during the natural winter bloom.

| Location | Summer: percent coverage of algae in exclosure and control plots* | | Winter: peak percent coverage of algae in control plots during the winter bloom† |
|---|---|---|---|
| | Exclosures | Controls | Controls |
| Sunset Bay | | | |
| Median (range) | 73 (65–98)‡ | 2 (0–9)‡ | 42 (0–81)‡ |
| No. plots | 9 | 7 | 9 |
| South Cove | | | |
| Median (range) | 87 (61–94)‡ | 9 (0–77)‡ | 25 (4–96)‡ |
| No. plots | 15 | 12 | 21 |

* Summer values are for the first census after each plot was constructed and include data from only those plots which were constructed and censused in the same summer.

† The peak winter values are the medians of the highest percent coverages recorded for each plot during the winter bloom; these are the maximum values of algal coverage found in the control plots at any time of year.

‡ Within each site in the summer algal coverages were significantly higher in the exclosure plots than in the control plots ($P < .0005$ for both sites). Within sites algal coverages in the exclosure plots during summer were also significantly higher than those in the control plots during the natural winter bloom ($P < .005$ at Sunset Bay and $P < .001$ at South Cove). All comparisons are by the Mann-Whitney U test, Zar 1974.

exclosures that had been censused at intervals not exceeding 1 mo. All exclosure plots started in the winter months had well-developed stands of *Bangia* and *Urospora* at the time of the first census, 29 d after exclosure construction. None of the 15 exclosure plots started in the summer months contained *Bangia* or *Urospora* at the first census, 30 d after their construction (Table 3). (However, exclosures constructed before the summer months still contained stands of these algae at this time, and in a separate set of three exclosures constructed in the summer but at a lower tidal level [≈1 m above mean lower low water], stands of *Bangia* and *Urospora* established within a month.)

The group referred to as microalgae was prevalent throughout the study plots and was the first group to increase in abundance following the removal of limpets. In the exclosure plots, this microalgal cover was composed primarily of mats of blue-green algae, diatoms, and sporelings of macroalgae. In the control plots, however, the microalgae were predominantly thin films of blue-green algae, which in the field appeared as transparent stains on the surface of the rock. These were present in minute crevices on the surface of the sandstone rock, even when they had disappeared as visible algal cover; hence, probably, their persistence. During the late summer months, small samples (<1 cm$^2$) of the rock surface were chipped away from areas of the study sites that were heavily grazed and appeared barren of algae to the naked eye. Under 500× magnification and ultraviolet light, *Oscillatoria*-like and *Dermocarpa*-like blue-green algae were found in the deeper interstices among the surface sand grains of the rock.

TABLE 3. Comparison between summer and winter in the time ($t$) required for limpet exclosure plots to develop stands of the filamentous algae *Bangia* and/or *Urospora* following construction of the plot. Comparisons are of plots constructed in the months of July and August for summer and in the month of November for winter. See text for further explanation.

| Season | Initial number of plots | Time to develop stands of *Bangia* and/or *Urospora* (d) | | |
|---|---|---|---|---|
| | | $t \leq 30$ | $31 < t < 42$ | $42 < t < 70$ |
| | | Number of plots | | |
| Summer | 15 | 0 | 9 | 6 |
| Winter | 7 | 7 | ... | ... |

Algal coverage within any season varied considerably among the exclosure plots, apparently as a result of grazing by herbivores other than limpets. The lowest percent coverages were in the exclosure plots that contained the most refuges for littorinid snails, amphipods, and other small herbivores, refuges such as empty barnacles and the crevices between barnacles and in the rock itself. Following the removal of littorinid snails from small clumps of barnacles in each of seven exclosure plots, algae grew up to and over the barnacles, indicating that the absence of algae did not result from some action of the barnacles themselves. The relationship between refuges and algal coverage is difficult to quantify because of the problem of quantifying refuge potential. In addition, the relationship between refugia and algal coverage can vary from season to season. To avoid this problem I compared refugia in sets of exclosures that were constructed and censused on the same dates, but which differed in having either extensive algal cover (≥80%), or more sparse algal cover (<50%). Plots with more dense algal cover contained fewer crevices and barnacles than those with sparser algal covers (Table 4).

