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INTERACTIONS OF SEASONALLY CHANGING PHYSICAL FACTORS AND GRAZING AFFECTING HIGH INTERTIDAL COMMUNITIES ON A ROCKY SHORE

by

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A DISSERTATION

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SECTION I

INTRODUCTION

On the rocky shores along the coast of Oregon, the algae and invertebrates that live at the uppermost intertidal levels are exposed for long periods above the tide and receive the least benefits of the climate moderating effects of the sea. The physical stresses usually considered the most lethal to these organisms are desiccation, high temperatures, and insolation, all of which are more severe during the drier, warmer, and sunnier months of summer, and less severe during the wet, cool, overcast winter weather.

The group of organisms showing the most response to the seasonal changes in the physical environment are the algae. During the winter months there is a "bloom" of algae that covers much of the surface of the high intertidal rocks, but in the summer most of the algae disappear, leaving large areas of barren rock surface, sparsely populated by a few invertebrates and perennial algae. Reductions in algal abundance during drier conditions and increases in algal abundance during wetter conditions is a general feature of high intertidal rocky shores (Aleem 1950, Lawson 1957, Lewis

1964).

Explanations for the seasonal fluctuations in the abundance of algae, as well as for the low densities and varieties of organisms in the high intertidal zone, have generally centered on the lethal effects of physical factors when these organisms are exposed above the level of the tide. These explanations are derived from, and are supported by, the close correlations between increased exposure to physical stresses and reductions in the abundances and variety of intertidal organisms. The sparsest populations and the fewest species are usually found during the periods of the year and on the locations of the shore that are the driest, warmest, and most sun-exposed. Variations in the abundances of algae appear most closely correlated with changes in exposure to desiccation (Dayton 1971, Lawson 1957, Lewis 1961, 1964).

In addition to the abiotic stresses, the high intertidal algae must also cope with large populations of grazing animals, especially the gastropods, which at lower intertidal levels have been shown to have a marked effect on species composition and abundance of the algae (Castenholz 1961, Dayton 1971, Jones 1948, Lodge 1948, May, et al., 1970, Smith 1968, Southward 1964). Castenholz (1961) working at a tidal level just below the one being considered in this paper, but on the same area of the Oregon coast, found that some decreases in algal abundance in the summer were due to grazing by several species of gastropods, and suggested that the winter increase in algal abundance may be due to reductions in the numbers and/or activities of these grazers, as well as to reductions in algal mortality from physical factors at higher intertidal levels.

The following study is an attempt to define how biotic and abiotic factors operate to control the abundances and influence the varieties of organisms found at the uppermost tidal levels of the wave-exposed rocky habitats at several sites on the coast of Oregon.

SECTION II

PHYSICAL AND BIOLOGICAL DESCRIPTIONS OF THE STUDY SITES

Physical Description

The studies described here were done on the outer coast of Oregon, in the vicinity of Cape Arago, 43° 18' N. latitude, 124° 25' longitude, about 18 km west of the city of Coos Bay.

The study sites were at various locations along the coast from the south jetty of the entrance to Coos Bay extending south to the area called South Cove or South Bay at Cape Arago, a distance of approximately 8 km.

Most of the experiments and observations were done at two sites: at a rocky point on the west side of the area called South Cove at Cape Arago, and on a large rock formation that is located on the north side of a small bay called Sunset Bay. In the following, these two sites will be referred to only as Cape Arago and Sunset Bay.

At the Cape Arago site, most of the rock surfaces studied were nearly horizontal, while at Sunset Bay the rock surface ranged from nearly horizontal to vertical. The non-vertical rock surfaces at Sunset Bay were on south, southwest, and west facing slopes. Several offshore reefs and a large, flat bench extending seaward from the study area protected the Sunset Bay site from wave action except during the higher tides. The site at Cape Arago was somewhat less protected from wave action.

The tides along this shore are of the mixed semi-diurnal type: there are two unequal high tides and two unequal low tides each day. In the U.S. system, tide heights are measured from the level of the mean lower low tides, the "0.0" level. On this part of the coast the average daily tide range, that is, the distance from the level of mean lower low tides to the level of the mean higher high tides is approximately 2.1 m. The mean tide level is 1.2 m.

In the study areas, the natural rock shore is sandstone. A feature of this shore is a bench, or shelf, that occurs along the shore at about the level of the mean high tides (1.8 m). (These benches are found along many shores, and theories of how they are formed at a consistent, high, tide level are described by Bartrum (1926).) The position of this bench will be used as a reference level, and, unless noted otherwise, all the experiments and observations described here were at levels of the rock above the level of this bench. These are the uppermost levels of the intertidal shore and correspond to the Zone 1 in the scheme of Ricketts, Calvin, and Hedgpeth (1969).

The wet and dry seasons in the high intertidal habitat are a result of both seasonally changing atmospheric conditions and yearly cycles of the tides. In the late autumn, winter, and early spring the weather is cooler and wetter, and the high rocks receive more spray and wash from the waves generated by winter storms. (Since this habitat is so often above the level of the tide the length of time it is wet is largely dependent on the amount of wash and spray it receives from the waves.) In addition, during the daylight hours of winter the tides are higher, while in summer there are fewer high tides during the daylight hours, and the high rocks are exposed on the average for periods of more than 8 hours per day to the drier, warmer, sunnier weather. This pattern of the tides through the year is shown in Figure 1. The pattern of the weather itself may be modified in some summers by cool, wet fogs.

Biological Description

About a dozen species are common in the high intertidal study areas at Cape Arago and Sunset Bay (Table 1).

Fig. 1.--The number of daylight hours per day the rock surface above the 1.5 m (5 ft) tide level is exposed above the level of the tide. The high intertidal study areas described in this paper are at, or above, the 1.8 m tide level. Thus, if the waves do not exceed 30 cm, the 1.8 m tide level and above is exposed to the air for an average of eight or more daylight hours per day in the period from March through September.

These data are derived from a table of predicted hourly tide heights provided by the National Oceanic and Atmospheric Administration, National Ocean Survey, for the period 1 October 1972 to 31 October 1973. Daylight hours are defined as one-half hour before sunrise to one-half hour after sunset.

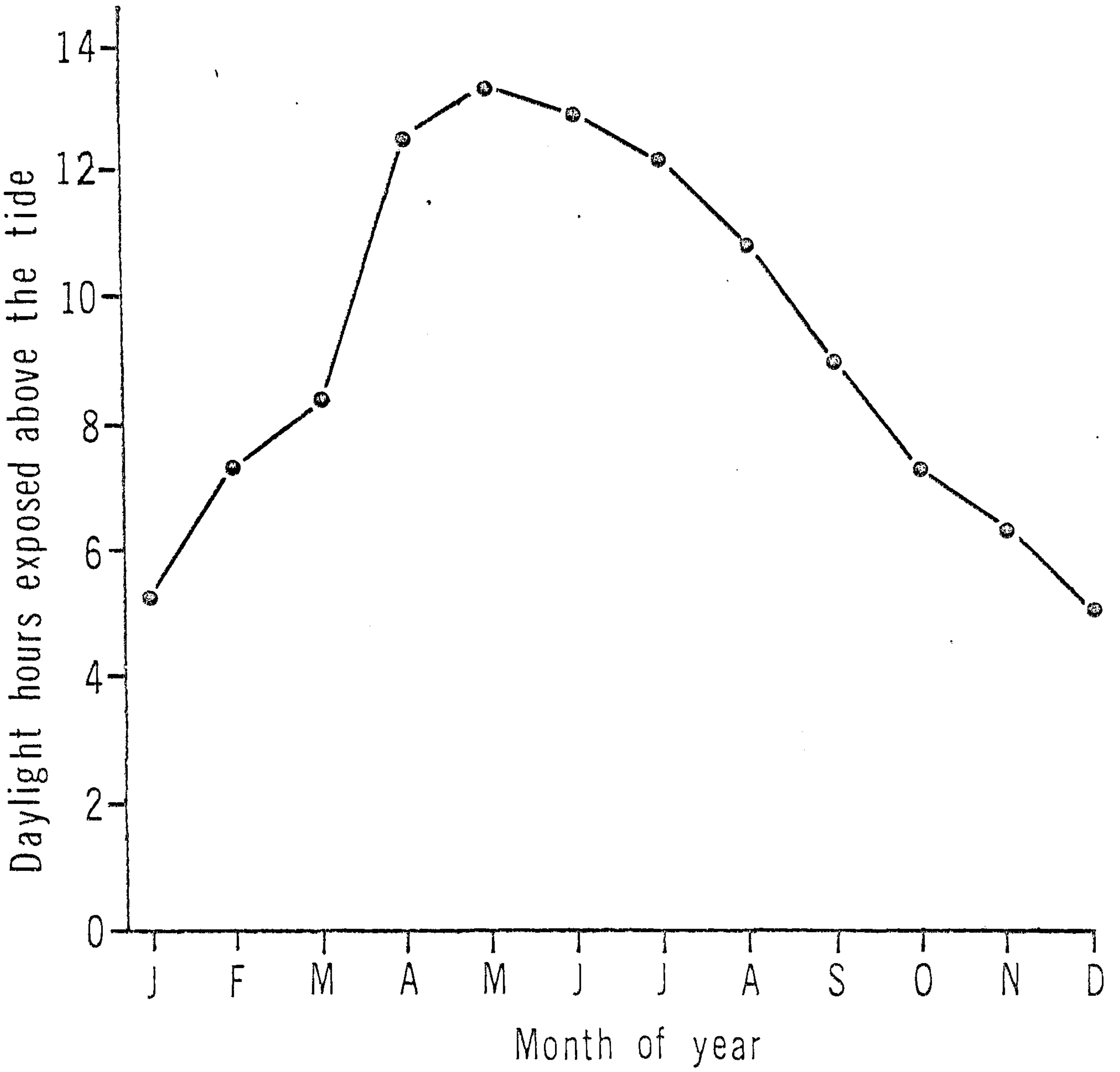

Daylight hours exposed above the tide
14
12
10
8
6
4
2
0
J
F
M
A
M
J
J
A
S
O
N
D
Month of year

TABLE 1.--The macroalgae and invertebrates common in the study areas.

	Genus and Species	Phylum
A. Macroalgae		
1. Transient algae with filamentous thalli	Bangia fuscopurpurea	Rhodophyta
	Bangia vermicularis	Rhodophyta
	Urospora pencilliformis	Chlorophyta
2. Transient algae with membranous thalli	Ulva spp.	Chlorophyta
	Enteromorpha vexata	Chlorophyta
	Porphyra perforata	Rhodophyta
	P. pseudolanceolata	Rhodophyta
	P. schizophylla	Rhodophyta
3. Perennial algae	Ralfsia spp.	Phaeophyta
	Iridaea flaccida	Rhodophyta
	Gigartina papillata	Rhodophyta
	Endocladia muricata	Rhodophyta
B. Invertebrates	Genus and Species	Common Name
1. Herbivorous gastropods	Acmaea (=Collisella) digitalis	limpet
	Littorina scutulata	littorine snail
	Littorina sitkana	littorine snail
2. Herbivorous Chironomid flies	Saunderia (=Camptocladius) marinus	midge
	Paraclunio alaskensis	midge
3. Barnacles	Chthamalus dalli	acorn barnacle
	Balanus glandula	acorn barnacle

The Algae

Not listed in Table 1 are the species of diatoms, blue-green algae, and lichens, which, at times, may be abundant at the highest tidal levels. Most of these are difficult to identify to genus or species with the naked eye. The algae listed are identifiable to genus with the unaided eye, but the specific distinctions for the annual or transient algae must, in many cases, be made by microscopic examination. Moreover, the divisions into species in these types of algae are based largely on certain differences in morphology, which, for these species, are highly variable; therefore, many of these species may be artificial, as discussed below.

The transient algae: annuals and ephemerals. --The term "transient," as used here, is a somewhat arbitrary term used here to categorize the algae which usually exist in any one area for only a short period of time. They have the following characteristics in common: They are all of simple structure, being either filamentous or membranous sheets of cells, one to two cell layers in thickness. They are rare or absent on the high intertidal rocks in the summer dry season but are very abundant in the winter months, forming much of the wet-season algal bloom. These types of algae are also fast growing, and are usually among the first species present in sequences of succession (Northcraft 1948).

Bangia and Urospora are two filamentous, hair-like algae that often grow intermingled with one another, forming thick mats, especially during the beginning of the wet season algal bloom.

The two species of Bangia may actually be the same species, B. fuscopurpurea being a more mature stage of B. vermicularis (Smith 1969).

The Urospora that has been encountered in this study resembles most closely the descriptions (Doty 1947, Smith 1969) for U. pencilliformis (Roth) Areschoug.

The Ulva species are difficult to tell apart, although the species collected in summer closely resemble Doty's (1947) description of U. californica Wille.

Enteromorpha vexata forms large patches at the highest intertidal levels (2-3 m) at South Cove. The thalli of these plants are commonly infected with a fungus, Turgidosculum ulvae (Reed) J. and E. Kohlmeyer. E. vexata has previously been put in the genus Ulva. The genera Ulva and Enteromorpha are similar, both being membranous green algae, two cell layers thick, but in the genus Enteromorpha, the two cell layers are at least partially separated, forming a hollow space. The variability of this characteristic has been demonstrated by Fjeld (1970) who has described the genetics of, and has cultured hollow, Enteromorpha-like plants from a wild-like Ulva species.

The Porphyra species found in the study areas have been identified by Thomas Mumford as the three species listed in Table 1; it is possible, however, that although these species are morphologically distinct, they may, in actuality, be produced by the same alternate stage, the "Conchocelis" stage, in the life cycle of these Porphyra spp. (Mumford 1973).

The perennial algae.--Ralfsia is a black encrusting alga that resembles a patch of tar on the rocks. Although it is common in other areas with each plant covering upwards from 10 cm^2 of the rock surface, in the study areas it was rare and the plants were smaller, most of them covering on the order of one square centimeter or less. The species of Ralfsia were not identified, and it should be noted that the members of this genus are now thought to be alternate stages in the life cycles of two other algal genera, Scytosiphon (Tatewaki 1966) and Petalonia (Edelstein et al., 1970).

Iridaea flaccida (Setchell and Gardner) Hollenberg and Abbott is a leafy red alga which was found mainly growing out of cracks and other sheltered microhabitats in the high intertidal areas studied here, and rarely exceeded 10 cm in length and 5 cm in width.

Gigartina papillata is another leafy red alga about the same size as Iridaea flaccida commonly found growing out of cracks in the surface of the rock, but it also grows out on the open surface of the rock.

Endocladia muricata is a distinctive, common alga of the high intertidal zone. The thalli of this plant are many branched, not leafy, and form spreading, bushy clumps 3-6 cm high.

The Invertebrates

In terms of biomass, the limpet, Acmaea (=Collisella) digitalis (Rathke) is the most common herbivore on the high, wave-exposed rocks in the study areas. The two littorine snails, Littorina scutulata Gould, and Littorina sitkana Philippi are common in the study areas only where large barnacles, clumps of perennial algae, or crevices in the rock provide protection from wave action (see Behrens 1974).

The larvae of the two Chironomid flies, Paraclunio alaskensis Coquillet and Saunderia marinus Saunders feed mainly on diatoms, green algae (Ulva and Enteromorpha), and blue-green algae (Leonard 1972, Morley and Ring 1972). At times these flies are abundant everywhere in the study areas, especially at South Cove. The adults apparently emerge at low tide, mate, oviposit, and are swept away by the next high tide (Saunders 1928, Morley and Ring 1972).

Chthamalus dalli Pilsbry is a smaller barnacle than Balanus glandula Darwin. If the two attempt to occupy the same space Balanus usually wins by undercutting or crushing Chthamalus (Connell 1961). On other shores, Chthamalus usually occupies a zone above that of Balanus, but in the areas studied here both species occurred up to the highest tidal levels. Of the two types, Balanus glandula is less able to become established in areas grazed by limpets (Dayton 1971).

SECTION III

EXPERIMENTS AND OBSERVATIONS

Method of Making Limpet Exclosures

To see what changes might occur on the high intertidal rocks if grazing by limpets were reduced, limpets were excluded from areas of the rock surface by use of strips of copper paint as barriers. The composition and application of this paint is described below in the form of instructions for others that may want to repeat the technique.

Materials

The base of the paint is the following:

Shining Armor brand copper paint
number 606
Manufactured by the Illinois Bronze Powder and
Paint Co., Lake Zurich, Illinois 60047

Description of paint:

a styrene lacquer, with xylol solvent,
with 15% by weight 99.9% pure electrolytic
copper powder (manufacturer's pers. comm.)
This paint is only available in 59 ml (2 fluid
oz.) jars.

The copper content of this paint is increased by adding an additional 29 g of copper powder to each jar (59 ml) of the commercially available paint. The copper powder is from the following source:

Luco brand "Copper Lining Bronze"
Manufactured by the Leo Uhlfelder Company
420 South Fulton Avenue
Mount Vernon, New York 10553

Description of copper powder:

"pure copper material" plus approximately 1% stearic acid (manufacturer's personal communication).

Methods of applying paint to rock:

1. The rock surface must be clean and dry for the paint to adhere. The paint may be applied directly to a dry rock surface that is free of a visible algal film; otherwise the rock must be thoroughly cleaned with a wire brush and scraper (only where paint is to be applied), and then dried with a propane torch.

2. Paint is applied to the surface of the rock with a brush, following the instructions on the original jar of paint (i.e., flow on in one direction, avoid too much brushing, keep paint stirred).

3. The paint is applied in a strip approximately 3-4 cm wide.

4. The paint need not be thoroughly dry before being covered by the tide. If necessary, the paint may be dried by applying the flame of the propane torch directly to the paint.

5. It is necessary that the particles of the copper powder be exposed at the surface of the paint: if a layer of lacquer covers the

copper powder, the paint will be ineffective as a barrier to limpets. If the copper particles are properly exposed at the surface, the color of the paint will gradually become greenish. If the paint remains a bright metallic copper, the protective layer of lacquer will have to be removed by sanding, or by some other method that will expose the underlying copper, or the strip will have to be repainted.

6. It is best to apply the paint to areas where water draining over the paint will drain away from the area being studied to avoid possible toxic effects of copper compounds on the organisms within the exclosures. This can be accomplished in several ways: a. Exclose large areas so that the ratio of the copper painted perimeter is low in relation to the area of the interior. b. Exclose areas raised above the surrounding substratum. c. On vertical surfaces U-shaped, open-topped exclosures can be used providing the top of the exclosure extends above the range of the limpets.

7. The paint will have to be repaired more often where there is abrasion from sand and debris, and where the rock could not be thoroughly dried before applying the paint.

Limpets from inside the new exclosures were removed or killed, but not put in the adjacent areas outside the exclosures where they would have boosted the surrounding densities of limpets. Any limpets that subsequently invaded an exclosure were replaced outside the exclosure.

For this study, this method of excluding limpets had the advantage, as compared to cages and raised fences, of not providing shade or retaining moisture that would reduce the physical stresses of exposure to summer weather conditions. In addition, raised barriers and large meshed screen cages attract and harbor littorine snails, amphipods, and other grazers which would otherwise not be in the area. The strips of copper paint acted as barriers only to limpets; littorine snails and other grazers may have had their movements retarded by the paint, but were not prevented from entering an area. Using this method, exclosures were set up on an area of barren rock surface on a trial basis in the late spring of 1971. Within several weeks the rock surfaces within these limpet exclosures were covered with a film of algae (diatoms, blue-green algae, and sporelings of other algae).

Effects of Excluding Limpets in the Summer Dry Season

Methods

During the warm dry summer period, limpet exclosures were set up on the driest, most sun-exposed portions of barren high intertidal rocks to determine if desiccation, high temperatures, or direct sunlight could prevent algal growth even in the absence of limpet grazing. In July and August of 1971, 13 exclosures ranging from approximately 0.15 to 3 m^2 were constructed on unshaded, horizontal, and south, southwest, and west facing vertical or sloping rock surfaces at the 2 to 3 m tide levels. The remaining, adjacent surface of the rocks at the same tide levels were used as "controls."

Results

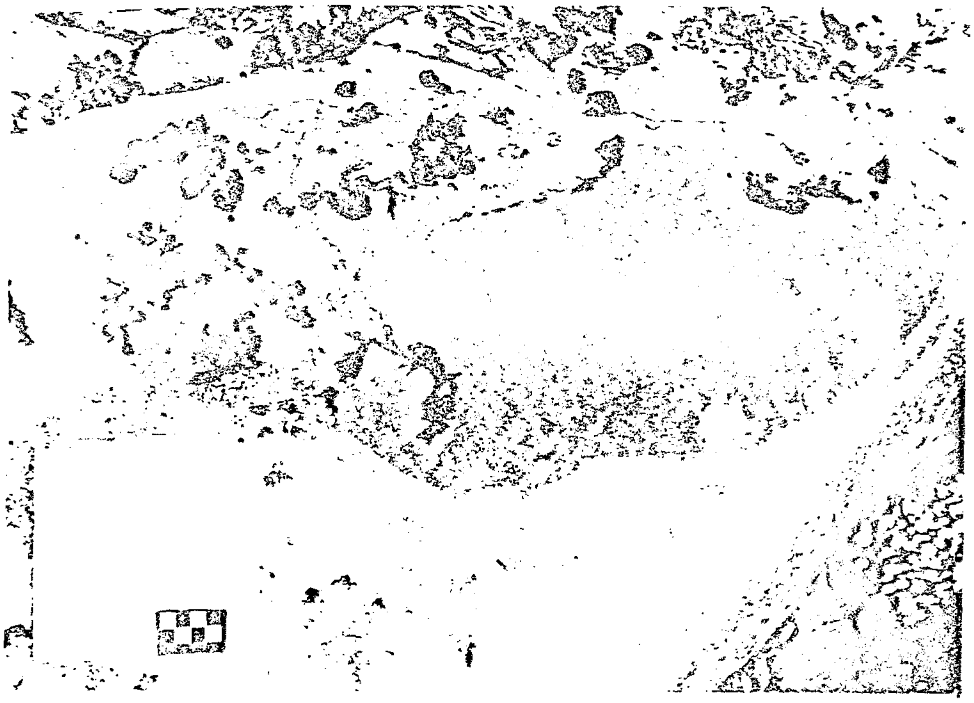
Within two to three weeks the rock surfaces inside the exclosures had become noticeably darker in color due to a growth mainly of blue-green algae. This was followed by a growth of diatoms, filamentous algae (*Bangia* and *Urospora*), and membranous algae (*Ulva*, *Enteromorpha*, *Porphyra*) in that order. The first growths of algae in some of these exclosures are shown in Figures 2a, 2b, 3a, 3b, 3c, and 3d.

Effects of Excluding Limpets at All Seasons of the Year

Methods

To compare the development of algal covers with and without limpet grazing in the different seasons of the year, groups of exclosures and control areas were established at the Cape Arago and

Fig. 2a,b.--Exclosures constructed at Cape Arago on 2 July 1971 shown 13 August 1971, 42 days later. These exclosures are approximately at the 2.5 m tide level. The dark area within the exclosures is due to a growth of diatoms, blue-green algae, and sporelings of other algae. For scale, the black square on which the date is printed measures 15.3 x 15.3 cm. The four white squares on the black square are 1 cm^2 each.



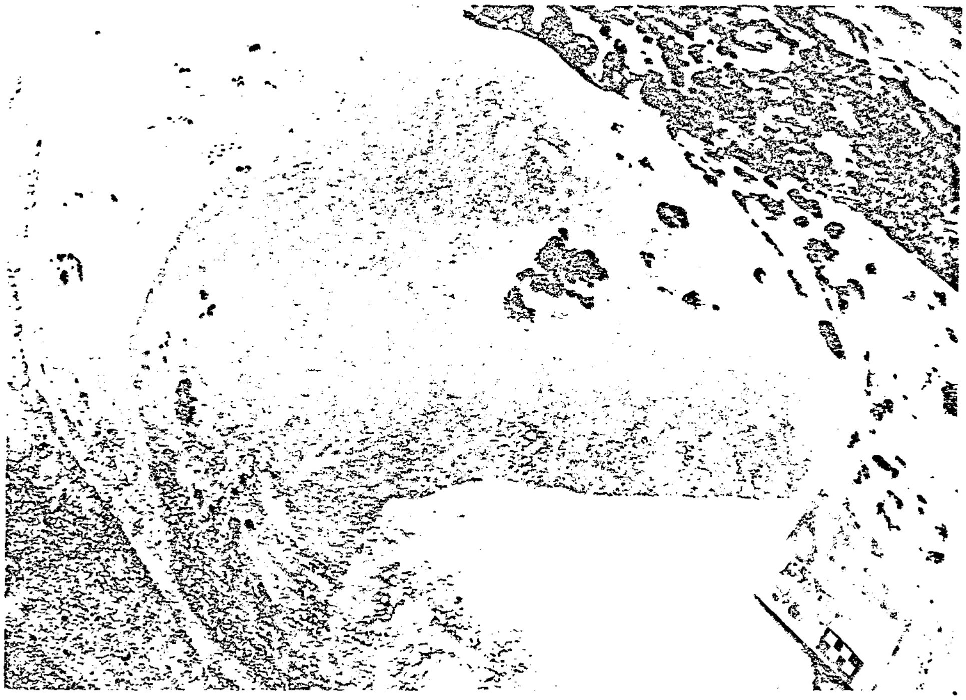
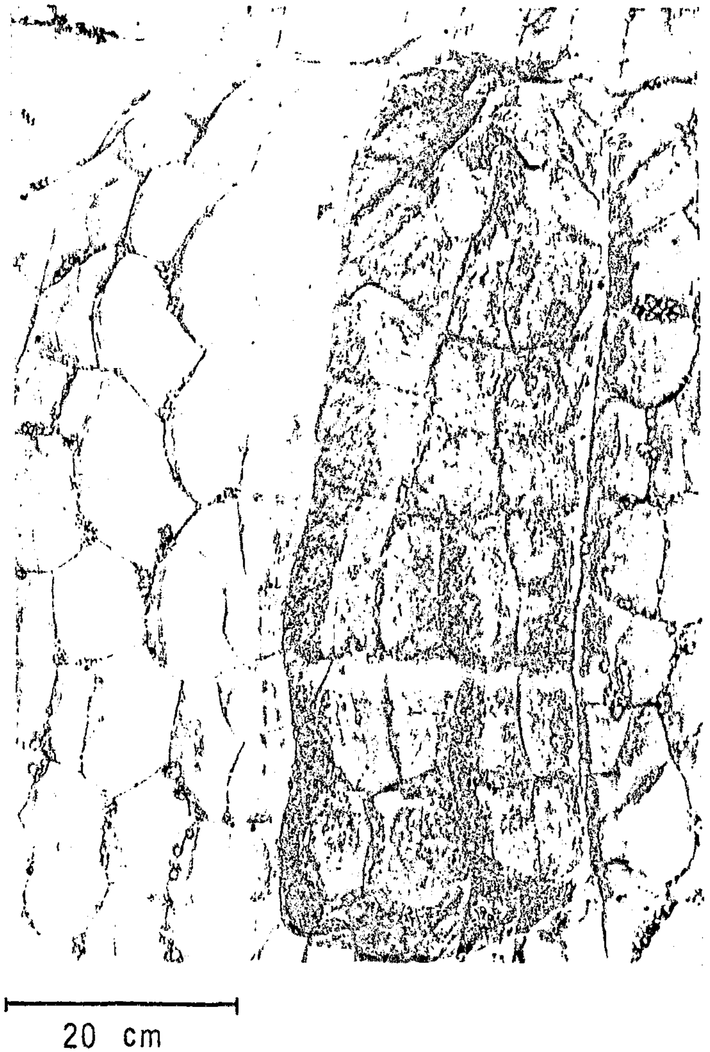
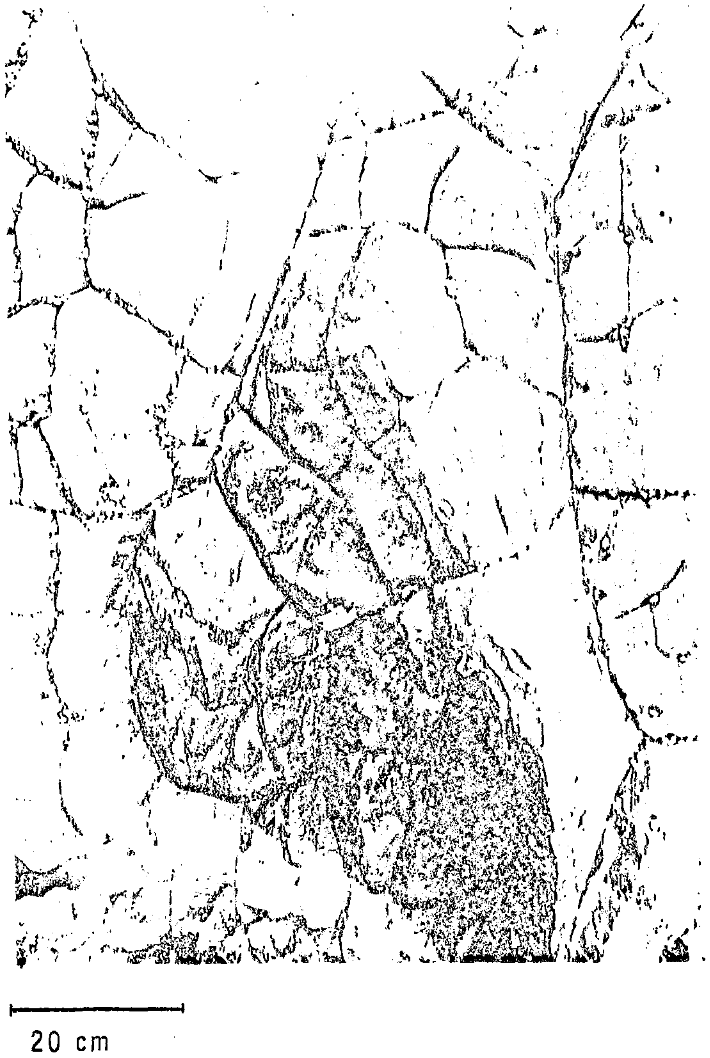
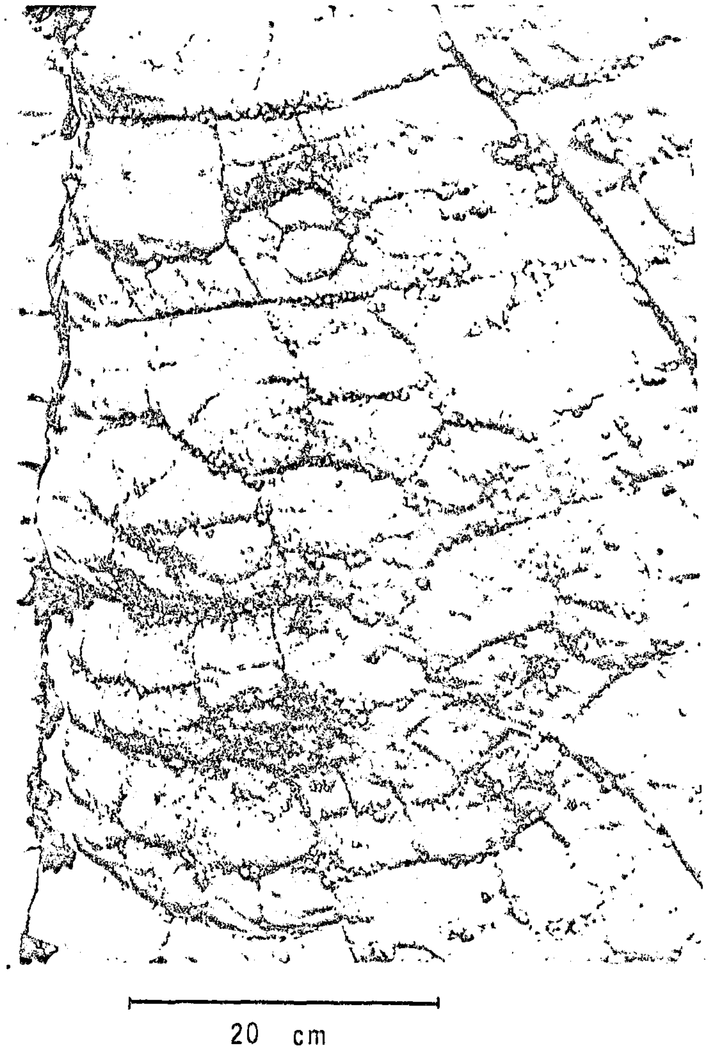


Fig. 3a, b, c, d. --Exclosures constructed on the high intertidal rocks at Sunset Bay on 16 July 1971, shown 28 days later. Scale shown in each picture. The exclosure in Figure 3c is covered mainly with diatoms, the exclosures in the other three figures are covered with a mixture of diatoms, blue-green algae, and sporelings of other algae.


20 cm


5 cm


20 cm


20 cm

Sunset Bay locations at 3 to 4 month intervals, using the following procedure:

1. Both locations were surveyed to determine the number of sites that were suitable for enclosing with copper paint (see Methods).
2. Four to five exclosures and controls were set up at a time.
3. The sites to be used for each group were selected randomly from all the possible sites using a table of random numbers. The same procedure determined whether a site would be used for an exclosure or control.
4. The shape and size of an exclosure or control varied depending on the site used. At the Cape Arago location the average area of the exclosures and controls was significantly less than that of the exclosures and controls at Sunset Bay, but more exclosures and controls were constructed at Cape Arago (Table 2).
5. Controls were constructed by marking a site with patches, rather than a solid line, of copper paint.
6. In order to follow the progression of events within the exclosures and controls, 35 mm color transparencies were taken of each exclosure and control at approximately

TABLE 2.--Comparisons of sizes of areas of rock surface in the randomized series of exclosures and controls set up at seasonal intervals at Cape Arago and Sunset Bay

Treatment	Total Area of Replicates (cm^2)	Number of Replicates	Mean Area Per Replicate (cm^2)	Standard Deviation of Areas (cm^2)
Cape Arago				
Exclosures	36,805	24	1534	642
Controls	30,205	21	1438	632
Sunset Bay				
Exclosures	32,854	13	2527	945
Controls	38,070	13	2928	1294

Note: There was no significant difference between the average areas of the exclosures and controls at either location ($p > .4$). The average areas of controls and exclosures at Sunset Bay were significantly larger than those at Cape Arago ($p < .001$).

monthly intervals. Small samples (less than 1 cm^2) were scraped from the surface of the rock if the identity of the organisms there was in doubt. Care was taken to disturb these sites as little as possible.

7. Connell's (1970) method, slightly modified, of superimposing an array of points on a projection of each transparency was used to estimate the percent cover of organisms within the exclosures and controls. The ways this method was modified and employed are described below. The percent covers of algae and invertebrates, or areas of bare rock, were estimated by projecting the array of points onto a projection of the color transparencies and counting the number of points that were centered on algae, barnacles, or bare rock. The assumption is that the proportion of the number of points which fall on a type of organism is proportional to the abundance of that organism.

The array of points used in this method was constructed as follows: a piece of graph paper, the size of which was proportional to a projection of a 35 mm transparency, was divided into 130 squares. Using coordinates from a table of random numbers, two points (one marked as an "x," the other as an "o") were randomly placed in each of these 130 squares, producing a somewhat uniform dispersion of points, that, on a smaller scale, were randomly placed. This method of arranging the points was used for the following reason: placing the points by the more usual method of using coordinates for the full area produced several large clumps of points that would have severely biased the measurements of the algal cover if a clump of these points fell on a clump of the algae or an isolated patch of bare rock. A strictly uniform array of points would not be satisfactory either, since there were uniformities within the exclosures and controls, such as regular patterns of straight crevices, that would be over represented if the two uniformities lined up with one another. A compromise was the one used here. After the points were placed on the paper, it was subsequently sampled with a quadrat the same size as that in which each set of the two points were placed. The quadrat was placed randomly on the paper, using coordinates from a random numbers table; 30 samples were taken. Using this information, the distribution of points on the piece of paper was analyzed for randomness by comparing the distribution of the observed number of points per sample with the expectation from the poisson distribution and testing this with the Chi-squared test. The two distributions did not differ significantly ($p > .98$).

The same array of points was used to census each control and exclosure. To maintain the greatest possible degree of independence between each census of a given site, each color transparency of a site was projected in a different way: rightside up, upside down, reversed, etc. In addition, because the camera was hand held when the census transparencies were taken, the orientation of the image of a site on the transparency varied; this also helped to assure that the points would not fall on the same places of each site at each census.

In performing the actual censuses the size of the projected transparency was adjusted until approximately 100 points (either the x's or the o's) fell within the area to be censused. For larger exclosures, more points were used: the density of points could be doubled by using both the x's and the o's. Only the object at the exact center of the x or the o was recorded as being touched by that point. No censuses were made of transparencies of poor quality.

Results

Excluding limpets from an area of rock in any season resulted in a growth of algae similar to, but usually more extensive than, that of the natural winter bloom. In addition, during the summer barnacles settled in some exclosures and grew in greater densities than observed in any of the controls.

The percent covers of all sessile organisms in the exclosures and controls are graphed individually in Figures 1A to 9A in the appendix. The percent cover for the plants (algae and lichens) alone are graphed individually in Figures 10A to 18A in the appendix.

This same information is shown in Figures 4-7 for the continuous period from 22 June 1972 to 4 August 1973 at Cape Arago and for the period of 13 August 1971 to 5 October 1972 at Sunset Bay.

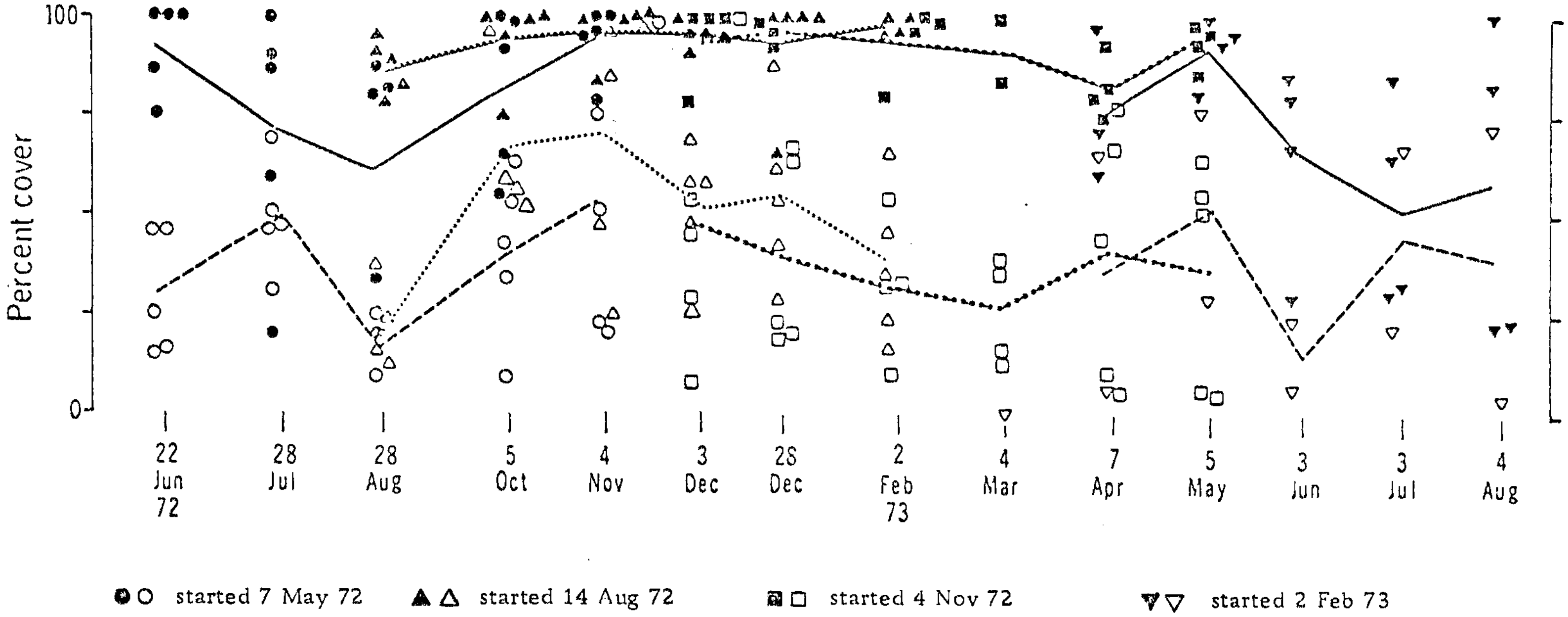
The non-plant cover is essentially barnacle cover; the only other sessile animals found in these censuses were mussels, but these were very rare, contributing less than two percent of the cover in the few exclosures in which they were found.

Seasonal Differences in Algal Development Within Exclosures

Following the removal of limpets, algal covers in the exclosures developed more rapidly in the wet-season months than the dry-season months. These differences are difficult to quantify in exact terms, however, because of the period of time between each census, and because no measurements were made of biomass per unit area. It was apparent from examining the color transparencies that after a given period of time, the growth of the algae in exclosures started in the wet season was more luxuriant than in exclosures started in the [illegible]er months of the year. This was more obvious during the first

Fig. 4.--Percent covers of sessile invertebrates and plants within the limpet exclosures and controls at Cape Arago. Information for an individual set of exclosures and controls is only shown for the six month period following the establishment of that set. The sessile invertebrates are mainly barnacles, and the plants are mainly algae including the blue-green algae, diatoms, and the red, brown, and green algae, plus some lichens. Solid symbols are for exclosures, open symbols for controls. Solid lines and broken lines connect, respectively, the average percent covers for the exclosures and the controls.

Not shown in this figure are the percent covers for the set of exclosures and controls started on 23 August 1971, which were not continuous in time with the data for the sets shown here. The data for the 23 August 1971 set are shown in Figures 1A and 10A in the appendix.


Percent cover
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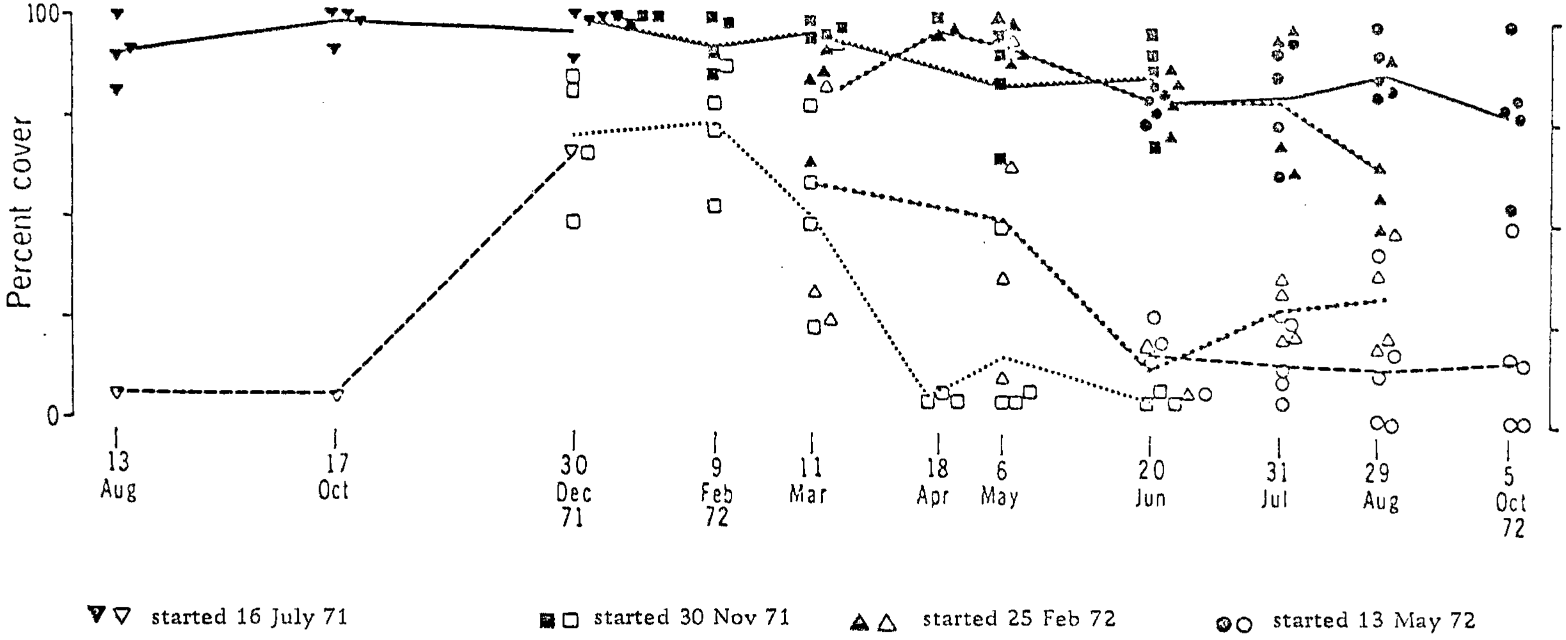
22 Jun 72
28 Jul
28 Aug
5 Oct
4 Nov
3 Dec
28 Dec
2 Feb 73
4 Mar
7 Apr
5 May
3 Jun
3 Jul
4 Aug
●○ started 7 May 72
▲△ started 14 Aug 72
▣□ started 4 Nov 72
▼▽ started 2 Feb 73

Fig. 5.--Percent covers of sessile invertebrates and plants within the limpet exclosures and controls at Sunset Bay. Information for an individual set of exclosures and controls is only shown for the six month period following the establishment of that set. The sessile invertebrates are mainly barnacles, and the plants are mainly algae including the blue-green algae, diatoms, and the red, brown, and green algae, plus some lichens. Solid symbols are for exclosures, open symbols for controls. Solid lines and broken lines connect, respectively, the average percent covers for the exclosures and the controls.

The set of exclosures and controls beginning 16 July 1971 is not part of the randomized series but is at the same location as the other exclosures and controls (see text for further explanation).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Percent cover
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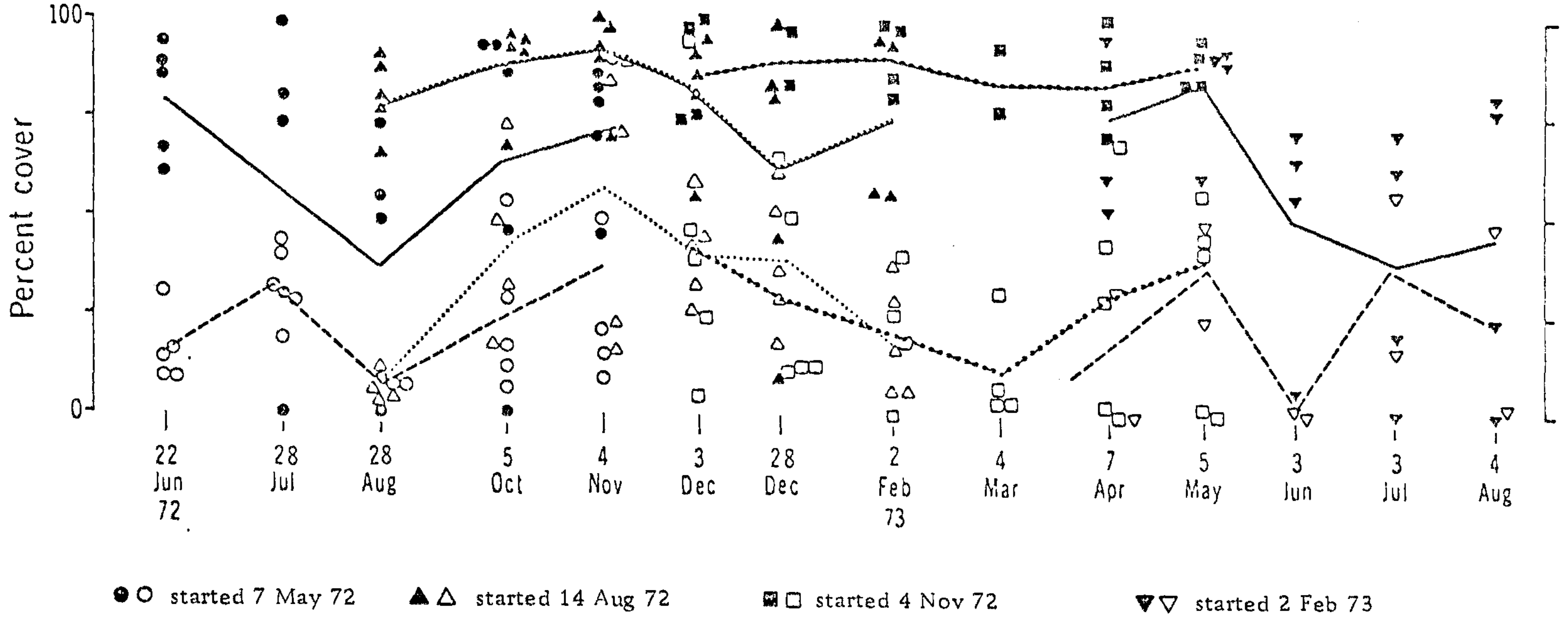
17 Oct
30 Dec 71
9 Feb 72
11 Mar
18 Apr
6 May
20 Jun
31 Jul
29 Aug
5 Oct 72
▼▽ started 16 July 71
■□ started 30 Nov 71
▲△ started 25 Feb 72
●○ started 13 May 72

Fig. 6.--Cape Arago percent covers of plants only within the limpet exclosures and controls. See titles for Figures 2 and 3 for more details.