Reduced coverages of algae within certain exclosure plots were associated with several species of chiron-

TABLE 4. Comparison of amount of refuges for small herbivores in limpet exclosure plots with sparser (<50%) and denser (≥80%) covers of algae. This comparison has been limited to exclosures that were constructed and censused on the same dates. At both sites there were more barnacles in the plots with sparser algal cover (at $P < .01$ for South Cove and $P < .02$ for Sunset Bay). At South Cove there were also more crevices in the plots with sparser algal cover ($P < .025$); at Sunset Bay there were no crevices in either category of exclosure plots. (Statistical comparisons are by $t$ test, Zar 1974.)

| | | Exclosures with <50% algal cover | | | Exclosures with ≥80% algal cover | | |
|---|---|---|---|---|---|---|---|
| Location | Date examined | Exclosure identification number | Barnacles (percent coverage)* | Crevices (total cm of crevice per $m^2$ of plot) | Exclosure identification number | Barnacles (percent coverage)* | Crevices (total cm of crevice per $m^2$ of plot) |
| South Cove | 28 Jul 1972 | 240 | 20 | 254 | 242 | 10 | 0 |
| | | 241 | 30 | 506 | 239 | 7 | 40 |
| | 28 Dec 1972 | 37 | 20 | 236 | 40 | 18 | 0 |
| | | 104 | 40 | 194 | 39 | 4 | 0 |
| | | | $\bar{x}$ 27.5 | 297.5 | | 9.75 | 10 |
| Sunset Bay | 31 Jul 1972 (set A) | 17 | 55 | 0 | 1 | 7 | 0 |
| | 31 Jul 1972 (set B) | 11 | 25 | 0 | 4 | 0 | 0 |
| | | | | | 20 | 11 | 0 |
| | | | | | 21 | 5 | 0 |
| | 29 Aug 1972 | 19 | 13 | 0 | 9 | 10 | 0 |
| | | | $\bar{x}$ 31 | 0 | | 6.6 | 0 |

* Barnacle coverage includes only those barnacles with basal diameters ≥3 mm.

omid fly larvae (mostly species of *Saunderia* and *Paraclunio*) (see Robles and Cubit 1981).

Seasonal variations in abundance of algal forage were reflected in the size-specific body masses of the limpets. For this analysis, two groups of *C. digitalis* were collected from the study area at Sunset Bay, one in winter (25 February 1972) and one in summer (6 August 1973). A third group was collected as they died after being stranded above the water level at South Cove. The limpets (whose positions previously had been marked on the rock) had not moved during the several weeks they had been out of the water. Some fell from the rock when lightly touched with a finger and appeared desiccated. As has been observed by Frank (1965) under these conditions, the bodies of the limpets were shrunken within their shells and barely spanned the distance from the point of attachment within the shell to the surface of the rock below. At most, only a thin median strip of the foot was attached to the rock. Most of these limpets, however, revived when placed in seawater. Those that did not showed no signs of decomposition and were used for this analysis.

The ash-free, size-specific body masses of the limpets collected from Sunset Bay in the winter averaged ≈204 mg/cm$^3$ of shell volume as compared with 158 mg/cm$^3$ for the limpets collected from the same location in summer. There were only 77 mg of tissue (ash-free dry mass) per cm$^3$ of shell for the limpets that died at South Cove in the fall (Fig. 4).

The measurements of areas grazed on the natural rock wall at South Cove indicated that the area cleared per limpet was reduced in winter (15 cm$^2$/individual) as compared with summer (43 cm$^2$/individual; Table 5). As the cleared areas expanded in summer, the algal mat that separated some adjacent grazing patches was eaten away, with the result that more limpets were found in fewer, but larger, cleared areas. There was a positive (but not statistically significant) correlation between the number of limpets in a cleared area and the area cleared per limpet. However, it is unlikely this produced the winter-summer difference in the amount

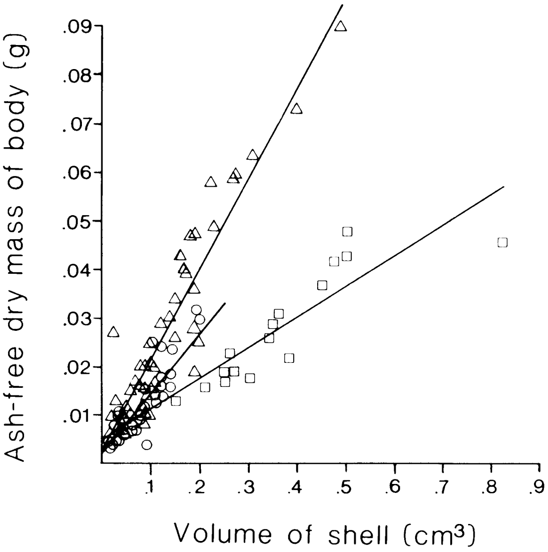

FIG. 4. Comparison of the amount of body tissue per unit volume of shell for limpets collected in the winter (△) and summer (○) at the Sunset Bay study site. The third group (□) was collected at South Cove after dying during a period when it had been continuously exposed above the tide for a period of several weeks. The probabilities that these slopes are equal are <.005 between the winter and summer group at Sunset Bay and <.001 between the group from South Cove and either group from Sunset Bay (by analysis of covariance). See Results for further explanation.