100
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Percent cover
22 Jun 72
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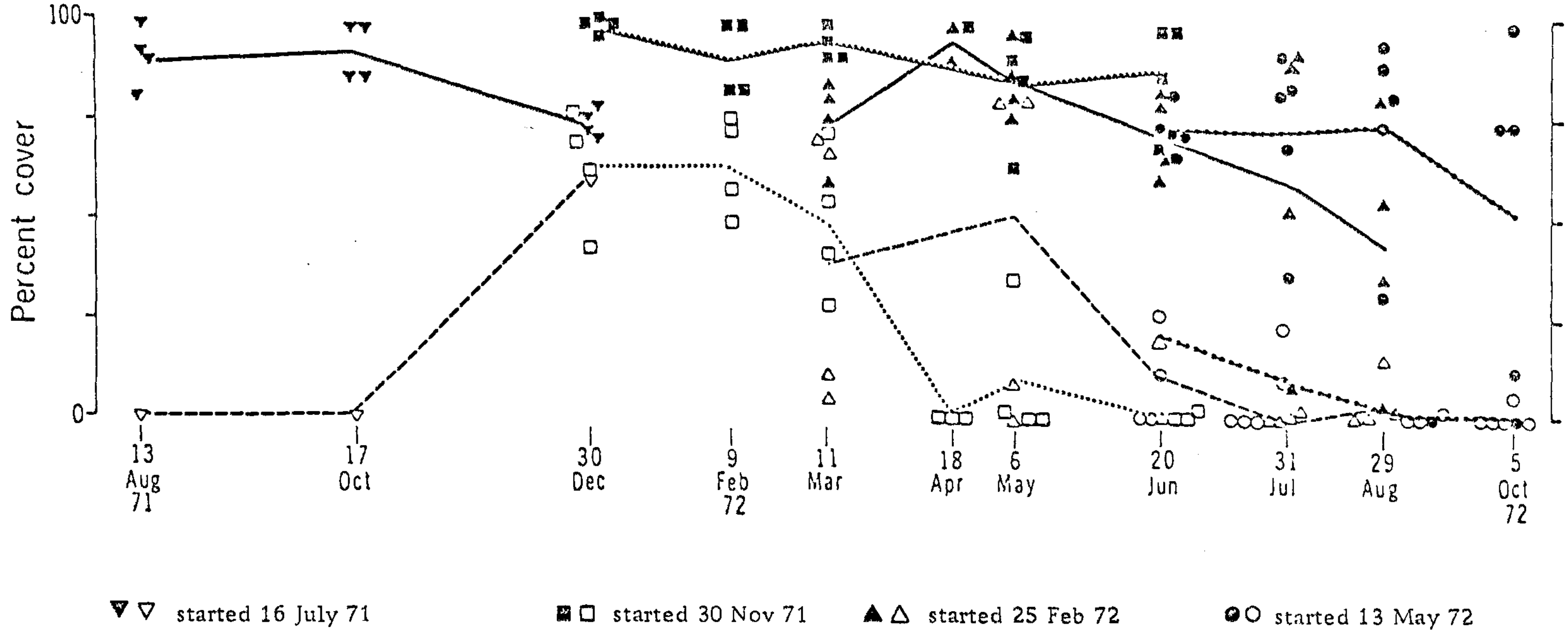
● ○ started 7 May 72
▲ △ started 14 Aug 72
▣ □ started 4 Nov 72
▼ ▽ started 2 Feb 73

Fig. 7.--Percent covers of plants only within the limpet exclosures and controls at Sunset Bay. See titles for Figures 2 and 3 for more details.


100
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Percent cover
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30 Dec
9 Feb 72
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18 Apr
6 May
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31 Jul
29 Aug
5 Oct 72
▼▽ started 16 July 71
■□ started 30 Nov 71
▲△ started 25 Feb 72
●○ started 13 May 72

month of development within the exclosures. The rate at which species appeared was also greater in the wet season. For example, *Bangia* and *Urospora* were usually the first macroalgae to appear in the exclosures. Censuses were taken of 22 exclosures at frequent enough intervals to contrast the rates at which *Bangia* and *Urospora* became established following the removal of limpets. Seven of these 22 exclosures were started in the wet season (November 1971, 1972) and the remaining 15 were started in the dry season (July and August 1971, 1972). All of the exclosures started in November had well developed stands of *Bangia* and *Urospora* by the time the first census was taken (29 days after the exclosures had been made). In contrast, none of the 15 exclosures began in the dry season had yet developed any *Bangia* or *Urospora* cover when they were examined within 30 days after they had been established (some of these are shown in Figures 2a, 2b, 3a, 3b, 3c, 3d). Six of these 15 still had no *Bangia* or *Urospora* cover six weeks after they had been established. All of these exclosures had covers of *Bangia* and/or *Urospora* within 10 weeks.

Seasonal Differences in Percent Covers in Exclosures and Controls

The percent covers in both the exclosures and the controls tended to be higher in the wet season months, during the period when there was the natural bloom of algae on the high intertidal rocks. At Cape Arago the average total cover (Figure 4) for all the exclosures was over 90 percent from November to March, while in the dry seasons it dropped as low as 60 percent (in August 1972) and 52 percent (in July 1973).

In the controls at Cape Arago, the highest percent covers were also recorded in the wet season (the highest was 70% in November) and the lowest percent covers (22%in August 1972 and 15% in June 1973) were recorded in the dry season months (Figure 4).

The first series of exclosures and controls shown for Sunset Bay in Figures 5 and 7 are not part of the randomized series, but are part of the summer series described earlier which were located on the drier portions of the rock. However, since the sites of these exclosures are interspersed with those of the randomized series, they are included here to provide more information for the dry season months. The percent cover shown as the "control" was obtained from a series of color transparencies which encompassed almost the entire remaining surface of the rock at the tidal level used for the subsequent series of randomized exclosures and controls; thus, it is probably less biased by sample size than the regular series of controls. It is important to note that the information for this particular first series of exclosures and controls is used only here in the "percent cover" descriptions and is not part of any of the analyses described in the following sections.

In the controls, the percent covers at Sunset Bay showed the same seasonal patterns as those at Cape Arago, but at Sunset Bay there were greater differences between the percent covers in the dry and in the wet seasons. In the dry seasons the differences between the percent covers in the exclosures and the percent covers in the controls were greater than in the winter months when the natural winter bloom of algae in the controls produced covers usually less than, but within the range of, the covers in the exclosures.

Seasonal Comparisons of *Ulva*, *Enteromorpha*, and *Porphyra* Present in the Exclosures and Controls

Because percent covers do not take into account biomass per unit area, the graphs in Figures 4 through 7 do not adequately represent the magnitude of the differences between the amounts of algae in the controls and in the exclosures. This was especially true in the dry season, when the algal covers in many of the controls consisted of thin films of blue-greens, and the algal covers in the exclosures were often of various species of macroalgae.

The presence or absence of *Ulva*, *Enteromorpha*, and *Porphyra* was recorded for each exclosure and control area at every monthly census from the time each area was first censused to January 1974, when all censuses were stopped. Figures 8 and 9 show the number of exclosures and controls that contained any of these genera in any of the twelve months of the year for all the years that these exclosures were censused. Through the summer months, most of the exclosures, but few of the controls, contained these leafy algae. Porphyra completely disappeared from most of the controls at both Cape Arago and Sunset Bay during the summer months, but was more abundant in the exclosures, especially at South Cove (Figures 10 and 11).

During any time of the year, most of the exclosures and controls that contained any of these leafy algae at all contained Ulva and/or Enteromorpha. Comparisons of the number of exclosures and controls containing these two genera are shown in Figures 12 and 13.

At Cape Arago, Ulva was present in over 50% of the exclosures during most of the months of the year (Figure 14), but at Sunset Bay, Ulva disappeared from many of the exclosures in summer. In the controls at Sunset Bay, Ulva was completely absent in the months of July through October (Figure 15). Ulva disappeared at Sunset Bay during the periods in April and May when low daytime tides occurred

Fig. 8.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Cape Arago in which any of the leafy, transient algae (Ulva, Enteromorpha, or Porphyra) were present. The number of exclosures or controls on which the percentages are based is shown above each bar.

Fig. 9.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Sunset Bay in which any of the leafy, transient algae (Ulva, Enteromorpha, or Porphyra) were present. The number of exclosures or controls on which the percentages are based is shown above each bar.

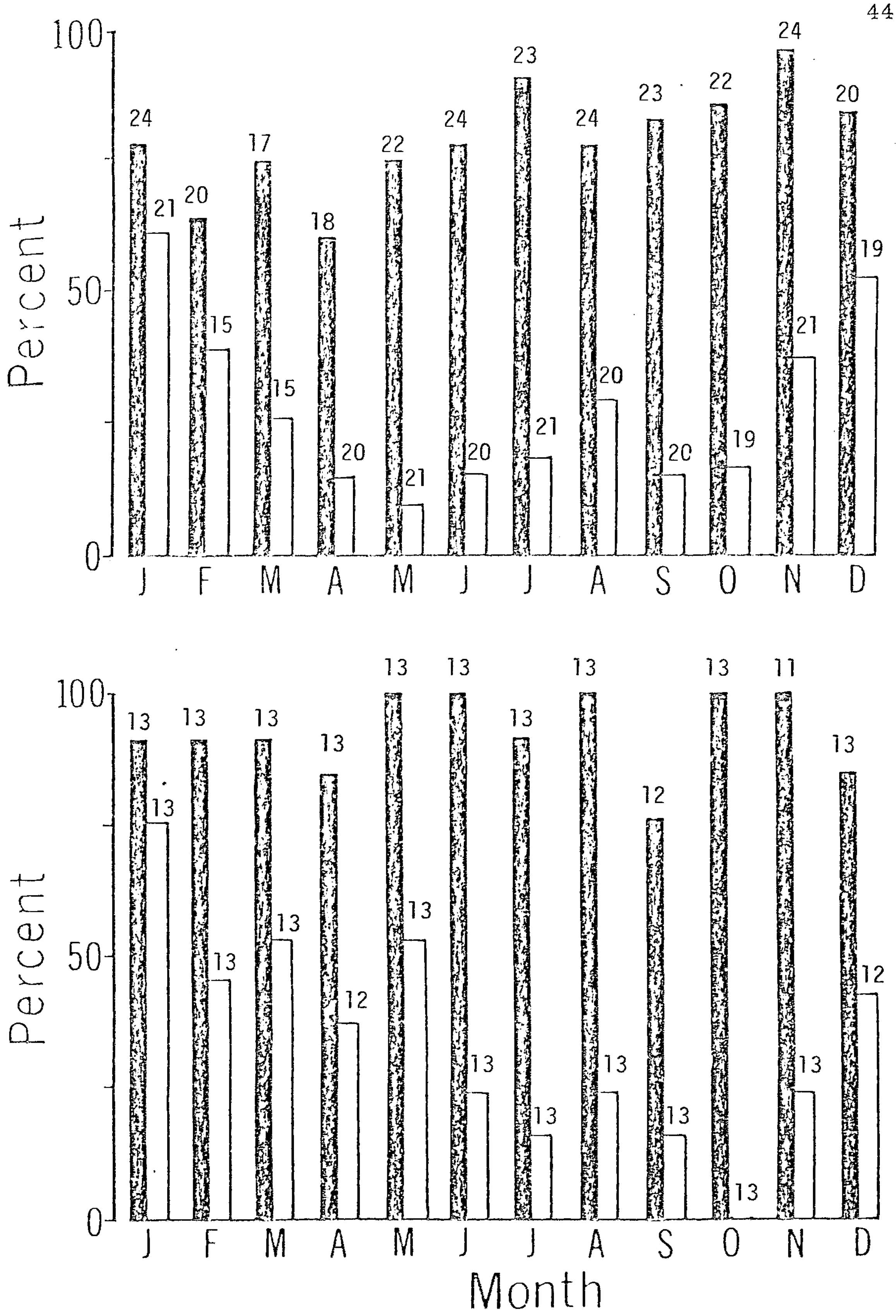
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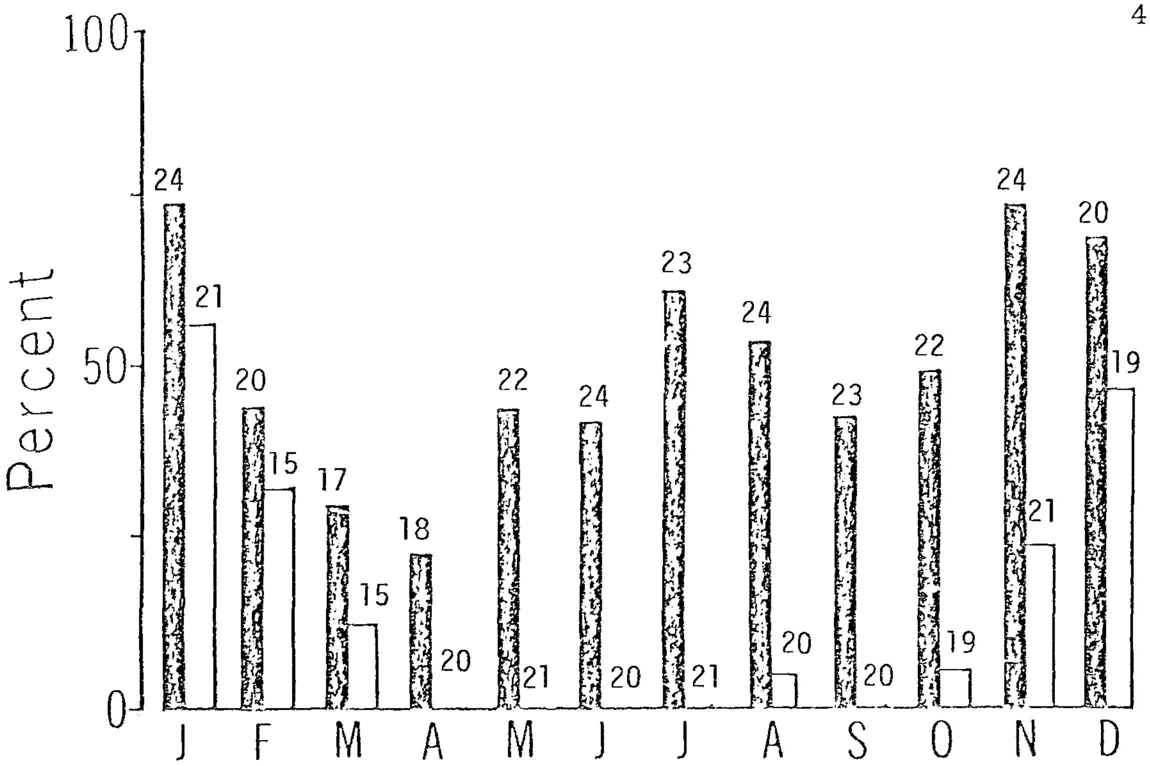
Fig. 10.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Cape Arago in which any of the *Porphyra* species were present. The number of exclosures or controls on which the percentages are based is shown above each bar.

Fig. 11.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Sunset Bay in which any of the *Porphyra* species were present. The number of exclosures or controls on which the percentages are based is shown above each bar.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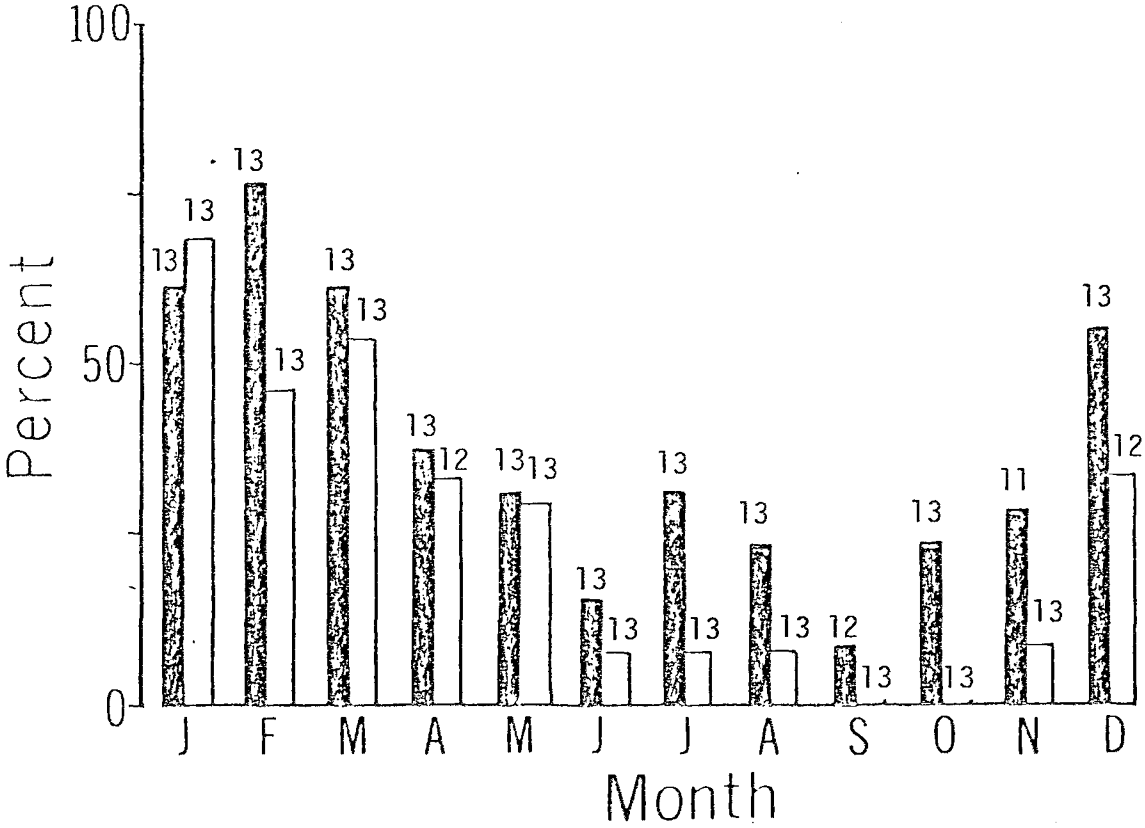
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Fig. 12.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Cape Arago in which Ulva, Enteromorpha, or both were present. The number of exclosures or controls on which the percentages are based is shown above each bar.

Fig. 13.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Sunset Bay in which Ulva, Enteromorpha, or both were present. The number of exclosures or controls on which the percentages are based is shown above each bar.

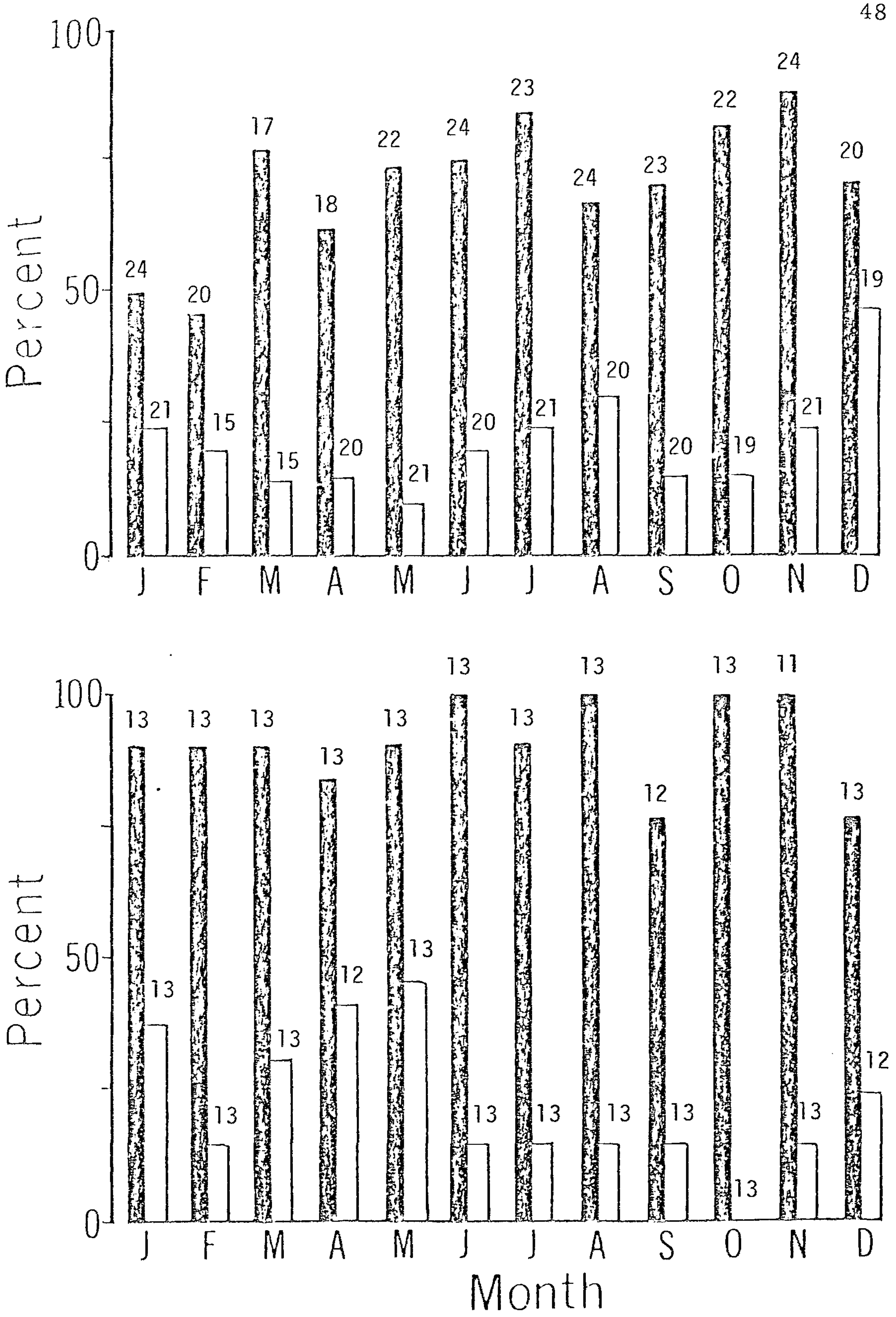
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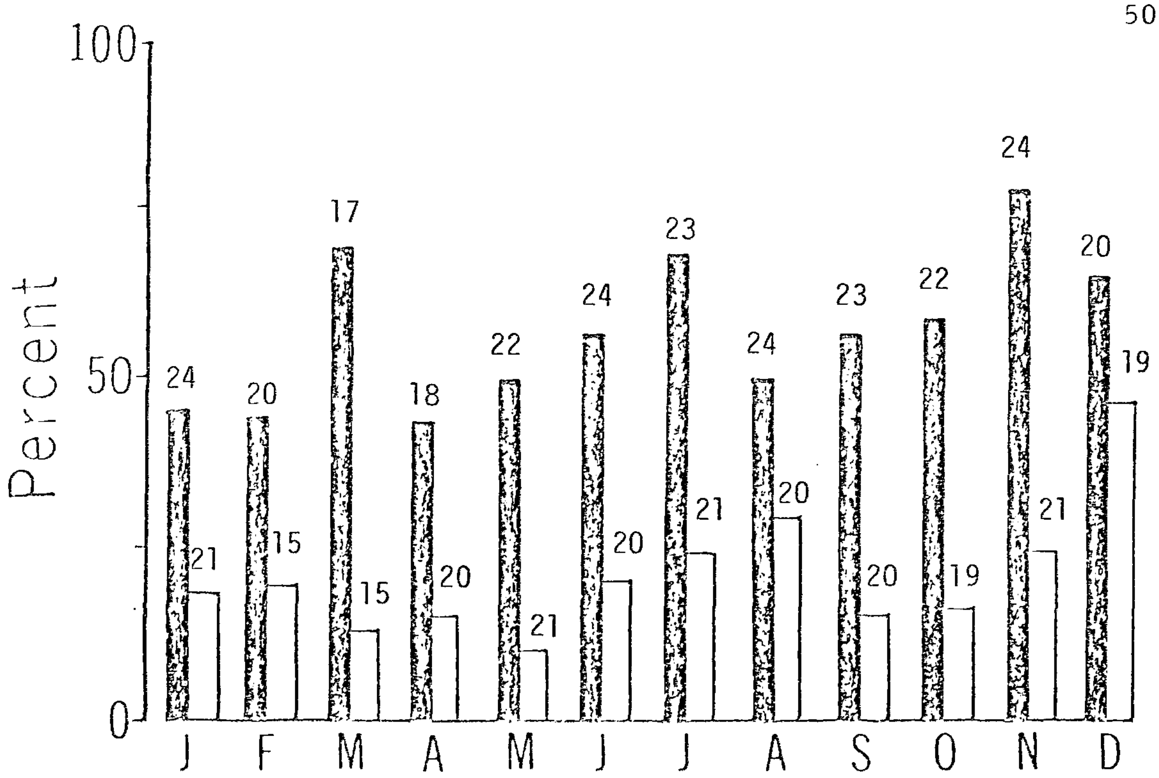
Fig. 14.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Cape Arago in which _Ulva_ was present. The number of exclosures or controls on which the percentages are based is shown above each bar.

Fig. 15.--Monthly percentages of exclosures (solid bars) and controls (open bars) at Sunset Bay in which _Ulva_ was present. The number of exclosures or controls on which the percentages are based is shown above each bar.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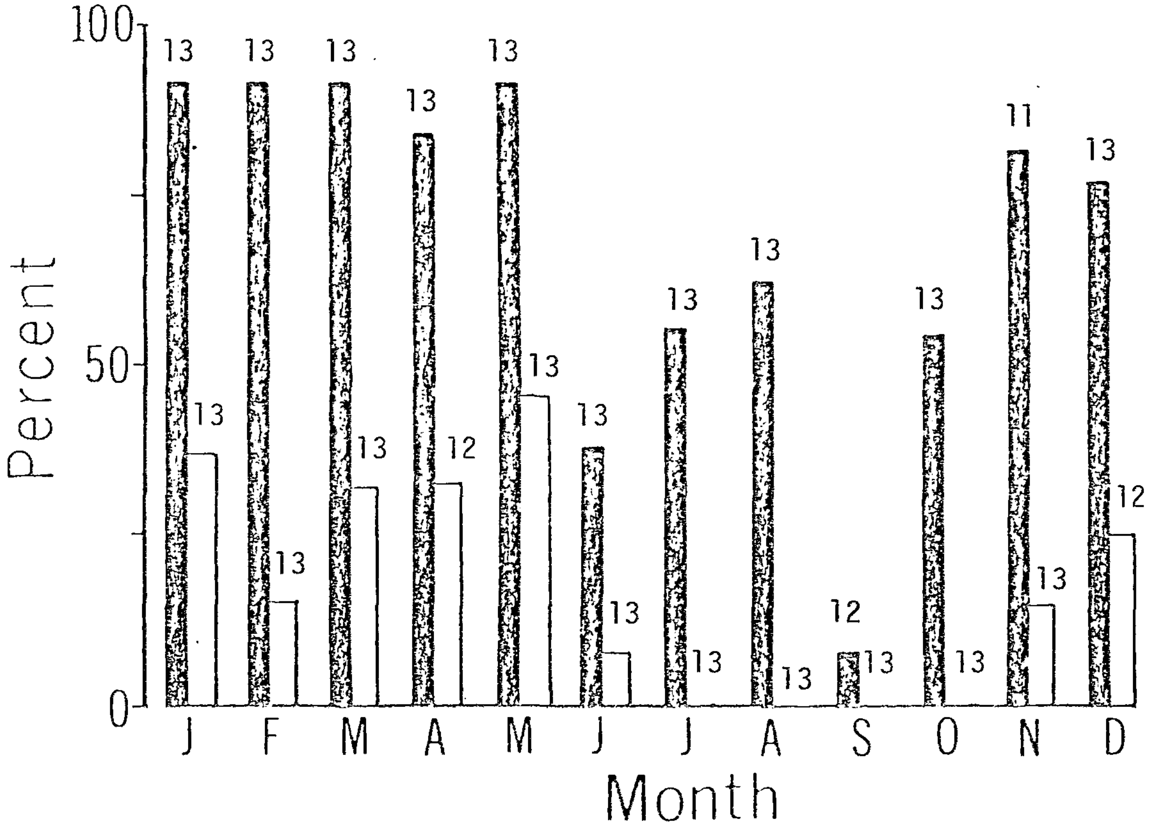
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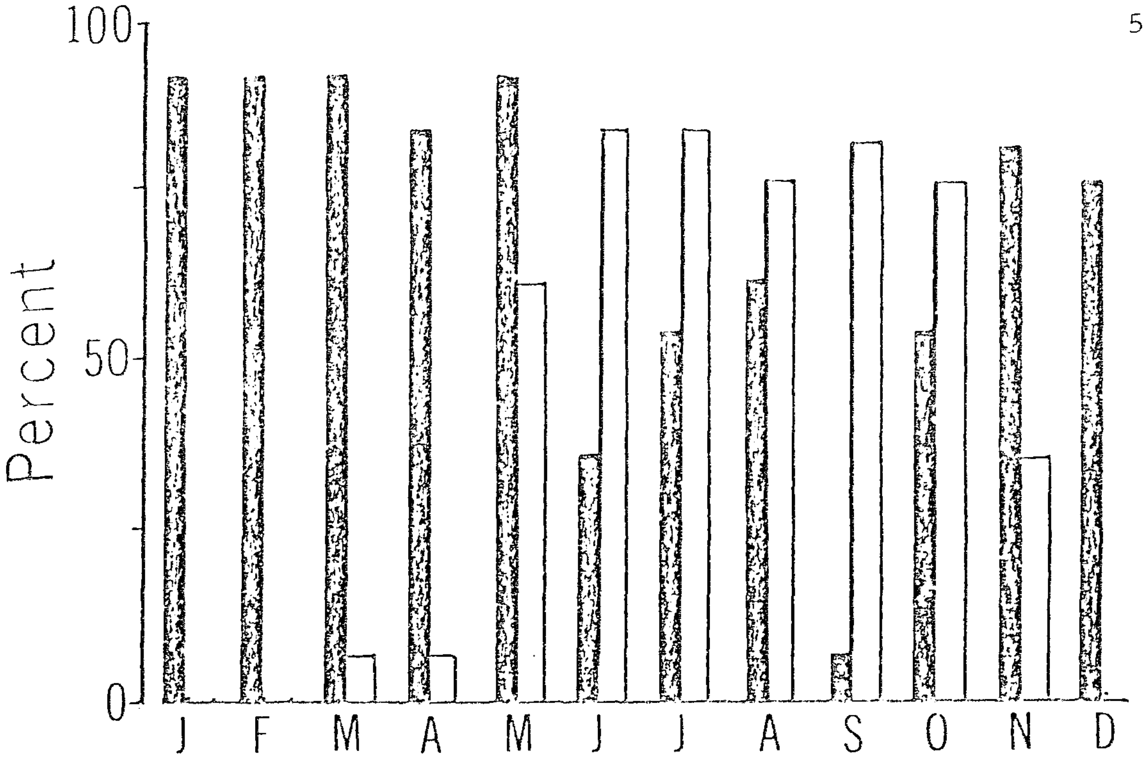
during warm sunny weather and the Ulva lost its green color.

This loss of color is commonly referred to as "bleaching," implying destruction of the pigments of the cells by physical factors such as sunlight and is a usual event during the combination of low tides and warm, sunny weather in spring. Suggesting that contents of the cells were not necessarily destroyed, were observations at a nearby location (Yoakam Point) where "bleaching" Ulva occupied a sloping wall that drained into a series of shallow tidepools. During the period when the Ulva thalli were losing their color, the tidepools were filled with a turbid green suspension of flagellated cells, apparently zoospores of the Ulva. If this is correct, the loss of color in the Ulva plants is a result of the contents of the cells of Ulva being released as reproductive cells rather than the cell contents being destroyed by the warm sunny weather. Fjeld (1970) has reported that nearly the whole thallus of Ulva may produce swarm cells, and this can be prevented if the plants are kept at low temperatures (5° C).

At Sunset Bay, as Ulva disappeared from the exclosures in summer, Enteromorpha vexata appeared. Figure 16 shows the relation between the absence of Ulva and the presence of Enteromorpha in the exclosures at Sunset Bay. Figure 17 shows the number of exclosures compared to the number of controls containing

Fig. 16.--Monthly percentages of exclosures containing Ulva (solid bars) and Enteromorpha (open bars) at Sunset Bay. The bars for September are a percentage of 12 exclosures, for November of 11 exclosures, and of 13 exclosures for all the remaining months.

Fig. 17.--Monthly percentages of exclosures (solid bars) and controls (open bars) in which Enteromorpha vexata was present at Sunset Bay. The number of exclosures or controls on which the percentages are based is shown above each bar.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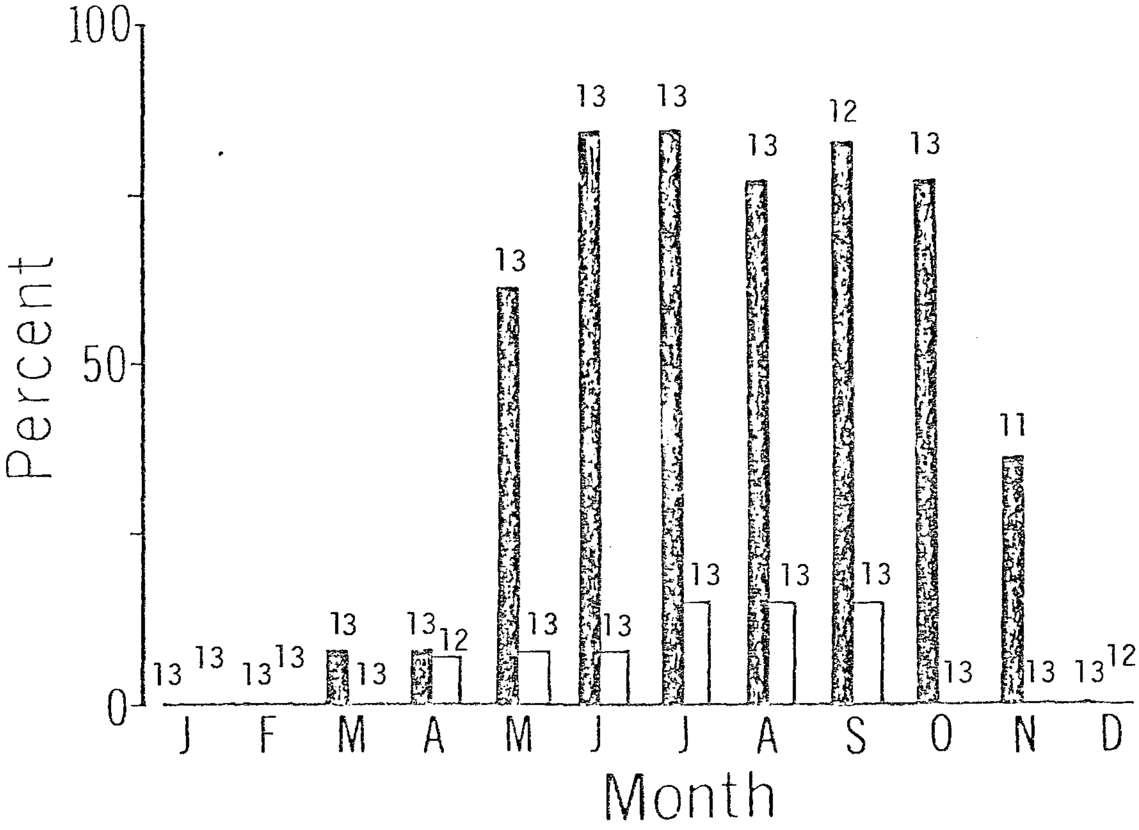
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E. vexata at Sunset Bay; most of the exclosures but few of the controls contained Enteromorpha. Similar figures were not made for the exclosures at Cape Arago because during the summer Enteromorpha tended to grow interspersed with the Ulva, making the visual identifications of Enteromorpha questionable, and therefore unreliable when the Ulva was abundant. At Cape Arago, Enteromorpha was found only one in one control. Since the problems of identifying the Enteromorpha did not affect the information in Figures 6 and 10, where either Ulva and/or Enteromorpha could be present, the positive identifications of Enteromorpha were used in the figures. At both Cape Arago and Sunset Bay Enteromorpha was absent from the exclosures and the controls in most of the winter months.

Resistance to Grazing Conferred on Enteromorpha vexata by a Fungal Symbiont

The only areas other than in the limpet exclosures where Enteromorpha vexata was abundant through the summer months was on a high (approximately 2.5 to 3 m tidal level) rock wall at Cape Arago about 20 m away from the exclosure and control series. Here E. vexata was abundant in all months of the year, but, unlike most of E. vexata in the exclosures, this E. vexata was mostly infected by fungi, especially during the summer. That this infected Enteromorpha was able to survive through the summer, when Enteromorpha in general was not able to survive outside the limpet exclosures suggested that either these infected plants were not accessible to the limpets or other grazers, or that the plants were resistant to grazing. The first possibility did not seem likely, since the infected Enteromorpha were adjacent to large concentrations of both littorine snails and limpets and were in an area where the algivorous chironomid flies were abundant.

Since the limpets Acmaea digitalis were difficult to maintain in the laboratory, littorine snails, Littorina scutulata, were used instead to test the hypothesis that the infected Enteromorpha was more resistant to grazing than the uninfected plants. The following procedure was used.

1. Groups of snails were put into ten 30 ml beakers along with whole thalli of infected and uninfected Enteromorpha vexata.
2. Four to eight snails were used per beaker, depending on the sizes of the snails (if the snails were larger, fewer were used).
3. One thallus of each type of plant (infected and uninfected) was put into each beaker. The thalli obtained in the field

were easily divided into two categories: those which were dark in color and were covered with numerous black dots (reproductive structures, i.e., perithecia, of the fungi) and those which were light green in color and on which there were no perithecia. The latter plants were considered to be uninfected, although they may have been lightly infected, or the infection could have been in its incipient stages.

4. A piece of nylon mesh cloth with openings approximately 1 mm in diameter was used to cover the mouth of each beaker and was held on with a rubber band.
5. The snails were kept in the beakers with the algae for 14 days; however, for the first eight days the beakers were kept constantly submerged in rapidly aerated water at 13° C and the snails did not feed. For the last six days the snails were kept in a covered aquarium which was briefly filled with seawater several times a day and then drained, simulating a wetting by a high tide. Under these conditions, the snails fed until the experiment was ended.
6. Since the amounts of the two types of algae eaten were so disparate, the amount of each type eaten was visually estimated several times. To bias the errors of this method against the hypothesis, the highest estimates of

the amounts eaten of the infected *E. vexata* were used, and for the uninfected plants the lowest figures were used.

The results of this experiment are shown in Table 3. The *Littorina scutulata* showed a clear preference for the thalli of *Enteromorpha vexata* that were not infected with the fungus.

This resistance to grazing conferred by the fungus apparently comes at the expense of growth for the *Enteromorpha*. Twenty flasks of Erdschreiber's medium containing infected thalli of *Enteromorpha* were kept in a greenhouse for a year. During this time the infected thalli did not grow, although they may have reproduced, since the flasks did become filled with a growth of uninfected *Enteromorpha* plants. (It may also be possible that these uninfected plants came from spores that had been attached to, but which were not actually produced by, the infected plants.)

Relative Resistances of *Ulva* and *Porphyra* to Grazing

Field observations indicated that grazers also showed a preference for *Ulva* over *Porphyra*. Where both types of algae were present littorine snails were found feeding more often on the *Ulva*. During the wet season, if both types of algae were adjacent

TABLE 3.--Feeding preferences of *Littorina scutulata* for thalli of the alga *Enteromorpha vexata*, infected and not infected with the fungus *Turgidosculum*

	Percent of *Enteromorpha* thallus eaten	
Replicate	Infected thallus	Uninfected thallus
1	35	50
2	20	100
3	10	100
4	10	100
5	10	100
6	5	100
7	2	100
8	0	100
9	0	50
10	0	90

to a refuge harboring littorine snails, or a homing area for limpets, *Porphyra* generally occupied the space nearer the grazers, while the *Ulva* was found further away. In situations where the limpets left visible trails on the surface of the rock, these trails went directly from the homing area to the location of the *Ulva*; apparently the limpets were bypassing the *Porphyra* plants that were nearer the homing area to feed on the *Ulva*.

Grazer preference for *Ulva* versus *Porphyra* was tested using *Littorina scutulata* in a procedure similar to that used testing preferences for infected versus uninfected *Enteromorpha* but with the following modifications:

1. Three treatments were used, ten replicates of each: one treatment contained *Ulva* only, one contained *Porphyra* only, and one contained equal amounts of *Ulva* and *Porphyra*.
2. Instead of using whole thalli, disks were cut out of the thalli. These disks were 2.8 cm in diameter.
3. Two disks were placed in each beaker, so that ten beakers had two disks of *Porphyra*, ten had two disks of *Ulva*, and ten had one disk each of *Ulva* and *Porphyra*.
4. Ten small *Littorina scutulata* approximately 5 mm in greatest whorl diameter were placed in each beaker.
5. The mouths of the beakers were covered with nylon mesh and the beakers were laid on their sides in a large tank. Fresh seawater was automatically filled and was drained from the tank eight to twelve times each 24 hours.
6. At the end of 12 days, the amount of each disk removed by the snails was measured by tracing the outline of the remaining parts of the disk on graph paper.

The results of this experiment are shown in Table 4. The littorine snails showed a clear preference for the *Ulva*, eating more than ten times as much of the *Ulva* thalli as of the *Porphyra* thalli. W[illegible]n the *Porphyra* was presented alone, the snails ate significantly

TABLE 4. --Feeding preferences of littorine snails, _Littorina scutulata_, for _Ulva_ and _Porphyra_ in the laboratory

	Treatment 1 _Ulva_ only	Treatment 2 Both _Ulva_ and _Porphyra_	Treatment 3 _Porphyra_ only
Amount of algae given to snails in each replicate (ten replicates of each treatment)	12.2 cm^2	6.1 cm^2 each alga	12.2 cm^2
Percent _Ulva_ eaten	34.2	33.8	--
Percent _Porphyra_ eaten	--	0.15*	1.3*

*Percent _Porphyra_ eaten in treatments 2 and 3 different at $p < .01$.

more of it than when it was presented in combination with the preferred Ulva.

Relationships of Barnacles, Grazers, and Algal Cover

During the six month period following the establishment of the exclosures, the lowest percent covers of algae (Figures 6 and 7) were in those exclosures containing the most refuges for littorine snails, amphipods, and other grazers not often found out on the broad open surfaces of the rock in the wave-exposed study areas. The refuges used by these grazers are usually barnacles, crevices in the rock, and clumps of perennial algae such as Endocladia and Gigartina. In the exclosures these refuges were often, but not always, surrounded by an area of bare rock or reduced algal growth, while the portions of the exclosure away from these refuges had a dense growth of the transient or annual types of algae. Table 5 compares on the same dates sets of exclosures that were started at the same time. These exclosures were selected from two categories: those with the least amount of algal cover (50% or less) and those with the greatest amount of algal cover (80% or more). Inspection of Table 2 shows that the group of exclosures with the least algal cover had more barnacles and crevices than the group with the most algal cover, although the amount of perennial algae was about the

TABLE 5. --Limpet exclosures containing the most algal cover (≥ 80%) and the least algal cover (< 50%) compared for the amounts of refuges they contain for Littorinid snails and other grazers

Location	Date Examined	Exclosures with less than 50 percent algal cover					Exclosures with 80 percent or more algal cover				
		Exclosure identification number	Percent of area covered with non-perennial algae	Percent cover of large barnacles*	Total length of crevices, cm	Percent cover of perennial algae**	Exclosure identification number	Percent of area covered with non-perennial algae	Percent cover of large barnacles*	Total length of crevices, cm	Percent cover of perennial algae**
South Cove	28 July 1972	240	0	20	80	0	242	98	10	0	1
		241	27	30	120	0	239	81	7	10	1
	5 Oct 1972	240	0	20	80	1	242	93	7	0	1
		241	34	19	120	7	239	86	5	10	7
							238	90	12	20	4
	28 Dec 1972	37	43	20	20	0	40	82	18	0	0
		104	8	40	30	1	39	99	4	0	0
Sunset Bay	31 July 1972 series a	17	6	55	0	1	9	90	7	0	0
							1	89	7	0	0
	31 July 1972 series b	11	36	25	0	1	4	89	0	0	2
							20	81	11	0	0
							21	82	5	0	0
	29 Aug 1972	17	1	61	0	1	9	80	10	0	0
		19	40	13	0	1					
	5 Oct 1972	11	11	40	0	1	21	98	4	0	0
Averages of figures in columns			18.7	31.2	40.9	1.2		88.4	7.6	2.9	1.1

* "Large barnacles" were those Balanus glandula with basal diameters greater than 3 mm.

** "Perennial algae" refers to Endocladia muricata and Gigartina spp.

same for the two groups.

Mass settlements of barnacles, Balanus glandula, over the areas within limpet exclosures were only observed in exclosures that were established in the summer months. The newly settled Balanus were, at first, overgrown by algae, but as the barnacles grew, the algae on and around the barnacles disappeared, apparently as a result of the grazers which located among the barnacles as the barnacles became large enough to provide shelter.

Areas of rock surface occupied by dense stands of the transient types of algae (those listed as such in Table 1 and which are fed upon by most grazers) and clumps of barnacles rarely overlapped. Barnacles did not become established in areas occupied by dense transient algal growth, and the transient algae rarely became abundant in or near clumps of Balanus. Most exclosures contained a few clumps of Balanus when constructed, and in time more barnacles settled and grew in the area of bare rock that generally surrounded these original groups of barnacles. As the new settlement of barnacles grew, the algae around them were eaten, leaving more space open for further settlement of barnacles. Through this process patches of barnacles gradually spread over the areas of the exclosures, to the exclusion of most of the transient algae. The perennial red algae, however, were commonly found among the barnacles. The other barnacle, Chthamalus dalli, also settled in the areas of rock cleared around the larger Balanus glandula.

Between 15 May 1971 and 2 February 1973 a total of 47 limpet exclosures had been constructed on the high intertidal rocks at South Cove and Sunset Bay. In mid-October 1973, the last dry-season censuses were made. By this time 29 out of the 47 exclosures (62%) had less than 15% cover of the algae categorized as transients. In 17 of these 29 exclosures, the progressive loss of the transient algae was clearly associated with the progressive increase of clumps of Balanus glandula. In the remaining 12 of the 29 exclosures, the disappearance of the annual algae began in the areas adjacent to both barnacles and crevices in the rock. As discussed earlier, crevices in the rock also harbor grazers and, along with barnacles, were associated with the low percent covers of algae in some of the new exclosures.

The remaining 18 of the 47 exclosures still had over a 50% cover of the transient algae by the mid-October 1973 census. With one exception, all these exclosures only had a small section, or sections, containing clumps of barnacles. The one exception was exclosure number 36 at Cape Arago, which was anomalous in other ways. Besides having both an extensive cover of barnacles with a thick cover of Ulva and Porphyra growing on top of the barnacles, the body weights of limpets collected from this exclosure were very low and were comparable to those of the limpets that had died from desiccation and/or starvation after being stranded above the tide for several weeks (Figure 19). Exclosure 36 was probably in the wettest location of all the exclosures of this series: it was one of the most wave exposed exclosures of the randomized series, and was one of the first exclosures to be wetted during the rising tides and the last to be above the range of the waves as the tides ebbed.

Limpet Exclosures Constructed in Areas Where Littorine Snails Were Abundant

In addition to the areas already described, approximately twenty limpet exclosures made of the copper paint were constructed on large boulders in several other areas that were well protected from wave action, and where littorine snails as well as limpets were abundant out on the open surfaces of the rock. There was little or no growth of algae in these exclosures, the most growth of algae being a thin film of blue-greens and other microscopic algae that appeared occasionally in the wet season.

It was found in the laboratory that the littorine snails would not cross strips of Tree Tanglefoot, a sticky mixture of vegetable resins (The Tanglefoot Company, Grand Rapids, Michigan). When the limpet exclosures in the wave sheltered areas were ringed with Tanglefoot algae grew abundantly in the exclosed areas, indicating that non-limpet grazers were responsible for the lack of algal growth in the limpet exclosures made with copper paint. (This material probably also kept out crawling arthropods such as isopods and amphipods.) The constant accumulation of debris on the sticky Tanglefoot material made it impractical to maintain and rendered it ineffective in repelling grazers; consequently, the algal covers within these exclosures never progressed past the *Bangia*-*Urospora* stage before being removed by invading grazers.