TABLE 5. Winter–summer comparison of areas cleared by limpets in algal mats at South Cove.

| Season | Number of limpets† in cleared area | Total area cleared (cm$^2$)‡ | Area cleared per limpet (cm$^2$)§ |
|---|---|---|---|
| Winter | 1 | 12.6 | 12.6 |
| | 5 | 78.5 | 15.7 |
| | 7 | 95 | 13.6 |
| | 21 | 445 | 21.2 |
| | 27 | 330 | 12.2 |
| | 39 | 558 | 14.3 |
| | 89 | 810 | 9.1 |
| | 107 | 2695 | 25.2 |
| | | $\bar{x} \pm$ SD | 15.4 ± 5.2*** |
| Summer | 7 | 230 | 32.9 |
| | 11 | 512 | 46.5 |
| | 15 | 632 | 42 |
| | 247 | 9795 | 39.7 |
| | 400 | 22 310 | 55.8 |
| | | $\bar{x} \pm$ SD | 43.4 ± 8.5*** |

† The average length of the limpets (from subsamples) was 16.7 mm (SD = 5.17, $n = 84$) in winter and 16.8 mm (SD = 3.13, $n = 85$) in summer. This difference in lengths was not significant ($P > .25$, $t$ test).

‡ In both seasons the total area grazed in a patch was strongly associated with the number of limpets within the patch (winter: $r = 0.98$, $P < .001$; summer: $r = 0.99$, $P < .001$).

§ The area grazed per limpet was positively associated with the number of limpets within the patch, but was not statistically significant (winter: $r = 0.27$, $P > .25$; summer: $r = 0.65$, $P > .25$).

*** The area grazed per limpet was significantly larger in the summer months ($t$ test: $P < .0005$).

of area cleared per limpet. In both seasons, a much stronger correlation existed between the number of limpets in an area and the total area cleared by all limpets. In addition, for grazed patches with comparable numbers of limpets between winter and summer, the areas cleared per limpet were much larger in summer (Table 5). Between winter and summer there was also little difference in the mean lengths of the limpets (Table 5).

Thus, in the summer months, when algal covers were sparse (Figs. 2 and 3), the size-specific body masses of the limpets were reduced (Fig. 4), even though the limpets foraged over larger areas (Table 5). In contrast, during the winter months the limpets maintained greater size-specific body masses (Fig. 4) while grazing over smaller areas (Table 5).

## DISCUSSION

### *A proposed explanation for the seasonal variations in algal cover in the high intertidal zone*

The results of the preceding experiments demonstrate that in the uppermost intertidal zone of this rocky shore, stands of algae can become established and persist at all times of the year, providing herbivory is sufficiently reduced. Algal mortality caused directly by physical stress does not adequately explain the seasonal changes of algal abundance in this habitat. Delicate, filamentous or membranous algae such as certain species of *Urospora, Bangia, Porphyra,* and *Ulva,* that in this zone are normally considered to be winter transients or annuals, were present throughout the year in the limpet exclosures (see also Lubchenco and Cubit 1980). Development of algal covers was slower in the summer months, but physical stresses did not prevent the establishment of stands of algae, even on the portions of the shore that were exposed to the extremes of desiccation, high temperatures, and solar radiation. Algae were more abundant in the limpet exclosures during the summer months than within the control plots during the natural algal blooms in the winter months. These results are not limited to the climate of the Oregon coast; in the warmer, drier climate of the central California coast similar results were obtained by excluding herbivores from the high intertidal zone of the rocky shore (Robles and Cubit 1981, J. Cubit, *personal observation*).

The natural seasonal fluctuations in algal cover could be explained by variations in rates of consumption by herbivores, in rates of production by the algae, or by a combination of the two. For instance, in summer the reduction of overall algal cover may be a result of increased rates of herbivory or decreased rates of production per unit of algal biomass. (Here rates of production or photosynthesis refer to the amount of carbon fixed per unit of algal biomass per unit time.) The explanation most consistent with the results of this study and other investigations of algal production, limpet demography, and limpet behavior is that variations in rates of algal production, rather than in rates of herbivory, generate the seasonal changes in algal coverage that occur in the uppermost intertidal zone.