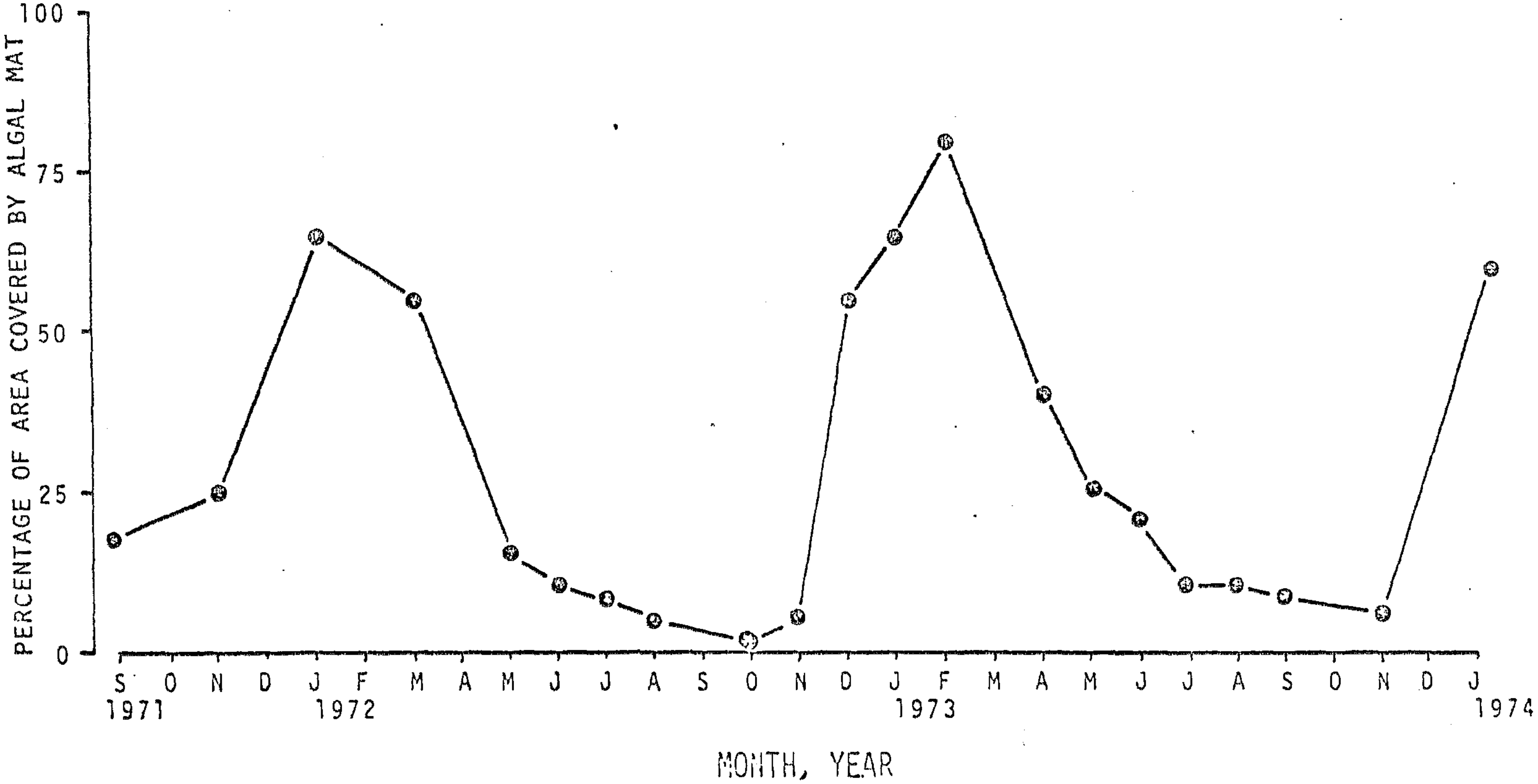
Observations on Seasonal Differences in Grazing by *Acmaea digitalis*

The areas of rock surface cleared by limpets was measured at two locations at Cape Arago. One location was a nearly horizontal, flat rock surface approximately 2.5 m^2 in area, bordered on one side by a crevice in which were most of the limpets that grazed on the flat surface of the rock. The other location was a rock wall on which there were many clumps of limpets, most of which were on the vertical surfaces of the wall.

Littorine snails were never observed in the first location, on the flat rock, and color transparencies were taken of this area of rock at approximately monthly intervals. In the winter months, during the algal "bloom," the limpets cleared only the area adjacent to the crevice, but by the end of the dry-season, in late summer and early fall, the limpets had removed nearly all of the non-perennial algae on the surface of the rock. The proportion of the surface of this rock that was covered with a mat of non-perennial algae was estimated from the color transparencies at various intervals in the period from 22 September 1971 to 21 January 1974 and is shown in Figure 18.

The fungus-infected Enteromorpha described earlier formed much of the algal cover on the rock wall, the other location where limpet grazing was measured. This Enteromorpha, as well as other algae, formed boundaries around the areas cleared by groups of limpets. These grazed areas were larger in the summer and were smaller during the winter algal bloom. In the winter, when the algae were abundant, small groups of limpets would be completely surrounded by a mat of algae. In summer, when the areas grazed bare by the limpets were enlarged, and the algae separating adjacent groups of limpets were removed, many groups of limpets would be found within fewer, but larger, areas of bare rock. The sizes of these areas that were cleared by the limpets were measured once in the summer and once in the following winter, and the number of limpets within these areas was counted. This

Fig. 18.--Seasonal changes in the size of an algal mat grazed by limpets at Cape Arago.


PERCENTAGE OF AREA COVERED BY ALGAL MAT
100
75
50
25
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J
1971
1972
1973
1974
MONTH, YEAR

information is shown in Table 6. The area cleared per limpet was approximately three times larger in summer than in winter.

The measurements in Table 6 do not take into account possible size differences between the limpets in the cleared areas in winter and summer. Color transparencies of portions of this rock wall had been taken in the same months the measurements of the grazing areas were made, but the transparencies did not cover all the portions of the rock wall on which the grazing areas were measured. To see if there was a difference in sizes between summer and winter of at least the limpets within the areas photographed, the transparencies were projected to the same scale and the lengths of these limpets were measured and compared. As shown in Table 7, the lengths of these limpets were very similar.

The Size-Specific Body Weights of Limpets in Relation to Algal Forage

The lack of algal forage in the late summer and early fall suggested that at this time the limpets might be affected by a shortage of food which, if true, should be reflected in lower weights of the soft body tissues for a given size of shell. Several collections of limpets that had been stored frozen were used to make the following measurements. These collections were of four types:

TABLE 6.--Summer and winter comparisons of areas cleared by limpets in algal mats on a high intertidal rock wall at Cape Arago

		Number of limpets in the Cleared Area	Total Area Cleared cm^2	Area Cleared Per limpet cm^2
Winter (29 December 1972)		1	12.6	12.6
		5	78.5	15.7
		27	330	12.2
		7	95	13.6
		21	445	21.1
		39	558	14.3
		107	2695	25.2
		89	810	9.1
	Totals	296	5024	17.0
Summer (27 June 1972)		247	9795	39.7
		15	632	42
		7	230	32.9
		11	512	46.5
		400	22310	55.8
	Totals	680	33479	49.2

TABLE 7.--Comparison of the sizes of limpets on the rock wall from which the grazing measurements were made at Cape Arago

	N	Average Length of Limpets (in special units of measure)*	Standard Deviation (in special units of measure)*
Summer (22 June 1972)	85	11.73**	2.19
Winter (28 Dec 1972)	84	11.66**	3.62

---

*These measurements were made from color transparencies which were projected so that the areas photographed were to the same scale. The projected scale was approximately 0.7 times the real size, and the lengths of the limpets were measured in millimeters from the projected image; therefore, these units are approximately 0.7 mm.

**The mean lengths of the limpets were not different at $p > .8$.

1. Limpets collected in summer (6 Aug 1973) from the Sunset Bay study area, but outside any exclosures or controls.
2. Same as above but collected in winter (25 Feb 1973).
3. Limpets that had been found inside exclosures, where food was abundant, in summer.
4. Limpets from very high tidal levels that had died in the late summer (5 Sep 1973).

These limpets had been stranded in a location that apparently had received no seawater for a period of several weeks during calm weather (with little wave action). During this period, the limpets, whose positions had been marked on the rock, had not moved. After several weeks under these conditions, some of these limpets fell off the rock when lightly touched with a finger and had a desiccated appearance. Many of these limpets revived when placed in fresh seawater and were replaced on the rock. Those limpets that showed no sign of movement after being in seawater for several hours were considered dead and used for these measurements.

Since limpets conceivably have more sand in their digestive systems in the summer when they must graze the surface of the rock more closely to get any algae that are there, ash-free dry weights were used. (The limpet bodies were dried at 100° C for 24 hours, weighed, and then ashed at 450-500° C for 24 hrs. The weights of these ashes were subtracted from the weights of the dried bodies.) The sizes of the shells were measured as the volume of the interior of the shell, which was determined by filling the shell from a 1 cc syringe with a 1:1 ethanol-water solution, which had less of a meniscus than pure water.

The relationships of ash-free, dry weights of the limpet bodies to volumes of their shells are compared in Figure 19. The limpets

Fig. 19.--Relationships of ash-free, dry weights of limpet body tissues to volumes of the shells, for limpets collected from various conditions. Place and date of collection is shown on each regression line (C.A. = Cape Arago, S.B. = Sunset Bay). Regression lines span distance of the maximum to minimum values used to calculate them. Regressions for limpets from exclosures are shown as dotted lines.

The size-specific body weights of the limpets from exclosure 9 were significantly greater than those of any of the other groups of limpets. The limpets collected from the open rock in summer and from exclosure 8 had significantly lower size-specific body weights than those collected in winter and from exclosures 13 and 58. Those limpets that died after being stranded above the tide had size-specific body weights that were significantly lower than those of all the other groups except the group collected from exclosure 36. The analysis of these data are shown in Table 8.

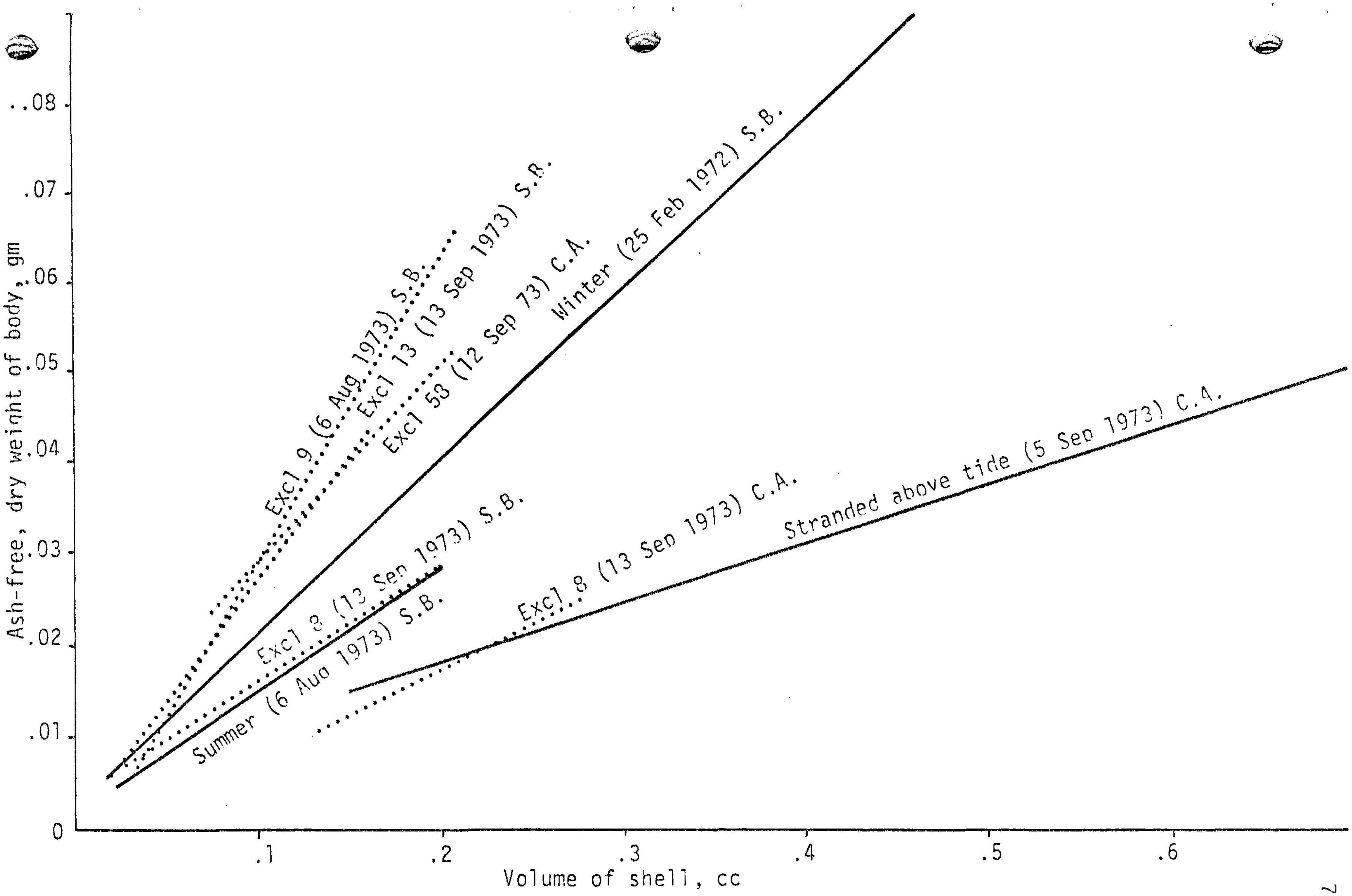

Ash-free, dry weight of body, gm
.08
.07
.06
.05
.04
.03
.02
.01
0
.1
.2
.3
.4
.5
.6
Volume of shell, cc
Excl 9 (6 Aug 1973) S.B.
Excl 13 (13 Sep 1973) S.R.
Excl 58 (12 Sep 73) C.A.
Winter (25 Feb 1972) S.B.
Excl 8 (13 Sep 1973) S.B.
Summer (6 Aug 1973) S.B.
Excl 8 (13 Sep 1973) C.A.
Stranded above tide (5 Sep 1973) C.A.

TABLE 8.--Analysis of regressions shown in figure 19

				Comparisons of regressions** (probabilities that slopes are equal)							
	N	Significance of regression*	Significance of correlation coefficients between weight and volume*	Excl. 9	Excl. 13	Excl. 58	Winter, open rock	Excl. 8	Summer, open rock	Excl. 36	Stranded, dead
Excl. 9	7	< .001	< .001		> .1	< .05	< .001	< .001	< .001	< .001	< .001
Excl. 13	6	< .01	< .01	> .1		> .25	> .25	< .025	< .005	< .001	< .005
Excl. 58	7	< .01	< .01	< .05	> .25		> .5	> .05	< .01	< .025	< .005
Winter, open rock	59	< .001	< .001	< .001	> .25	> .5		< .05	< .005	< .05	< .001
Excl. 8	6	< .01	< .01	< .001	< .025	> .05	< .05		> .5	> .25	< .001
Summer, open rock	41	< .001	< .001	< .001	< .001	< .01	< .005	> .5		> .25	< .001
Excl. 36	8	< .05	< .01	< .001	< .001	< .025	< .05	> .25	> .25		> .25
Stranded above tide, dead	16	< .001	< .001	< .001	< .005	< .005	< .001	< .005	< .001	> .25	

---

*Equations for regressions, significance of regressions, and Pearson product-moment correlation coefficients were obtained using the linear regression analysis program MSP106 of the University of Oregon Computing Center. (This program uses the method of Mendenhall 1967.)

**The ash-free, dry weight to shell volume relationships for the groups of limpets were compared using the Analysis of Covariance program (BMDO9V) of the Health Sciences Computing Facility, University of California, Los Angeles.

collected in winter had significantly higher body weights per unit volume of shell than limpets collected from the same area in the summer. In summer the limpets that had the greatest body weights in relation to shell volume came from exclosures, where food was more abundant than on the surrounding surface of the rock. However, limpets with relatively low body weights in relation to shell volume were found in other exclosures. The limpets with the lowest body weights per unit shell volume were those that were collected as they died on the high rocks.

Observations on the Growth of Endocladia muricata

In areas protected from strong wave action *Endocladia* plants grow in the unusual patterns, such as loops and circles, shown in Figure 20. Examination of the rock surface beneath these plants showed no irregularities underlying the patterns formed by the plants. It was also considered that littorine snails may become trapped within the clumps of plants and then eat out the interiors of the clumps. But this hypothesis was rejected after groups of marked *Littorina* placed within the clumps easily escaped and dispersed over an area of several square meters within a day.

Changes in individual patches of *Endocladia* were followed by photographing them approximately once a month. The clumps

Fig. 20.--Patterns in the growth of Endocladia muricata in an area sheltered from waves at Cape Arago.

were also examined visually for signs of grazing or other factors which could produce the patterns of their growth.

In summer, the cause of these patterns became apparent. During periods of calm weather with little, if any, wave action, the interiors of the *Endocladia* clumps became filled with sediment. Reducing conditions then developed within the masses of sediment as evidenced by the formation of black sulfides and the smell of hydrogen sulfide. The portions of the *Endocladia* branches enmeshed in this anaerobic sediment were killed; the next period of increased wave action removed the sediment, the killed branches, and any live branches attached to those that were dead, leaving a hollow space in the center of the clump. This sequence of events is illustrated in Figure 21. Fragments of branches that were attached to the rock at the outer edge of the clump regenerated a new clump in the shape of the perimeter of the previous clump.

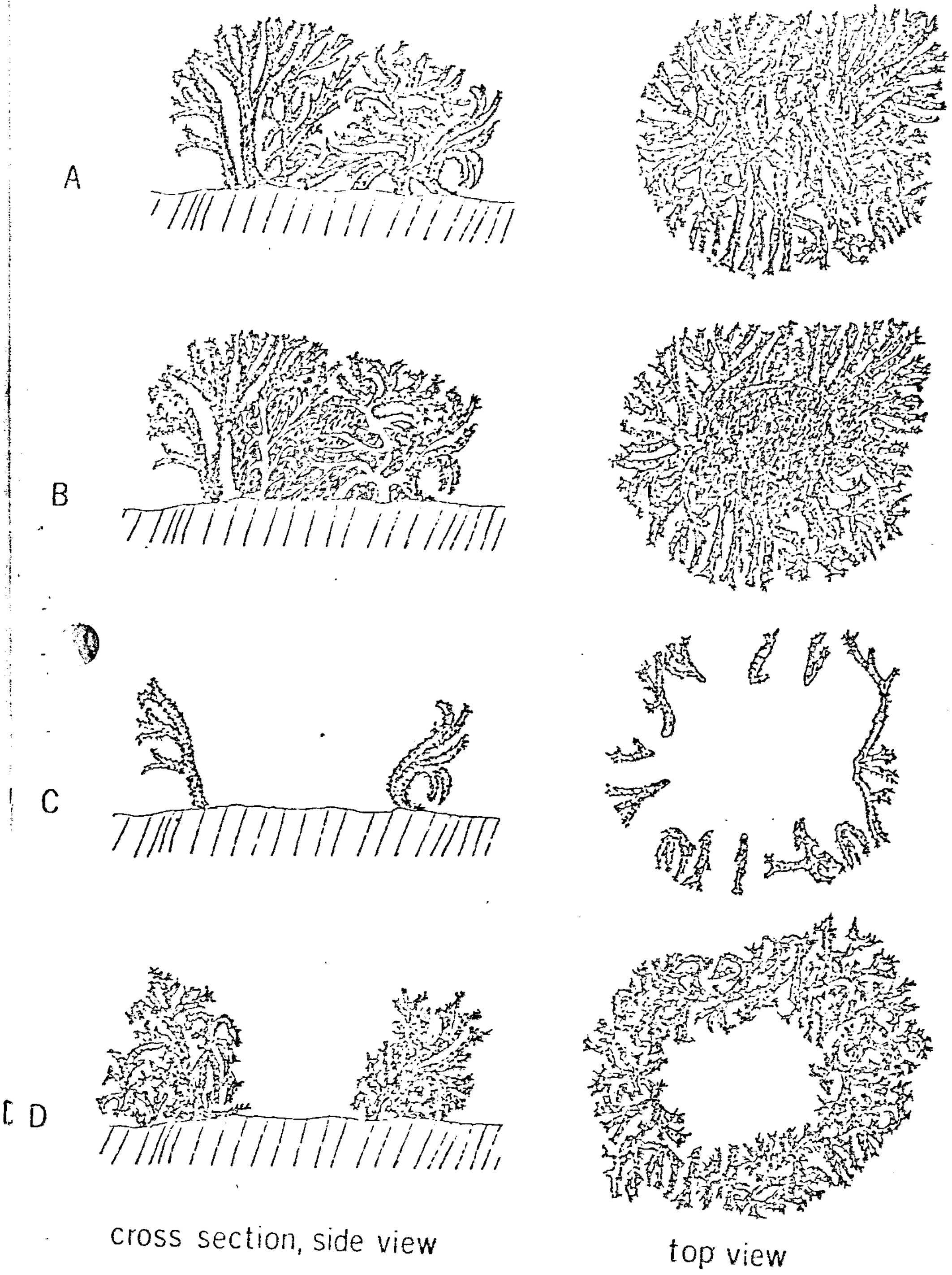
Fig. 21.--Schematic diagram of the process which produces patterns such as whorls, loops, and circles in the growth of clumps of the bushy red alga, Endocladia muricata. Figures are approximately one-half life-size, and the diameter of the branches has been exaggerated by a factor of 5 in scale to the rest of the plant.

A. Normal clump of Endocladia during periods when wave action is great enough to keep the interior of the clump free of sediment.

B. Accumulation of sediment in the interior of the clump of Endocladia. Unstippled branches are those that have died.

C. During the next period of increased wave action the sediment is removed from the interior of the clump. The dead branches and the live branches attached to them are also removed leaving only those branches that were attached to the rock surface outside the area of sedimentation and were not killed by being enmeshed in the sediment.

D. The intact branches that had been part of the fringe of the original clump regenerate a new clump in the approximate shape of the perimeter of the original clump.


A
B
C
D
cross section, side view
top view

SECTION IV

DISCUSSION

On the high intertidal rocks grazed by limpets, algae are only abundant during the wet season; during the dry season, algal covers naturally decline. The experiments with the limpet exclosures demonstrate that much of the reduction in algal abundance in the dry season is a result of limpet grazing. By excluding limpets from portions of the rock surface, algal covers became established and were maintained at all times of the year. Physical stresses did not prevent the establishment of algal covers even on the portions of the rock which were exposed to the extremes of desiccation, high temperatures, and solar radiation during the summer months. Genera of algae that are normally considered to be transient because they become rare or disappear in the summer months remained abundant in the limpet exclosures.

Although the physical conditions of summer did not exceed the tolerance limits of many of the high intertidal algae, development of the algal mats within the exclosures was slower in summer than in winter. This was probably a result of the high intertidal rocks being wetted for fewer daylight hours per day in the summer, and, thus, providing fewer growth hours per day for the algae (Castenholz 1961). Some loss of water increases the photosynthetic rates of some high intertidal algae (Johnson et al., 1974), but photosynthesis generally decreases as algae dry when exposed above the tide (Johnson et al., 1974, Stocker and Holdheide 1937).

The only algae that normally survive through the summer period of intense grazing are those in areas inaccessible to the limpets, and those which are resistant to grazing. Thus, in areas exposed to limpet grazing a perennial alga is also a grazer resistant alga.

As phyla, the red algae seem to be the most successful and the green algae the least successful at surviving in areas of heavy grazing. Glynn (1965) found that the limpets, *Acmaea digitalis* and *A. scabra*, and the littorine snails, *Littorina scutulata* and *L. planaxis*, living in association with the perennial red alga *Endocladia muricata* did not eat this alga, but instead fed mainly on blue-green algae, diatoms, and green algae (based on examinations of gut contents). In areas of concentrated grazing by sea urchins either there are no algae at all, or the red algae are abundant. If grazing by sea urchins is reduced, brown and green algae become more abundant (Irvine 1973, Kitching and Ebling 1961, Leighton et al., 1966, Paine and Vadas 1969). When various species of limpets and other gastropods have been removed from mid-intertidal rocky shores, green algae have flourished, followed, in some cases, by Fucus, a brown alga (Bellamy et al., 1967, Jones 1948, Lodge 1948, May et al., 1970, Mar. Biol. Assoc. U.K. 1968).

In the areas that I studied, the red algae Endocladia muricata and Gigartina papillata comprise nearly all of the biomass, or standing crop, of the algae that survive through the summer on rocks that are heavily grazed by limpets and littorine snails. In winter, the membranous green alga Ulva was cleared from areas near concentrations of littorine snails and limpets and was replaced by the membranous red alga Porphyra. In the laboratory, Porphyra was more resistant to grazing by Littorina scutulata than was Ulva.

There is some evidence that the green algae may be competitively dominant over the other algae, and would monopolize more of the intertidal zone if they were not so readily removed by the intertidal herbivores. As mentioned before in the study areas, Porphyra grew abundantly in the areas that limpets and littorine snails cleared of Ulva, and, in studies by other investigators, Ulva grew abundantly in areas cleared of limpets and other grazers. Rapidly photosynthesizing Ulva plants in tidepools have been observed to raise the pH (by depleting carbonates) to a level that kills other algae, including the red algae (Atkins 1922, Fjeldmann 1957).

This idea could be examined more closely by reducing the populations of all herbivores and noting the effects on the algal populations. To my knowledge, the closest "experiment" to this that has been done, was when the detergents used during the Torrey Canyon oil spill killed off most of the intertidal herbivores in some locations of the British coast (Bellamy et al., 1967, O'Sullivan and Richardson 1967). The aftermath of this was called the "green shore phenomenon" because the green algae (mainly Enteromorpha) then formed dense mats in the intertidal zone (Bellamy et al., 1967, Mar. Biol. Assoc. U.K. 1968). However, since some algae were also killed by the detergents, the subsequent abundance of Enteromorpha may have been some sort of "successional" event unrelated to grazing. (Enteromorpha, though, was one of the algae that was noted to be killed by detergents (Mar. Biol. Assoc. U.K. 1968).) A similar "greening" of the shore occurred at Heron island, off the coast of Australia following the destructive effects of a hurricane in 1967 and is apparently a common phenomenon following such storms (P. Frank, pers. comm.).

Many of the changes in the species composition of the algal covers within the limpet exclosures may have been due to littorine snails and other grazers removing the initial covers of the filamentous algae and the green algae Ulva and Enteromorpha, thereby opening up this space to other species. As described earlier, barnacles only became established in areas that had been cleared of these transient types of algae. In exclosures that were particularly free of littorine snails the filamentous algae and *Ulva* and *Enteromorpha* were persistent for long periods (2 to 3 years).

The only green alga to remain abundant in the presence of grazing on the high intertidal rocks through the summer as *Enteromorpha vexata* infected with the ascomycete fungus, *Turgidosculum*. Apparently the fungus provides some protection against herbivores: in the laboratory *Littorina scutulata* preferred the uninfected *Enteromorpha* to the infected plants. Another case of an ascomycete-algal association being grazer-resistant is the lichen, *Pygmaea pumila* (=*Lichina pygmaea*), which is the ecological equivalent of *Endocladia muricata* on some British shores (Glynn 1965). This is mentioned here because there is considerable evidence that the ascomycete fungi are closely related to the red algae. This evidence is usually used to support the hypothesis that the ascomycetes evolved from the red algae (for reviews see Denison and Carroll 1966, Kohlmeyer 1973). However, this evidence may also be used to support the hypothesis that the red algae evolved from some, perhaps lichen-like, association of ascomycete fungi with blue-green algae. Such an idea has previously been proposed by Richard M. Norris

(R.M. Norris pers. comm.).) In evolutionary schemes, the red algae are usually considered derived from the blue-greens because of similarities in photosynthetic pigments and other cellular components (reviewed in Christensen 1971, Hommersand and Searles 1971), and the similarities of the red algae to the ascomycetes are not considered.

As suggested by the Turgidosculum-Enteromorpha association, the selection for the hypothetical red algal type of blue-green-ascomycete association may have been the advent of grazing which removed free-living blue-greens and other types of algae from the surface of the rock, thereby leaving this space and other resources open to the red algae. Blue-green algae that form stromatolites were once abundant in the intertidal zone during the Precambrian but subsequently disappeared. Evidence from both present-day and fossil stromatolites indicates that the reduction in abundance and distribution of these types of blue-green algae is a result of grazing and other activities of animals (Awramik 1971, Garrett 1970). If the red algae are not closely related to the ascomycete-algal associations, then these two groups are a case of closely convergent evolution, both ecologically and morphologically.

During the summer months, when the algae grow more slowly, and most of the algal forage is consumed, the limpets appear to suffer from a shortage of food. At Sunset Bay, the size-specific body weights of Acmaea digitalis collected from the open rock surface were lower in summer than in winter (Figure 19). Frank (1965) found for this same species that gonads regressed and that rates of growth decreased in the summer. The mortality of high intertidal limpets also was greater during the summer (Breen 1971, Frank 1965). Haven (1973) found that growth rates of Acmaea digitalis and Acmaea scabra (sympatric with A. digitalis to the south of Oregon) were dependent on the food supply per limpet. Sutherland (1972) also noted many of these above relationsips for Acmaea scabra living at the high intertidal levels: in summer, mortality rates were higher, size-specific weights were lower, growth rates were lower, and gonads regressed.

The mortality of limpets living at the high intertidal levels in the summer has been attributed to desiccation (Sutherland 1970, Wolcott 1973). Such deaths occur during periods of calm seas and dry weather (Frank 1965, Sutherland 1970, Wolcott 1973). Under these conditions there is also very little growth of algae, and starvation cannot be ruled out as a cause or contributor to the deaths of these limpets. The limpets that died under these conditions at Cape Arago(Figure 16) had the least amounts of body tissue in relation to shell volumes of any of the limpets measured. Since Acmaea digitalis must expend material and energy to protect itself from desiccation (by sealing its shell to the substrate with a mucus sheet (Wolcott 1973)), starving limpets may be killed by exposure to desiccating conditions that would not be lethal to limpets with more adequate food resources. Wolcott (1973) has pointed out that, ". . . the finding of dead, dry animals in the field can mean either that the animals were killed by desiccation, or that the animals dried out because they were dead." It has also been suggested (Frank 1965) that since limpets only move on wet rock, dry summer conditions may reduce opportunities for grazing and have the same effect as a shortage of food.

During the wet season (roughly November to March), when algae are abundant in the high intertidal zone, limpets do most of their growing (Breen 1971, Frank 1965), their gonads increase in size (Frank 1965), and their size-specific body weights are greater (Figure 19). Since all these things require material and energy, it is unlikely that the increase in the abundance of the algae at this time is due to the limpets drastically reducing their consumption of algae. Nor is it likely that the wet season algal bloom is a result of a decrease in the abundance of limpets on the high rocks. At higher tidal levels densities of limpets, Acmaea digitalis, increase, rather than decrease, during the winter, due to an immigration of limpets from lower tidal levels (Breen 1972, Frank 1965). However, the amount of algae the limpets could potentially consume in winter may be reduced by the weather: limpets, like other poikilotherms, may have their metabolic rates, and thus their energy requirements, reduced by the cooler winter temperatures. Also, Acmaea digitalis ceases to move when sufficiently exposed to fresh water (Wolcott 1973), so grazing times may be shortened during winter low tides and heavy rains.

In the dry season, the direction of limpet migration is reversed, and the limpets migrate to lower levels of the rock. However, this downward migration is not as extensive as the upward migration in the wet season, so there is a net influx of migrants into the higher levels of the intertidal zone (Breen 1972, Frank 1965).

Limpets are able to adjust population densities through migration. In experiments where densities of limpets were artifically increased, the limpets responded by emigrating from the areas of higher density (Breen 1972, Frank 1965, Stimson and Black 1974). In crowded areas, the limpets migrated to the upper and lower extremes of their range where mortalities were higher (Frank 1965, Stimson and Black 1974). In the studies of Frank (1965) and Stimson and Black (1974) the density-dependent factor causing these migrations was not identified; however, these investigators suggested food concentration was a likely possibility. Breen (1971) tested this possibility by reducing the availability of food rather than increasing the numbers of limpets and obtained the same results: emigration from the experimental area.

The preceding information on seasonal changes in algal and limpet populations suggests that mortality and migration regulate limpet densities in relation to food supply, and that the carrying capacity of the high intertidal rocks is greater for limpets in the wet season than the dry season. The winter wet season is a period of growth and recruitment for populations of high intertidal limpets, but when these populations enter into the summer period of low algal productivity, they remove much of the standing crop of the algae, suffer from a reduction in the supply of forage, and, through emigration and mortality, their number are reduced to a level that is incapable of consuming the next winter's growth of algae at the rate it is produced. A result of this difference between the larger amount of algae produced and the smaller amount of algae consumed is a large standing crop of algae, or "algal bloom" in the winter months.

This explanation is somewhat different than the suggestion of Castenholz (1961) that reductions in the activities and/or densities of grazers may be responsible for the algae being more abundant in winter. Observations made during this study, and the observations made by other investigators indicate that Castenholz's (1961) explanation is probably correct for areas grazed by littorine snails, which were one of the main grazers in the area studied by Castenholz (1961). At Cape Arago littorine snails were rare in some locations in winter where they had been abundant in summer. This was probably a result of the increased force of the waves at these locations in winter. In such areas the littorine snails must either retreat into crevices or be dislodged by the waves (Behrens 1974, Lewis 1964).

From this study, biotic interactions, especially grazing in relation to algal production, appear to be the most important factors controlling the overall abundance, and perhaps the species composition, of organisms in high intertidal communities. The only clear case of abiotic factors directly controlling the abundance of a high intertidal organism was the example of clumps of Endocladia being killed back (in a density-dependent manner) by the accumulation of sediment within the clumps during calm weather. In all the other cases, physical factors influenced the abundance of algae by affecting the species interactions. During the dry season, the algae disappeared because they grew at a slower rate than they were removed by grazing, not because their "physiologically critical limits" were exceeded by the dry, warm, and sunny conditions in the summer months. The idea that biotic interactions have little effect on physically stressed communities (Dobzhansky 1950, Williams 1964) is obviously not the case in the area studied here.

It appears that there is an optimum range of grazing intensity necessary for many species to become established and maintained on the rocks. In the exclosures, the barnacles, Balanus and Chthamalus, only became established where littorine grazing had removed the mats of algae. However, outside the exclosures, where the rocks were also grazed by limpets, there was little or [illegible] recruitment of barnacles. Similarly, Porphyra was most abundant in areas where mats of Ulva had been cleared away by grazing but was rare in areas of heavy limpet grazing. Ulva, with very little resistance to grazing, was only abundant in the limpet exclosures and during those periods of the year on the open rocks when limpet grazing was reduced. If it were not for the seasonal fluctuations in productivity generating annual reductions in the intensity of grazing, Ulva would probably never be abundant on these rocks.

Since Balanus is able to competitively eliminate Chthamalus (Connell 1961), but Chthamalus is more resistant to grazing (Dayton [illegible]71), Chthamalus should survive best at that intensity of grazing just sufficient to eliminate Balanus. On some shores Chthamalus is more abundant at the higher tidal levels, just above where Balanus is abundant. This zonation may be a result of grazing, which is more intense at higher tidal levels in the summer, the period of the year when barnacles settle and are presumably most vulnerable to selective removal by grazers. If this is true, the upper limit of the Balanus zone is determined by grazing. This idea would be shown to be incorrect if exclusion of grazers from the Chthamalus zone did not result in a replacement of Chthamalus by Balanus. In the areas studied here, there was no Chthamalus zone because all barnacles were rare on the open surface of the high intertidal rocks. In the limpet exclosures, however, Balanus was abundant, especially in those exclosures started during the summer season of barnacle settlement. Chthamalus was only abundant in portions of the exclosures that were adjacent to crevices, clumps of Balanus, and in other areas of the exclosures that were regularly grazed by littorine snails.

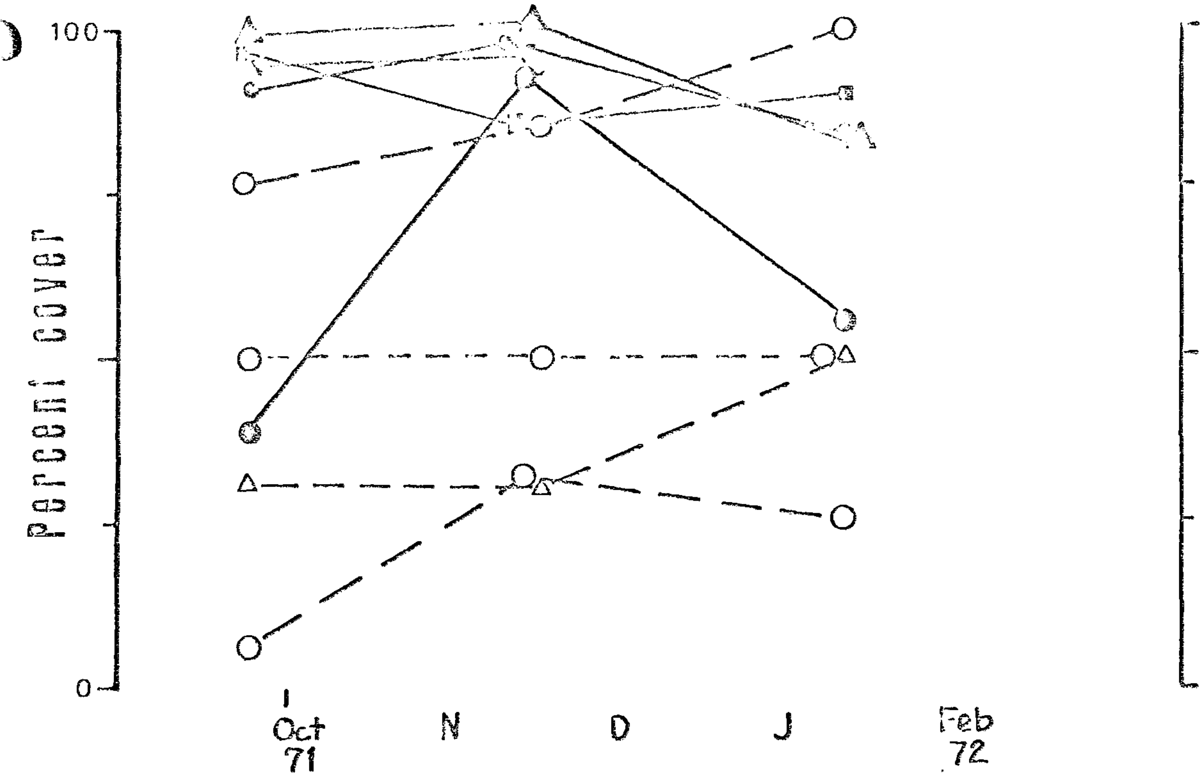
Lawson (1957) and Lewis (1964) have observed that the winter bloom and summer decline of algae on the high intertidal rocks is a result of a raising and lowering of the upper limits for these algae. As shown here, the factor limiting algal abundance at the higher levels was grazing.

The common idea that mainly physical factors limit the distribution and abundance of organisms at upper levels of the shore (see Connell 1972 for review), therefore, needs to be re-examined. The idea that competitive success at lower tidal levels comes at the expense of tolerance to physical factors at higher tidal levels (Baker 1909, Connell 1972, Walter and Stadelmann 1968) needs to be expanded to include grazing as one of the stresses or limiting factors at the higher levels of the intertidal shore.

APPENDIX

Fig. 1 A. Percent covers of plants and sessile invertebrates in exclosures and controls started on 23 Aug 1971 at Cape Arago. Solid symbols are exclosures, open symbols are controls.

Fig. 2 A. Percent covers of plants and sessile invertebrates in exclosures and controls started on 7 May 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.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Percent cover
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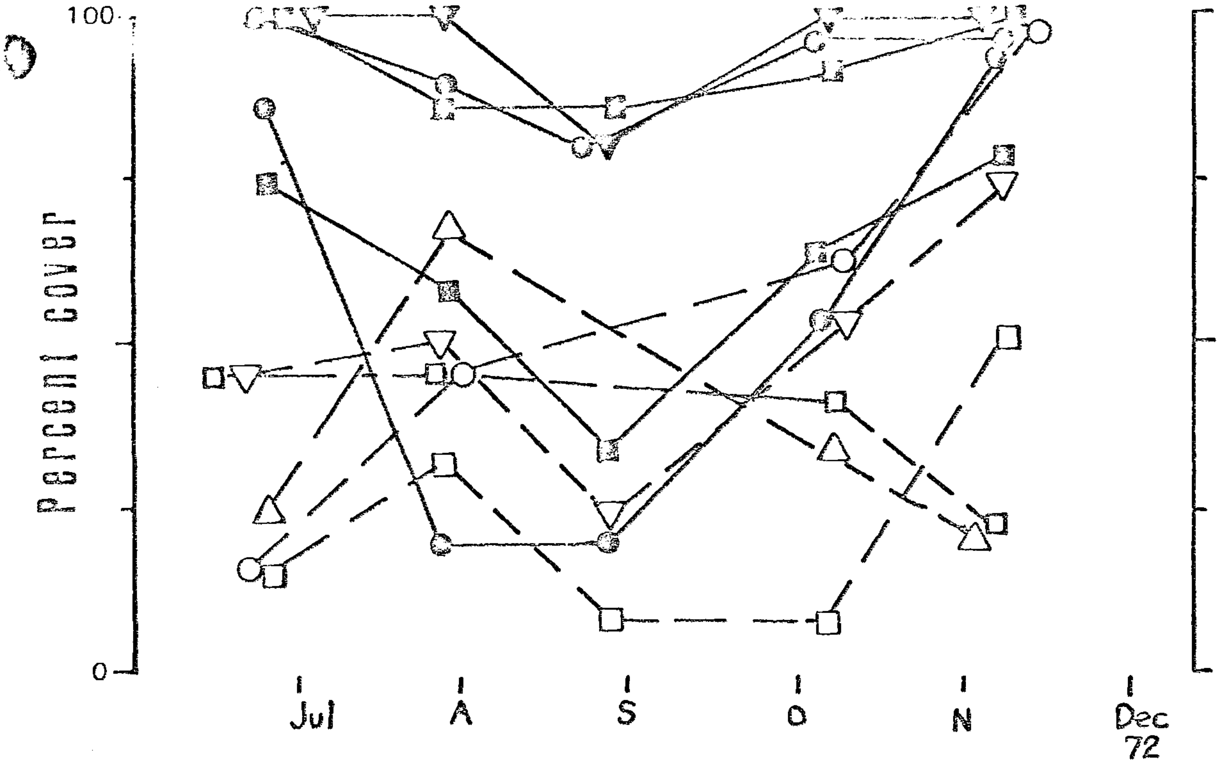
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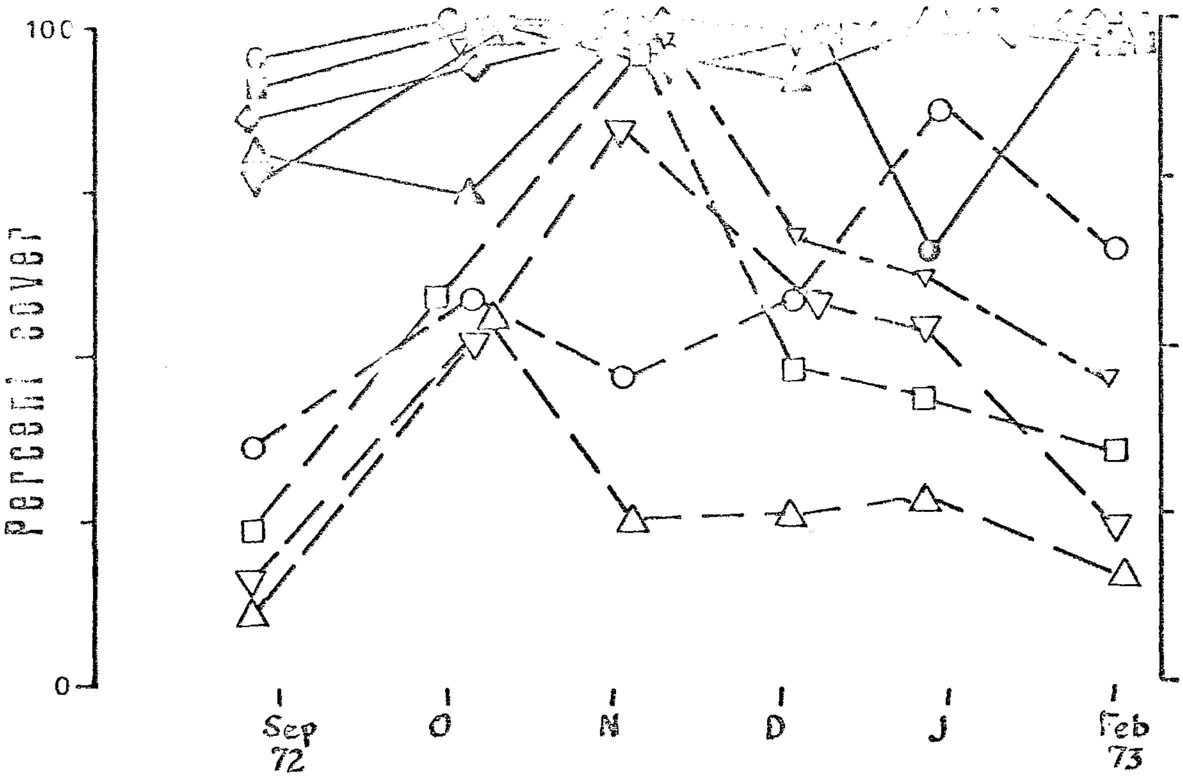
Fig. 3 A. Percent covers of plants and sessile invertebrates in exclosures and controls started on 14 Aug 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.

Fig. 4 A. Percent covers of plants and sessile invertebrates in exclosures and controls started on 4 Nov 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.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Percent cover
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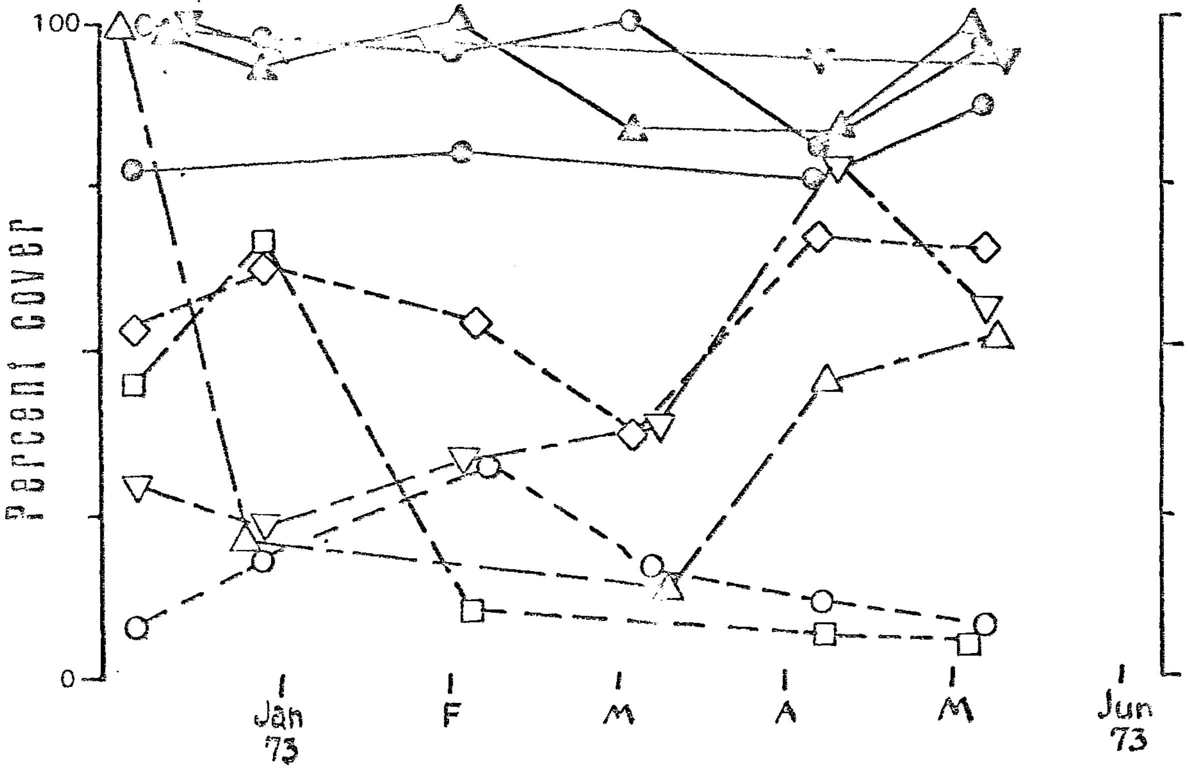
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Fig. 5 A. Percent covers of plants and sessile invertebrates in exclosures and controls started on 2 Feb 1973 at Cape Arago. Solid symbols are exclosures, open symbols are controls.