In the high intertidal zone, rates of algal production appear governed by moisture conditions during the daylight hours, which in turn depend on weather conditions, waves, and tidal patterns. Even for desiccation-tolerant algae, rates of photosynthesis are dependent on the availability of water. Photosynthetic rates of some high intertidal algae increase with initial water loss but eventually decrease as algae dry (Stocker and Holdheide 1937, Johnson et al. 1974, Quadir et al. 1979). In the summer months, daily growth periods are apparently shortened by desiccating conditions (Castenholz 1961). Consistent with this postulated difference in growth rates is the observation that within the exclosure plots, stands of *Bangia* and *Urospora* developed more slowly during the summer than in the winter months. Lower rates of primary production probably also explain the pattern of decreased coverages of algae in the exclosure plots in summer. In both summer and winter algae were removed from the plots by nonlimpet herbivores (see for instance Table 4) and by abrasion from wave-carried debris, but replacement was slower in the summer.

It is unlikely that the increased abundance of algae in the high intertidal habitat during the winter months is either a result of a seasonal decrease in the populations of the limpets or an interruption of their grazing activities. To the contrary, at the upper intertidal levels, populations of limpets are generally larger in winter, a result of immigration from lower levels and decreased rates of mortality (Frank 1965, Breen 1972). Limpets do not suspend their feeding activities in winter, as indicated by simultaneous increases in rates of shell growth (Frank 1965, Breen 1971), size of gonads (Frank 1965), and size-specific body masses (Fig. 4). The combination of these factors indicates an input of material and energy from active feeding.

The demographic pattern through the whole year suggests that the life history characteristics of the high intertidal limpets are strongly affected by seasonally varying rates of algal production. In a study of *Collisella digitalis* in Oregon, Frank (1965) found that rates of shell growth decreased in summer; these rates are apparently dependent on the supply of forage per limpet (Haven 1973). The rates of mortality for high intertidal *C. digitalis* are greater in the summer (Frank 1965, Breen 1971). Sutherland (1972) also noted many of the same relationships for *Collisella scabra* (sympatric with *C. digitalis* to the south of Oregon) living at the uppermost intertidal levels: in summer, rates of growth were lower, rates of mortality were higher, and both gonad and size-specific body masses decreased.

In the high intertidal zone, seasonal migration and mortality evidently adjust densities of *C. digitalis* populations relative to food supply. (Recruitment of juveniles apparently occurs at lower levels of the shore [Frank 1965]). This species migrates into the upper intertidal zone in winter, when algae are more abundant and emigrates to other parts of the intertidal zone in summer when algal forage is reduced (Frank 1965). Manipulative field studies indicate that such migrations are density-dependent on food supply. In experiments involving *C. digitalis,* artificially increasing the population densities of limpets on the shore resulted in emigration from the areas of greater density (Frank 1965, Breen 1972, Stimson and Black 1975). In these cases the limpets migrated to the upper and lower extremes of their ranges where rates of mortality were higher (Frank 1965, Stimson and Black 1975). In the above studies the density-dependent factor per se was not identified, although concentration of food was suggested as a likely possibility. Breen (1971) tested this idea by reducing the availability of food, rather than by increasing the density of limpets, and obtained the same results: migration of limpets from the experimental area. This density-dependent migratory behavior appears to be the primary mode of regulation of limpet populations (Breen 1972). The exclosure experiments demonstrate that the abundance of algal forage is, in fact, dependent on the population densities of the limpets, thus completing a feedback loop in the regulation of limpet population densities relative to food supply.

In addition to the mortality which results from migration into the upper part of the range, the limpets that remain in the high intertidal zone also experience increased rates of mortality in the summer months. This phenomenon which occurs during periods of calm seas and dry weather, has been attributed to desiccation or insolation (Lewis 1954, Frank 1965, Sutherland 1970, Wolcott 1973). However, there is also little growth of algae under these conditions, and density-dependent starvation cannot be ruled out as a cause of, or contributor to, the deaths of these limpets. For instance, *C. digitalis* protects itself against desiccation by sealing its shell to the substratum with a sheet of mucus (Wolcott 1973), and at some point of starvation, a limpet may not be able to produce this sheet. In addition, under dry conditions at South Cove, the emaciated and desiccated bodies of the limpets were barely able to span the distance between the point of shell attachment and the substratum below. As a result, they were easily dislodged and could have been carried away by waves (Wolcott 1973), strong winds, or predators. (Frank [1965] reports predation on limpets by a mouse under such circumstances.) At South Cove, limpets found dead under these conditions had the lowest size-specific body masses of all the groups of limpets measured (Fig. 4). Lewis (1954) attributes such instances of mortality to physical stresses alone because the limpets he studied had access to algae even at the highest intertidal levels. However, the algae were unidentified "Myxophyceae." If these algae were lichenized, as are many at this tidal level, they may not be readily consumed by herbivores (Cubit 1975). Mechanisms may exist through which rates of mortality from physical stress are influenced by a density-dependent factor such as food supply. The actual contribution of this type of mortality to population regulation, however, remains to be assessed. This hypothesis could be tested by experimentally increasing the supply of forage for limpets in high-stress conditions, or by transplanting groups of limpets from circumstances of (1) abundant and (2) scarce forage to areas of high stress and then comparing immediate rates of mortality between the two groups.

Since *C. digitalis* only moves on wet rock, it has also been suggested that dry summer conditions may reduce opportunities for grazing and have the same effect as a shortage of food (Frank 1965). Nonetheless, limpets graze away larger areas in the summer (Table 5), suggesting compensation for decreased algal production per unit area. Having to forage over larger areas may well be another increased cost associated with summer, since gastropod locomotion is relatively expensive (Denny 1980*a, b*).

In summary, in winter daytime conditions are wet, photosynthesis continues throughout the daylight hours, rates of primary production exceed rates of consumption by herbivores, standing crop increases, and the risk of a given alga being consumed by herbivores decreases. In the summer months, the algae often dry when exposed above the level of the tides, rates of photosynthesis and algal growth decrease, rates of production by algae fall below rates of consumption by limpets, and the limpets graze over larger areas, diminishing the standing crop of algae. As this happens, for any remaining algae the risk of being consumed by a herbivore increases. For an alga at this tidal level to survive through the summer it must either be in special circumstances of reduced herbivory, or possess its own protection against herbivory. For example, beds of algae persist on horizontal areas of the shore where oystercatchers consistently reduce limpet populations (Frank 1982). In the vicinity of limpets, however, resistance to herbivory is a necessary condition for surviving through the summer.

What prevents the number of limpets in the high intertidal zone from increasing to a level capable of consuming all of the winter forage? While winter is a time of abundant forage, summer is a time of scarcity, and limpet populations decline in density through emigration, increased rates of mortality, and lower rates of replacement. Consequently, the limpets cannot maintain population densities through the summer that are capable of consuming the next winter's crop of algae as fast as it is produced. Thus, algal consumption will lag increasing production, at least initially, in the following winter, resulting in a temporary increase of standing crop, or "bloom," of algae.

### *Comparisons with other plant-herbivore studies*

Similar interactions of vegetation abundance, herbivore populations, and productivity have been noted for terrestrial and other marine communities. Leigh (1975) and Leigh and Smythe (1978) suggest that populations of vertebrate folivores in a tropical forest in Panama are regulated by seasonal shortages in new leaves, as are herds of grazing animals in the Serengeti (Sinclair 1975). In the Sahelian region of Africa the survivial of vegetation within fenced areas demonstrated that the extensive reduction of plant cover during the severe drought of the early 1970s was caused by grazing, rather than by the direct effects of physical stress (Wade 1974). Cushing (1975) describes interactions between the seasonal abundance of planktonic algae and herbivores in arctic and temperate seas, which are also similar to the benthic system of limpets and attached algae described here.

This explanation for the seasonal changes in algal abundance is different from those proposed by Castenholz (1961) and Menge (1975) for areas grazed by littorinid snails. Based on studies on the Oregon coast, Castenholz (1961) suggested that blooms of algae occurred in the winter months because of reductions in the numbers and/or activities of *Littorina.* Similarly, Menge (1975) explained that winter increase in algal abundance on the New England shore resulted from a decrease in the activities of the *Littorina.* These snails retreated into crevices in the rock during the winter. Observations made during the present study agree with those of Castenholz (1961) and Menge (1975). Littorinid snails were rare in some locations in winter where they had been abundant in summer, probably as a result of increased winter wave action. Littorinid snails, poorly adapted for maintaining themselves on open rock surfaces exposed to heavy wave action, must retreat into crevices in the winter months or be washed away by the waves (Lewis 1964, Behrens 1974).

However, before the increase in algal abundance can be attributed to decreased activities of *Littorina,* it should be determined if individual snails actually consume less algae in the winter months or if the increased availability of algae at this time allows the snails to meet their nutritional requirements by grazing smaller, safer areas near crevices. For these snails there may be no advantage for adaptations to remain active on wave-exposed sections of the shore.