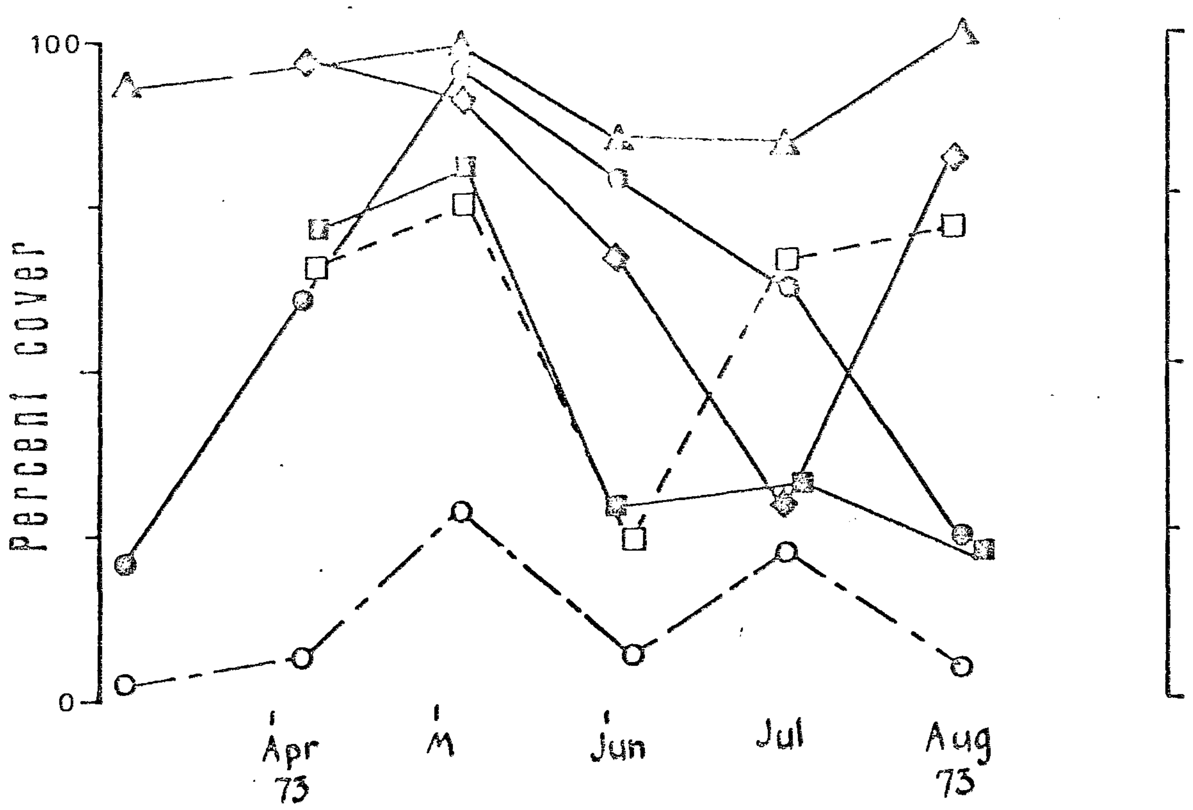
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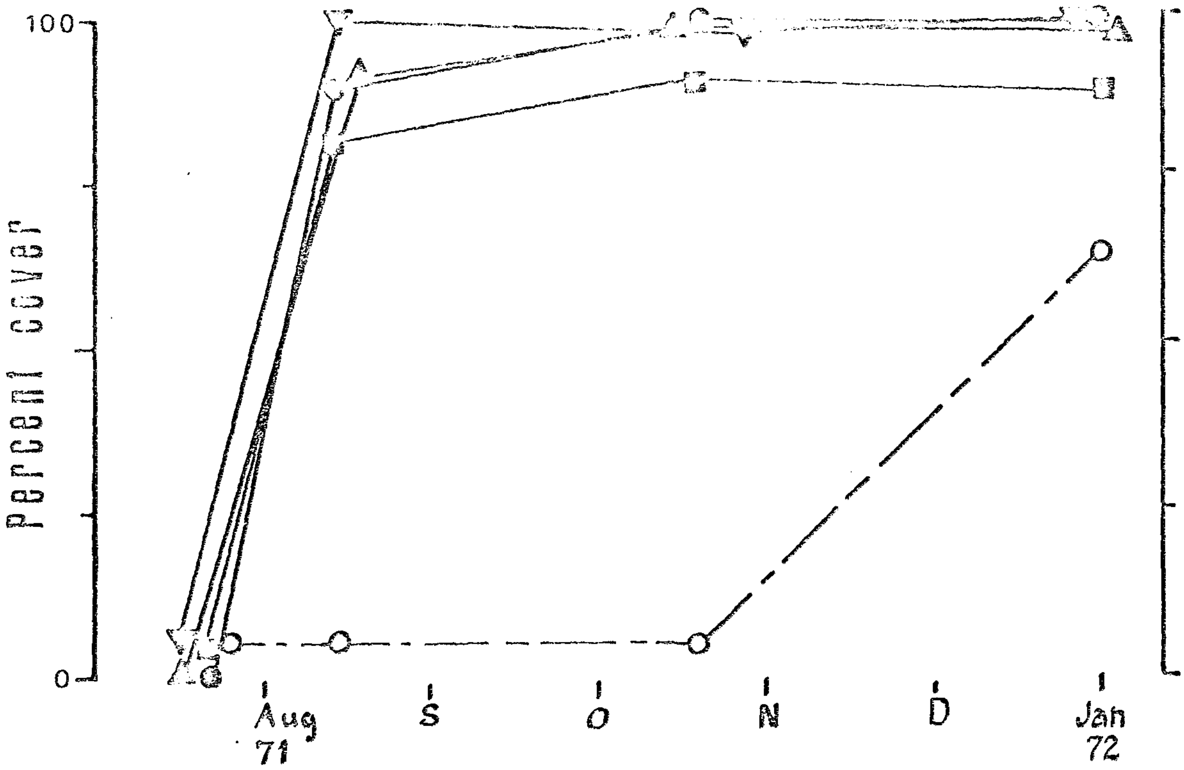
Fig. 6 A. Percent covers of plants and sessile invertebrates in exclosures and controls started 16 July 1971 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.

Fig. 7 A. Percent covers of plants and sessile invertebrates in exclosures and controls started 30 Nov 1971 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.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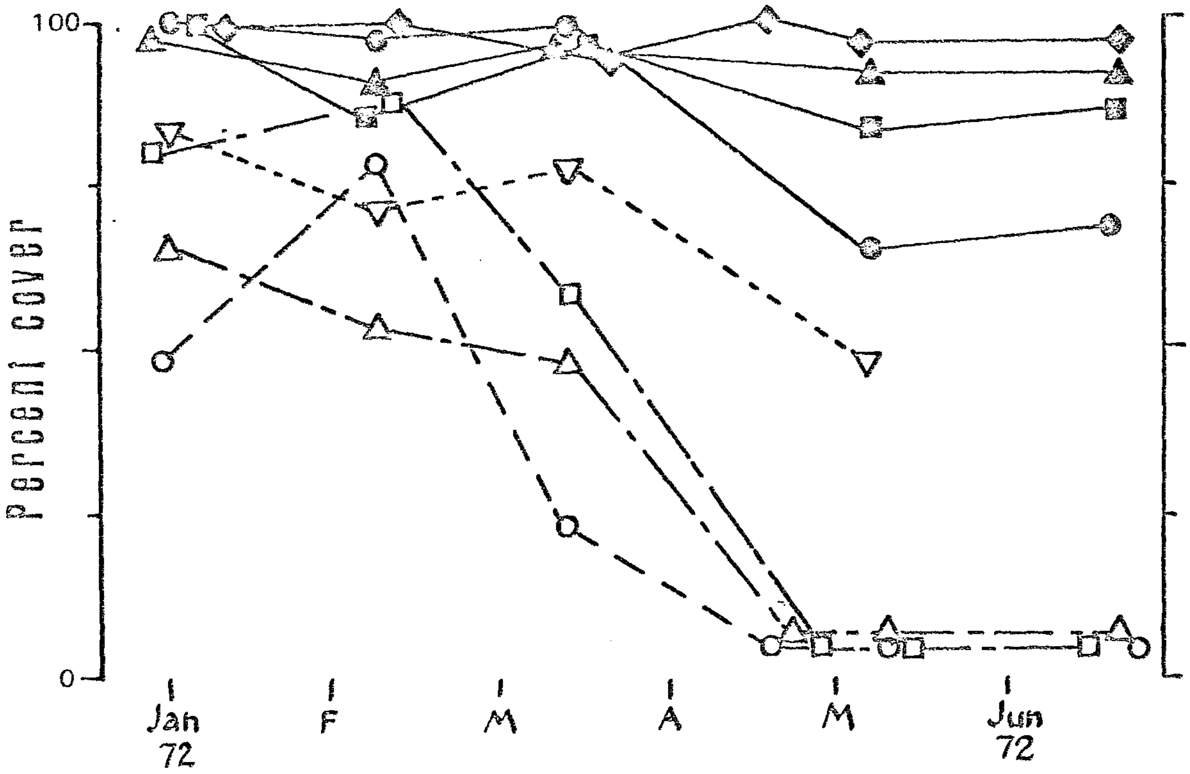
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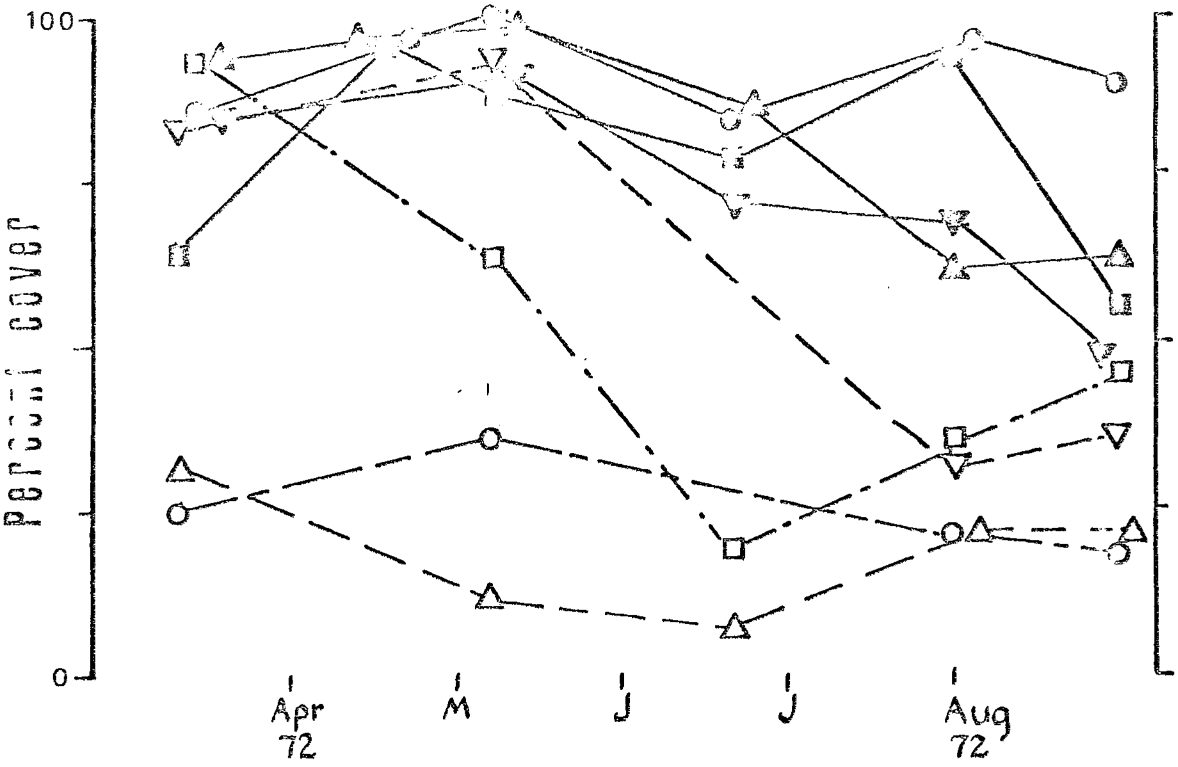
Fig. 8 A. Percent covers of plants and sessile invertebrates in exclosures and controls started 25 Feb 1972 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.

Fig. 9 A. Percent covers of plants and sessile invertebrates in exclosures and controls started 13 May 1972 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.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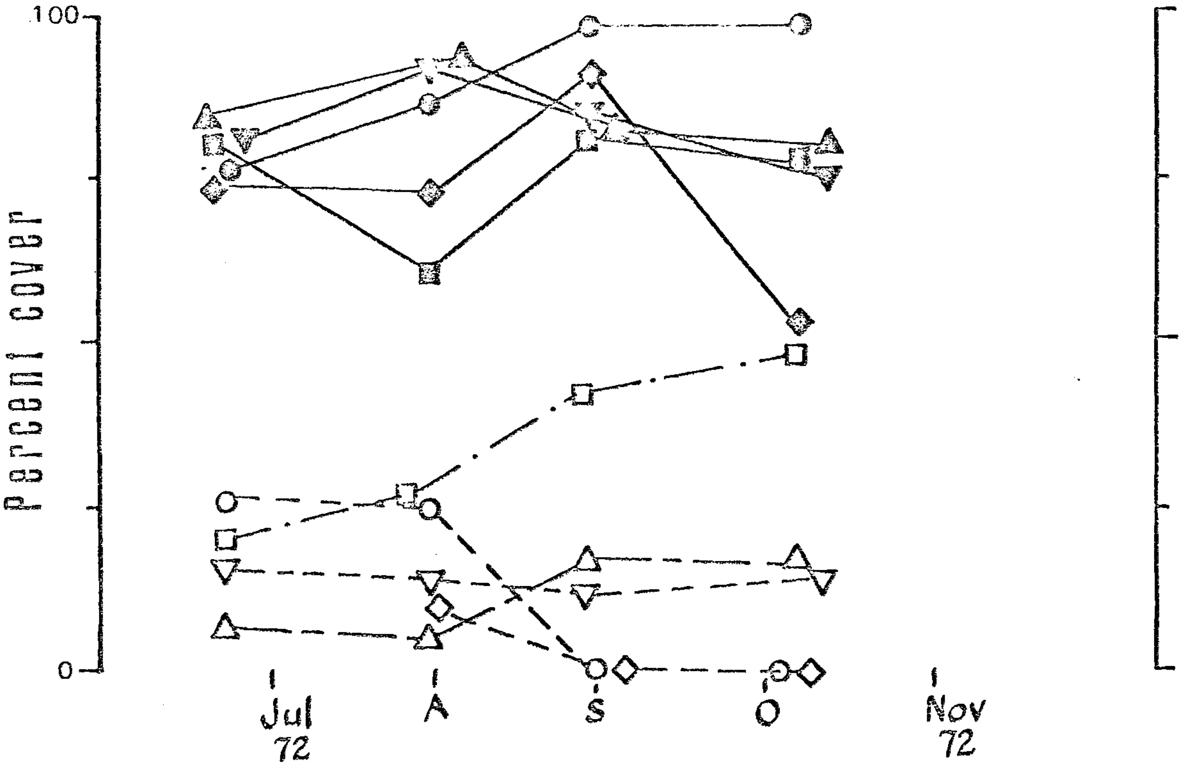
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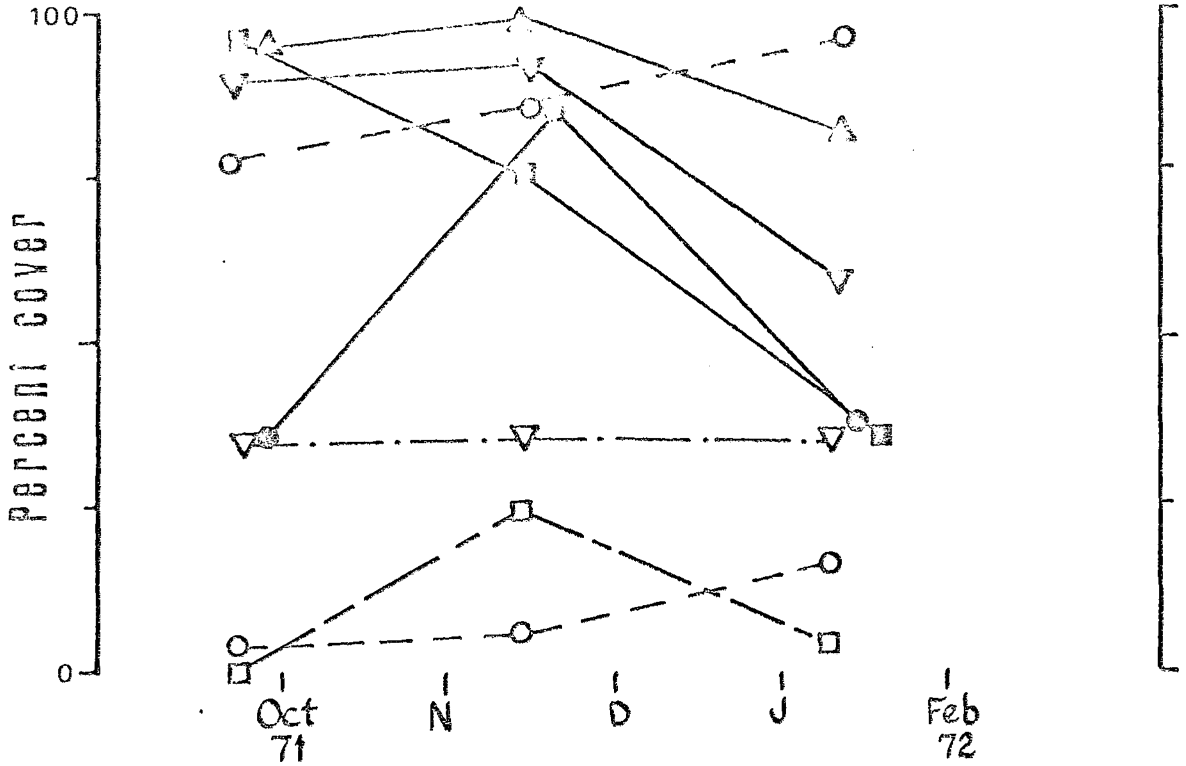
Fig. 10 A. Percent covers of plants only in exclosures and controls started on 23 Aug 1971 at Cape Arago. Solid symbols are exclosures, open symbols are controls.

Fig. 11 A. Percent covers of plants only in exclosures and controls started on 7 May 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.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Percent cover
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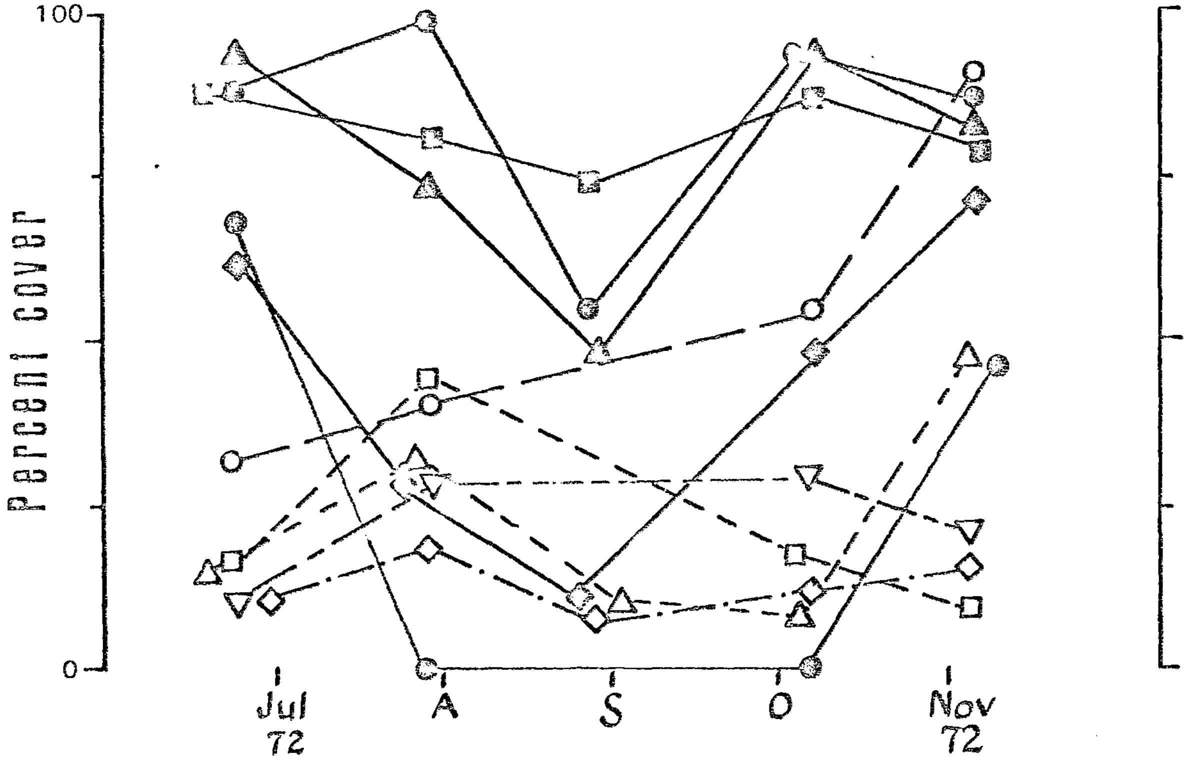
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Percent cover
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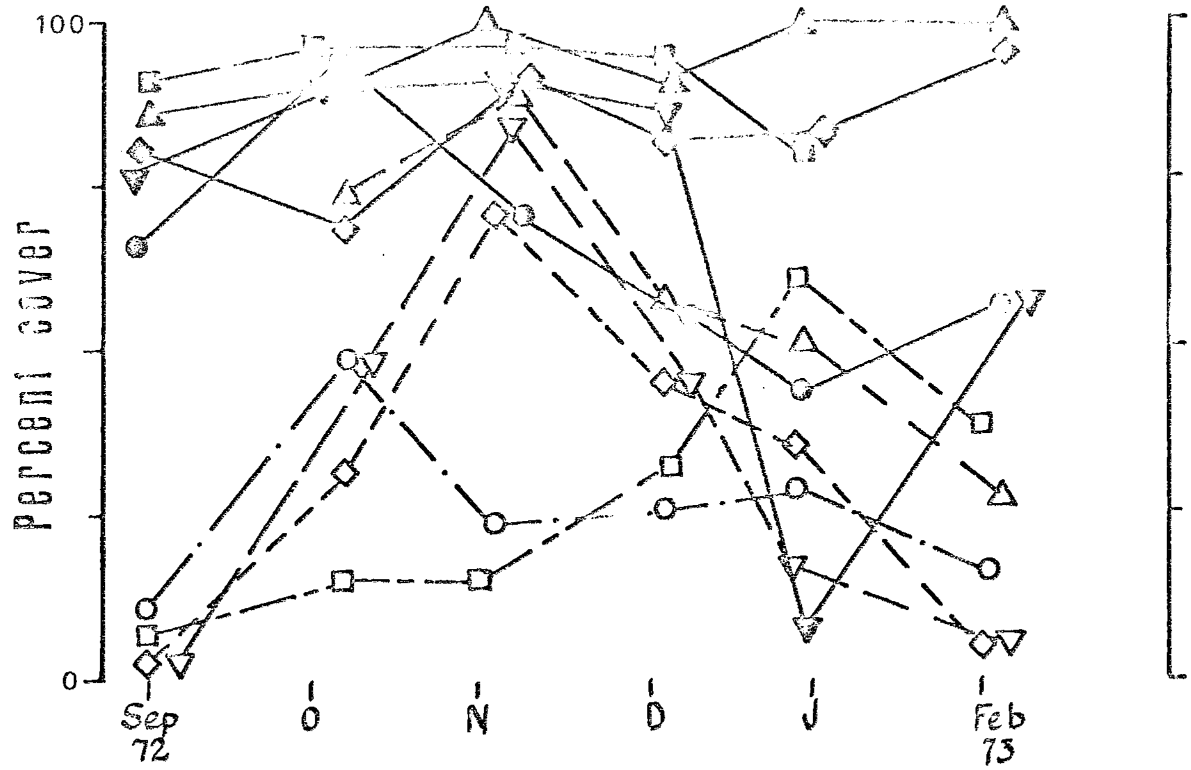
Fig. 12 A. Percent covers of plants only in exclosures and controls started on 14 Aug 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.