Studies of the feeding, growth, reproduction, and energetics of these snails in winter could establish if the snails actually slow or cease their activities. In this regard, Victor Chow (*personal communication*) has studied one species of *Littorina, L. keenae* (=*planaxis*), that is predominant in the high intertidal zone of the north-central California coast where winter algal blooms occur. In his study site at Bodega Head, reductions in snail abundance were associated with winter wave action, while shell growth, but not reproduction, continued through the winter.

In a midtidal study site at a latitude of ≈35° (as compared with 45° for the Oregon coast), Underwood (1980) also found that foliose algae will appear above the limits of their normal distribution on the shore if they are protected against herbivory. However, in this, probably harsher, environment the foliose algae only grew to maturity in the shade of cages. In open-topped cages the algae never developed past the sporeling stage.

### *Effects of seasonality on the species composition of high intertidal communities*

If these hypotheses are correct, the present species composition of these particular high intertidal communities is dependent on fluctuations in rates of primary production caused by seasonal changes in the physical environment. If rates of production were more constant over time, the limpet populations should approach an equilibrium with algal production, and there would no longer be seasons of reduced grazing pressure which presently give algae such as *Bangia, Urospora, Ulva,* and *Porphyra* the opportunity to establish, grow, and reproduce. Under more constant physical conditions, no matter how benign, these herbivore-susceptible algae should be much rarer, occurring primarily in circumstances where physical disturbances or predators reduce the activities and/or abundances of the herbivores (e.g., Frank 1982, Robles 1982). This effect could be produced equally well by less favorable winter conditions or more favorable summer conditions. Thus, the abundances of the transient species of algae could not be maintained indefinitely by prolonging winter weather conditions through the year.

We may also speculate that reducing the seasonal fluctuations in factors controlling primary production may increase the abundance of the more grazing-resistant species of perennial algae at the uppermost intertidal level. At present, these algae must compete with the transient species in the winter months and withstand the grazing pressure of the starving limpets in the summer months. Some evidence suggests that the simpler, faster growing, transient species of algae are competitively superior in establishment to the tougher, more complex, slower growing perennial species, and that some grazing may be necessary to open areas for the perennials (Branch 1975, Nicotri 1977, Sousa 1979, Lubchenco and Cubit 1980, Slocum 1980, Brawley and Adey 1981). Physical stress alone probably cannot explain the low abundance of perennial algae in the upper intertidal zone of the Oregon study areas. At least some perennial algae are evidently capable of tolerating extremes of desiccation, insolation, and high temperatures. Scattered individuals of *Ralfsia* sp., *Hildenbrandia* sp., *Blidingia minima* var. *vexata*, and *Endocladia muricata* occurred in the Oregon study areas throughout the year (Figs. 2 and 3). On rocky shores of the tropical and subtropical latitudes, certain species of algae (e.g., *Bostrychia*, *Calothrix*, and *Hildenbrandia*) are perennial at the uppermost intertidal levels, where physical conditions are probably much harsher than on the Oregon coast (Taylor 1945, Stephenson and Stephenson 1972, J. Cubit, *personal observation*). If physical conditions fluctuated less on the Oregon coast, there would probably not be such seasonal extremes of competition and herbivory, making the uppermost intertidal zone a more favorable habitat for perennial species of algae and producing more year-round algal coverage than now exists.

If the preceding is correct, community structure in the high intertidal zone is sensitive to changes in annual patterns of physical conditions, and even a small change of climate in one season could change the species composition and abundance of algae and herbivores on a year-round basis. As an example, a simple reduction in the wet fogs of spring and early summer at the Oregon study site would decrease the abundance of algal forage in the summer months and therefore increase it in the winter months. Conversely, prolonging foggy conditions through the summer would tend to equalize rates of primary production between summer and winter, thus decreasing the winter bloom of transient species, and perhaps increasing the overall abundance of the more grazing-resistant species of perennial algae. The possibility of long-term, cyclic changes of community composition in the high intertidal zone is suggested by the oscillations of climate and seasonal timing of the tides associated with the precession of the earth's orbit (see for examples Hays et al. 1976, Sergin 1980, Kukla et al. 1981).

## CONCLUSIONS

The prevailing idea that the lethal effects of physical stresses account for the disappearance of algae in the high intertidal zone during transition from winter to summer, as well as in the transition from lower to higher levels on shore, is inconsistent with the results of this study. As demonstrated by the increased abundance of algae at all times of year following the experimental removal of limpets, grazing must be considered as one of the factors contributing to the mortality and controlling the abundance of algae at the upper intertidal levels of the rocky shore.