Fig. 13 A. Percent covers of plants only in exclosures and controls started on 4 Nov 1972 at Cape Arago. Solid symbols are exclosures, open symbols are controls.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Percent cover
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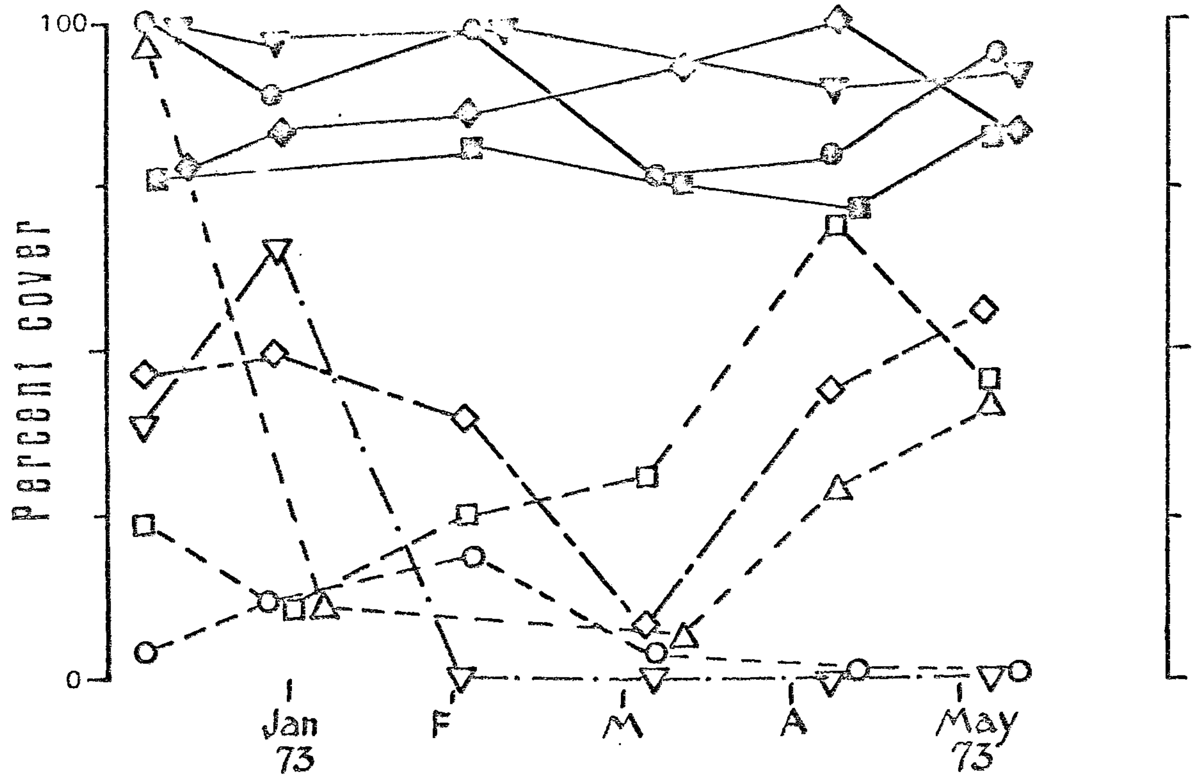
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Percent cover
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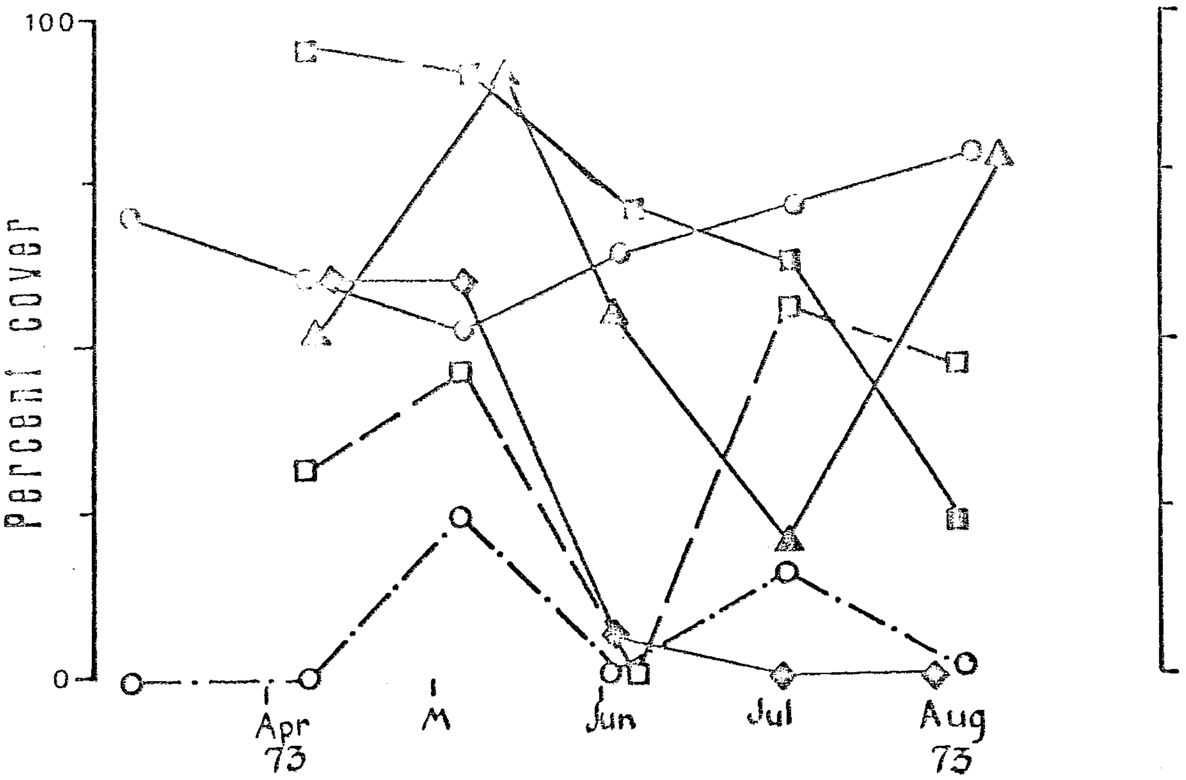
Fig. 14 A. Percent covers of plants only in exclosures and controls started on 2 Feb 1973 at Cape Arago. Solid symbols are exclosures, open symbols are controls.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Percent cover
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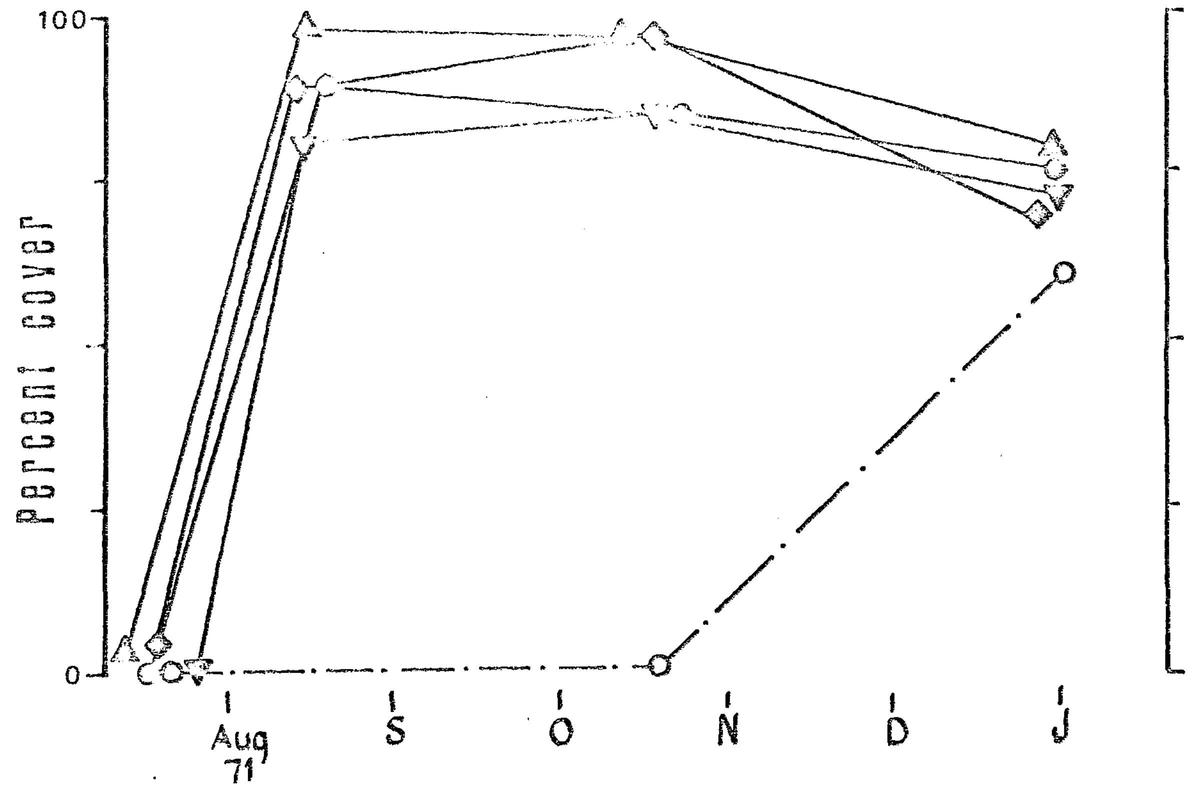
Fig. 15 A. Percent covers of plants only in exclosures and controls started on 16 July 1971 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.

Fig. 16 A. Percent covers of plants only in exclosures and controls started on 30 Nov 1971 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.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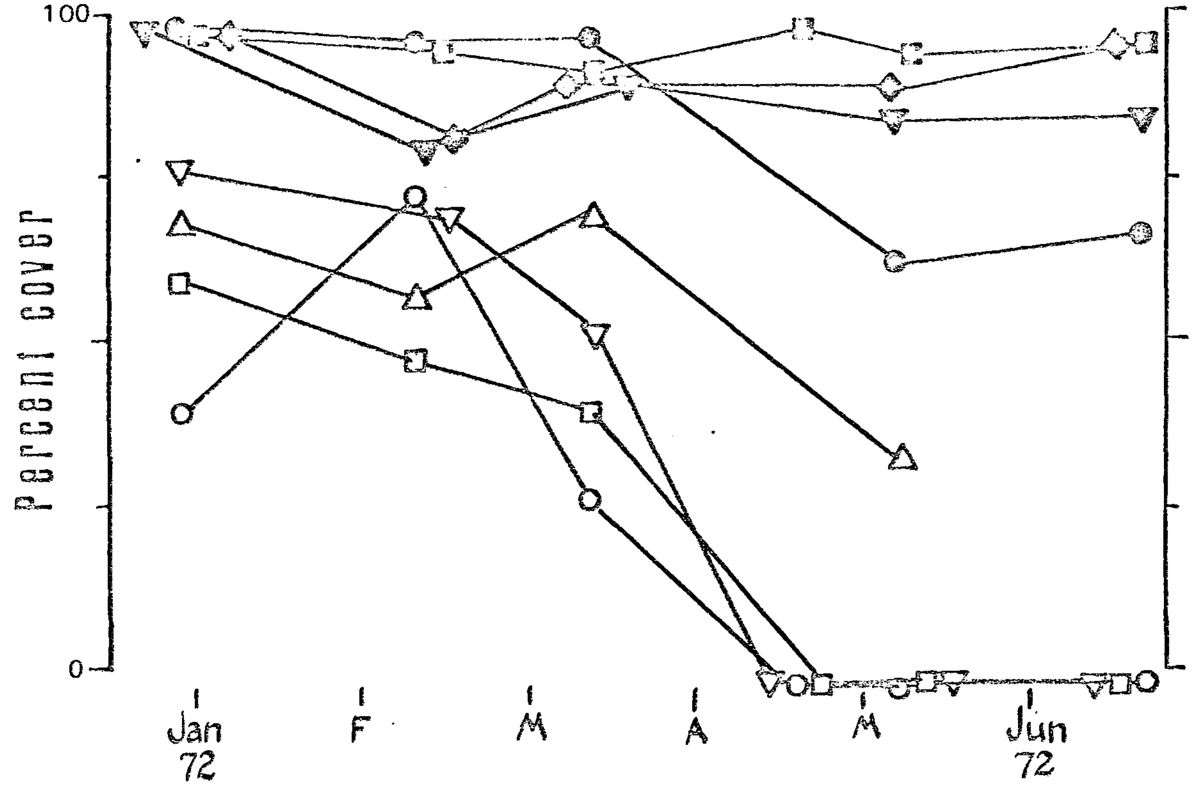
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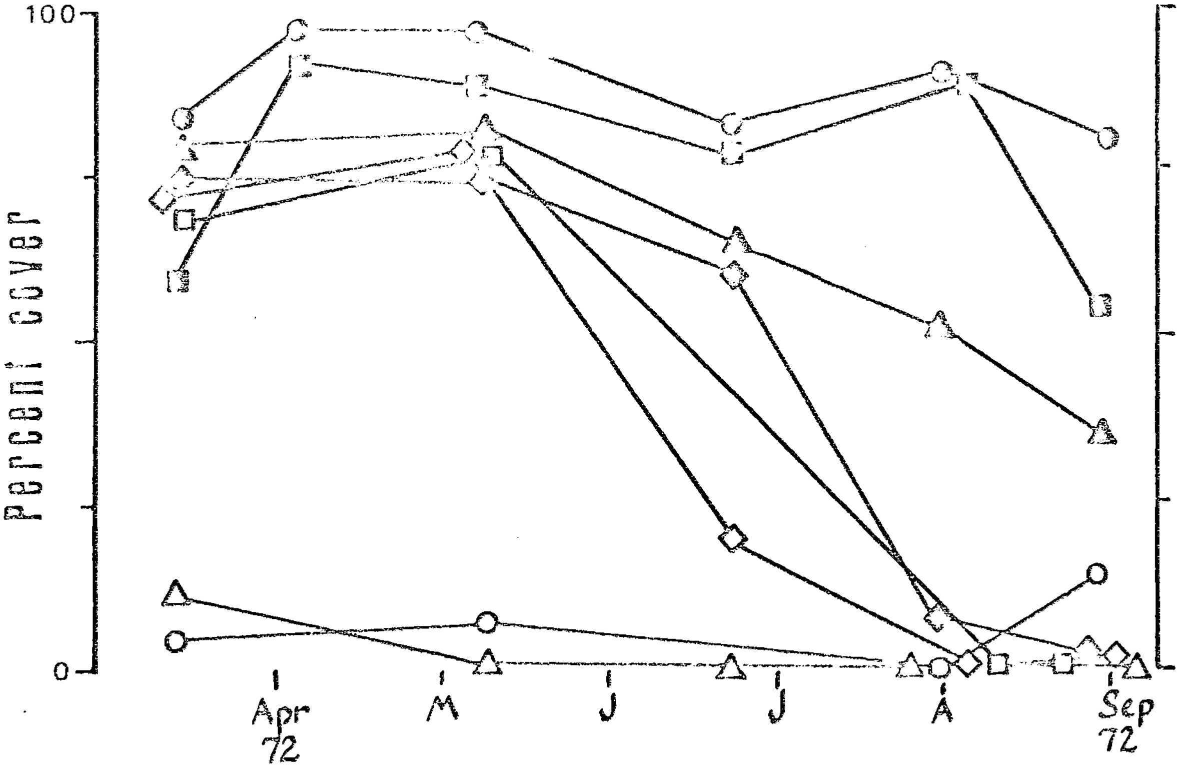
Fig. 17 A. Percent covers of plants only in exclosures and controls started on 25 Feb 1972 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.

Fig. 18 A. Percent covers of plants only in exclosures and controls started on 13 May 1972 at Sunset Bay. Solid symbols are exclosures, open symbols are controls.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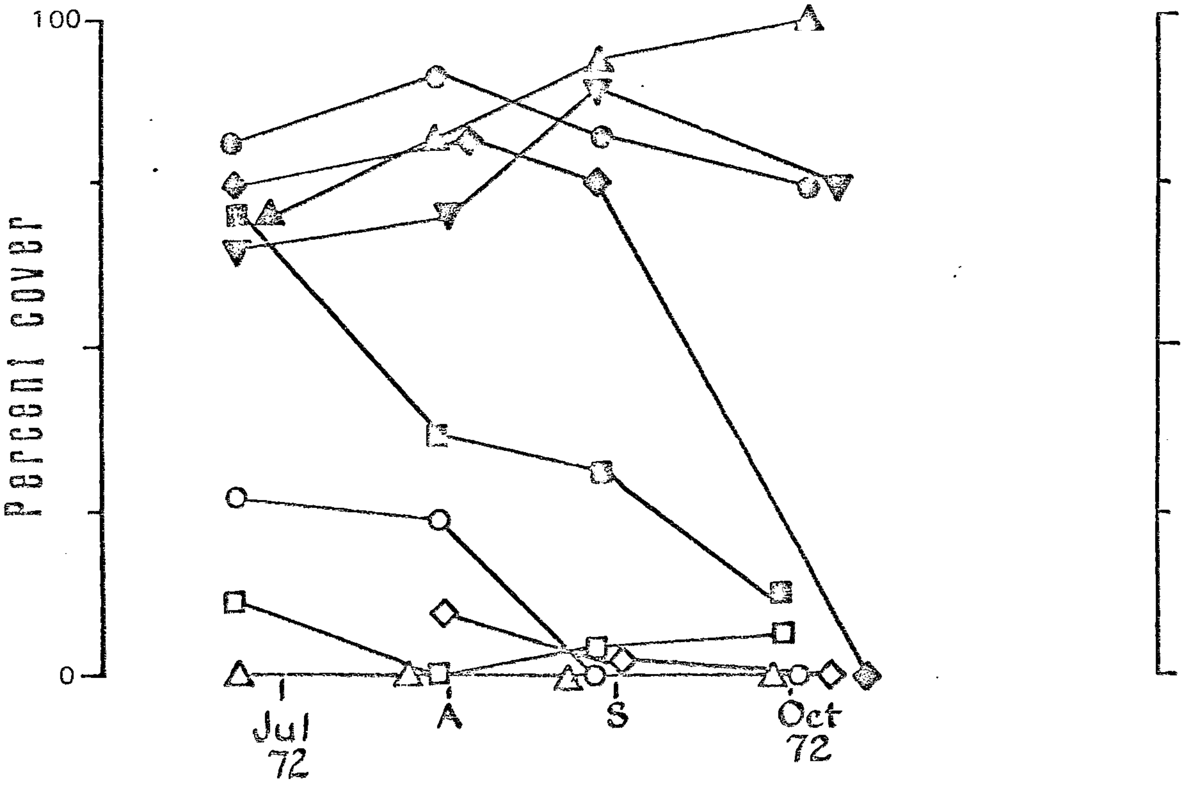
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Percent cover
Jul
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LITERATURE CITED

Aleem, A. A. 1950. Distribution and ecology of British marine littoral diatoms. J. Ecol. 38: 75-106.

Atkins, W. R. G. 1922. The influence upon algal cells of an alteration in the hydrogen ion concentration of sea water. J. Mar. Biol. Assoc. U. K. 12: 789-791.

Awramik, S. M. 1971. Precambrian columnar stromatolite diversity: reflection of metazoan appearance. Science 174: 825-826.

Bartrum, J. A. 1926. Abnormal shore platforms. J. Geol. 34: 793-806.

Behrens, S. 1974. Ecological interactions of three Littorina (Gastropoda, Prosobranchia) along the west coast of North America. PH. D. Dissertation, Univ. of Oregon.

Bellamy, D. J., P. H. Clarke, D. M. John, D. Jones, A. Whittick, T. Darke. 1967. Effects of pollution from the Torrey Canyon on littoral and sublittoral ecosystems. Nature 216: 1170-1173.

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

Breen, P. A. 1972. Seasonal migration and population regulation in the limpet Acmaea (Collisella) digitalis. Veliger 15: 133-141.

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

Christensen, Tyge. 1964. The gross classification of algae. In Algae and man, D. F. Jackson, ed. New York: Plenum Press, pp. 59-64.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42: 710-723.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40: 49-78.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 3: 61-104.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.

Denison, W. C. and G. C. Carroll. 1966. The primitive ascomycete: a new look at an old problem. Mycologia 58: 249-269.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Sci. 38: 209-221.

Doty, M. S. 1947. Part I: Chlorophyta and Phaeophyta. Farlowia 3: 1-65, pls. 1-10.

Edelstein, T., L. C-M. Chen, and J. McLachlan. 1970. The life cycle of Ralfsia clavata and R. borneti. Can. J. Bot. 48: 527-531.

Fjeld, A. 1969. A chromosomal factor exerting a predetermining effect on morphogenesis in the multicellular green alga Ulva mutablis. Genet. Res., Camb. 15: 309-316.

Fjeldmann, J. 1957. Ecology of the marine algae. In Manual of phycology, G. M. Smith, ed., pp. 313-334.

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

Garrett, P. 1970. Phanerozoic stromatolites: noncompetitive ecologic restriction by grazing and burrowing animals. Science 169: 171-173.

Glynn, P. W. 1965. Community composition, structure, and interrelationships in the marine intertidal Endocladia muricata-Balanus glandula association in Monterey Bay, California. Beaufortia 12: 1-198.

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

Hommersand, M. H. and R. Searles. 1971. Bibliography on Rhodophyta. In Selected papers in phycology, J. R. Rosowski and B. C. Parker, eds., pp. 760-767.

Irvine, G. V. 1973. The effect of selective feeding by two species of sea urchins on the structuring of algal communities. Paper given at the 54th annual meeting of the Western Society of Naturalists, University of San Diego, San Diego, Calif. December 27-29, 1973.

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

Jones, N. S. 1948. Observations and experiments on the biology of Patella vulgata at Port St. Mary, Isle of Man. Proc. Trans. Liverpool Biol. Soc. 56: 60-77.

Kitching, J. A. and F. J. Ebling. 1961. The ecology of Lough Ine. XI. The control of algae by Paracentrotus lividus (Echinoidea). J. Anim. Ecol. 30: 373-383.

Kohlmeyer, J. 1973. Spathulosporales, a new order and possible missing link between Laboulbeniales and Pyrenomycetes. Mycologia 65: 614-647.

Lawson, G. W. 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. J. Ecol. 45: 831-860.

Leighton, D. L., L. G. Jones, and W. J. North. 1966. Ecological relationships between giant kelp and sea urchins in Southern California. Proc. 5th Int. Seaweed Symp. E. G. Young and J. L. McLachlan, Ed. Pergammon Press, pp. 141-153.

Leonard, S. D. 1972. The natural history of Paraclunio alaskensis and Paraclunio trilobatus (Diptera, Chironomidae) two intertidal flies. M.A. thesis, Humboldt State College, Arcata, Calif., 49 pp.

Lewis, J. R. 1961. The littoral zone on rocky shores--a biological or physical entity? Oikos 12: 280-289.

Lewis, J. R. 1964. The ecology of rocky shores. London: English Universities Press, 323 pp.

Lodge, S. M. 1948. Algal growth in the absence of Patella on an experimental strip of foreshore Port St. Mary, Isle of Man. Proc. Trans. Liverpool Biol. Soc. 56: 78-85.

Marine Biological Association of the United Kingdom. 1968. "Torrey Canyon" pollution and marine life. J. E. Smith, ed. Cambridge: University Press, 196 pp.

May, V., I. Bennet, and T. E. Thompson. 1970. Herbivore-algal relationships on a coastal rock platform (Cape Banks, N.S.W.) Oecologia 6: 1-14.

Mendenhall, W. 1967. Introduction to probability and statistics. 2nd ed. Belmont, Calif.: Wadsworth.

Morley, R. L. and R. A. Ring. 1972. The intertidal Chironimidae of the British Columbia coast. II. Life history and population dynamics. Can. Ent. 104: 1099-1121.

Mumford, T. F., Jr. 1973. Some observations on the ecology and seasonal occurrence of the species of Porphyra from Washington and British Columbia. Paper given at the 54th annual meeting of the Western Society of Naturalists, University of San Diego, San Diego, Calif. December 27-29, 1973.

Northcraft, R. D. 1948. Marine algal colonization on the Monterey Peninsula, California. Am. J. Bot. 35: 396-404.

O'Sullivan, A. J., and Alison J. Richardson. 1967. The Torrey Canyon disaster and intertidal marine life. Nature 214: 448, 541-542.

Paine, R. T. and R. L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr. 14: 710-719.

Ricketts, E. G., J. Calvin, and J. W. Hedgpeth. 1969. Between Pacific tides. Stanford, Calif.: Stanford Univ. Press, 614 pp.

Saunders, L. G. 1928. Some insects of the Pacific coast of Canada. Entomol. Soc. Amer., Ann. 21: 521-545.

Smith, G. M. 1969. Marine algae of the Monterey peninsula. Stanford, Calif.: Stanford Univ. Press, 752 pp.

Southward, A. J. 1964. Limpet grazing and the control of vegetation on rocky shores. *In* Grazing in terrestrial and marine environments. D. J. Crisp, ed. Oxford: Blackwell pp. 265-273.

Stimson, J. and R. Black. 1974. Field experiments on population regulation in intertidal limpets of the genus *Acmaea*. Submitted to Ecology.

Stocker, O. and Holdheide, W. 1937. Die Assimilation Helgoländer Gezeitenalgen während der Ebbezeit. Z. Botan. 32: 1-59.

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

Sutherland, J. P. 1972. Energetics of high and low populations of the limpet, *Acmaea scabra* (Gould). Ecology 53: 430-437.

Tatewaki, M. 1966. Formation of a crustaceous sporophyte with unilocular sporangia in *Scytosiphon lomentaria*. Phycologia 6: 63-66.

Williams, C. B. 1964. Patterns in the balance of nature. New York: Academic Press.

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

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