These results did not fit the generalization that predation, used in the broad sense to include herbivory, is less severe when physical conditions are more harsh (Connell 1975, Menge and Sutherland 1976, Menge 1978). In the summer months, when the stresses of desiccation, insolation, and high temperatures are more severe in the high intertidal zone, a greater proportion of the standing crop of algae is removed by herbivores.

Explanations for patterns of temporal abundance and spatial distribution of organisms on intertidal shores typically dwell on the effects of agents of mortality (e.g., predation, herbivory, and physical stresses). However, if the explanations presented here are correct, among the primary variables that control the seasonal and spatial abundance of intertidal algae at the upper levels of the shore are those physical factors that do not necessarily cause mortality, but do influence rates of primary production and, consequently, rates of growth, survival, and reproduction relative to rates of herbivory. These relationships can also produce the strong correlations that exist between physical conditions and the distribution and abundance of intertidal organisms in time and space. Physical factors affect the abundance of species in the high intertidal zone not only through mortality caused by stress, but also through generating annual cycles in rates of primary production. In their seasonal oscillation, physical conditions in the high intertidal zone periodically shift the net outcome that occurs between rates of herbivory and rates of algal production, resulting in the development of a much different type of high intertidal community than would exist if the physical conditions, no matter how benign or severe, remained more constant over time.

## ACKNOWLEDGMENTS

I thank the following people for providing information and other assistance during this study: G. S. Caldwell, R. W. Castenholz, L. Cheng, V. Chow, C. J. Cogswell, C. I. French, C. K. Hunter, H. M. Howard, M. Leitschuh, P. Leon, S. D. Leonard, R. A. Lewin, A. C. Miller, T. F. Mumford, T. M. Niesen, J. N. Norris, A. C. Roman, D. C. Simpson, D. R. Strong, R. C. Terwilliger, J. A. West, C. E. Wickstrom, S.

Williams, and S. B. Yamada. I also thank P. Rudy for providing facilities at the Oregon Institute of Marine Biology and the Sigma Xi Foundation for a grant-in-aid of research. Support was also received from the Smithsonian Institution Environmental Sciences Program at the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute, and from the Department of Biology, University of Oregon, where this study formed part of a dissertation.

The manuscript was greatly improved by the comments of J. M. Burgett, J. Connor, P. W. Frank, S. D. Garrity, E. G. Leigh, Jr., S. C. Levings, W. P. Sousa, J. P. Sutherland, and A. J. Underwood.

I especially thank J. H. Connell, S. A. Cook, and P. W. Frank for their advice and discussion.

## LITERATURE CITED

Aleem, A. A. 1950. Distribution and ecology of British marine littoral diatoms. Journal of Ecology **38**:75–106.

Bartrum, J. A. 1926. Abnormal shore platforms. Journal of Geology **34**:793–806.

Behrens, S. 1974. Ecological interactions of three *Littorina* (Gastropoda, Prosobranchia) along the west coast of North America. Dissertation. University of Oregon, Eugene, Oregon, USA.

Branch, G. M. 1975. Intraspecific competition in *Patella cochlear* Born. Journal of Animal Ecology **44**:263–281.

Brawley, S. H., and W. H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology **61**:167–177.

Breen, P. A. 1971. Homing behavior and population regulation in the limpet *Acmaea* (*Collisella*) *digitalis*. Veliger **14**:177–183.

———. 1972. Seasonal migration and population regulation in the limpet *Acmaea* (*Collisella*) *digitalis*. Veliger **15**:133–141.

Carefoot, T. H. 1977. Pacific seashores. University of Washington Press, Seattle, Washington, USA.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology **42**:783–794.

Chapman, A. R. O. 1973. A critique of prevailing attitudes on the control of seaweed zonation on the sea shore. Botanica Marina **16**:80–82.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs **41**:351–389.

———. 1972. Community interactions on marine rocky intertidal shores. Annual Reviews of Ecology and Systematics **3**:169–192.

———. 1974. Ecology: field experiments in marine ecology. Pages 21–54 *in* R. N. Mariscal, editor. Experimental marine biology. Academic Press, New York, New York, USA.

———. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Cubit, J. D. 1975. Interactions of seasonally changing physical factors and grazing affecting high intertidal communities on a rocky shore. Dissertation. University of Oregon, Eugene, Oregon, USA.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, England.

Dayton, P. K. 1970. Competition, predation, and community structure: the allocation and subsequent utilization of space in a rocky intertidal community. Dissertation. University of Washington, Seattle, Washington, USA.

———. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351–389.

———. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs **45**:137–159.

Denny, M. 1980*a*. Locomotion: the cost of gastropod crawling. Science **208**:1288–1290.

———. 1980*b*. The role of gastropod pedal mucus in locomotion. Nature **285**:160–161.

Earle, S. A. 1972. A review of the marine plants of Panama. Bulletin of the Biological Society of Washington **2**:70–87.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565–581.

Fisher, R. A., and F. Yates. 1963. Statistical tables. Hafner, New York, New York, USA.

Frank, P. W. 1965. The biodemography of an intertidal snail population. Ecology **46**:831–844.

———. 1982. Effects of winter feeding on limpets by Black Oystercatchers. Ecology **63**:1352–1362.

Haven, S. B. 1973. Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. Ecology **54**:143–151.

Hays, J. D., J. Imbrie, and N. J. Shackleton. 1976. Variations in the earth's orbit: pacemaker of the ice ages. Science **194**:1121–1132.

Johnson, W. S., A. Gigon, S. L. Gulmon, and H. A. Mooney. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology **55**:450–453.

Kukla, G., A. Berger, R. Lotti, and J. Brown. 1981. Orbital signature of interglacials. Nature **290**:295–300.

Lawson, G. W. 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. Journal of Ecology **45**:831–860.

Leigh, E. G., Jr. 1975. Structure and climate in a tropical rain forest. Annual Review of Ecology and Systematics **6**: 67–86.

Leigh, E. G., Jr., and N. Smythe. 1978. Leaf production, leaf consumption, and the regulation of folivory on Barro Colorado Island. Pages 33–50 *in* G. Montgomery, editor. The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C., USA.

Lewis, J. R. 1954. Observations on a high-level population of limpets. Journal of Animal Ecology **23**:85–100.

———. 1964. The ecology of rocky shores. English Universities Press, London, England.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology **61**:333–344.

Lubchenco, J., and J. Cubit. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology **61**:676–687.

Menge, B. 1978. Predation intensity in a rocky intertidal community. Oecologia (Berlin) **34**:1–16.

Menge, B., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. American Naturalist **110**:351–369.

Menge, J. L. 1975. Effect of herbivores on the community structure of the New England rocky intertidal region: distribution, abundance, and diversity of algae. Dissertation. Harvard University, Cambridge, Massachusetts, USA.

Newell, R. C. 1979. Biology of intertidal animals. Marine Ecological Surveys, Faversham, Kent, England.

Nicotri, M. E. 1977. The impact of crustacean herbivores on cultured seaweed populations. Aquaculture **12**:127–136.

Quadir, A., P. J. Harrison, and R. E. DeWreede. 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. Phycologia **18**: 83–88.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. Between Pacific tides. Stanford University Press, Stanford, California, USA.

Robles, C. 1982. Disturbance and predation in an assemblage of herbivorous diptera and algae on rocky shores. Oecologia (Berlin) **54**:23–81.

Robles, C., and J. Cubit. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. Ecology **62**:1536–1547.

Sergin, V. Ya. 1980. Origin and mechanism of large-scale climatic oscillations. Science **209**:1477–1482.

Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropical grasslands ecosystems. Journal of Animal Ecology **44**:497–520.

Slocum, D. J. 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. Journal of Experimental Marine Biology and Ecology **46**:99–110.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs **49**:227–254.

Stephenson, T. A., and A. Stephenson. 1972. Life between tidemarks on rocky shores. W. H. Freeman, San Francisco, California, USA.

Stimson, J., and R. Black. 1975. Field experiments on population regulation in intertidal limpets of the genus *Acmaea*. Oecologia (Berlin) **18**:111–121.

Stocker, O., and W. Holdheide. 1937. Die Assimilation Helgolander Gezeitenalgen wahrend der Ebbezeit. Zeitschrift fur Botanik **32**:1–59.

Sutherland, J. P. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). Ecological Monographs **40**:169–188.

———. 1972. Energetics of high and low populations of the limpet, *Acmaea scabra* (Gould). Ecology **53**:430–437.

Taylor, W. R. 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. Allan Hancock Pacific Expeditions 12. University of Southern California Press, Los Angeles, California, USA.

Underwood, A. J. 1979. The ecology of intertidal gastropods. Advances in Marine Biology **16**:111–210.

———. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia (Berlin) **46**:201–213.

———. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. Journal of Experimental Marine Biology and Ecology **51**:57–85.

Wade, N. 1974. Sahelian drought: no victory for Western aid. Science **185**:234–237.

Wolcott, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." Biological Bulletin **145**:389–422.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.