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ANTECEDENT EVENT INFLUENCE ON BENTHIC MARINE ALGAL STANDING CROPS IN HAWAII

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Abstract: In non-monsoonal tropical areas, such as Hawaii, the somewhat random effects of storm waves may be the most influential environmental factors regulating the size of the harvestable frondose marine algal crop. Seasonal factors, such as light and temperature, seem to be less important as judged by regression and correlation analysis. With increasing time prior to the measurement of standing crop, the influence of light steadily decreased, that of storm waves increased to within three weeks before the sampling period after which it decreased, while the effect of temperature increased throughout.

INTRODUCTION

Since the time of Kjellman (1878) and Svedelius (1906) there has been little progress in understanding seasonal changes of benthic marine algal standing crops. At the same time it should be noted that in the tropics little has been done either to quantify the variations in standing crop or to relate them through empirical measurements to environmental variables. Insofar as is known little, if any, consideration has been given to the relative importance or the antecedent time aspects of the different possible factors which may influence the harvestable standing crop. While in polar and temperate latitudes seasonality is strongly related to seasonal light and temperature changes, this is less clearly seen in the tropics. In the latter regions it has, however, been related in a qualitative way (Svedelius, 1906) to the seasonally variable monsoons. For the intertidal algal populations of Ghana, Lawson (*e.g.*, 1957) has statistically related the seasonality in density of the intertidal populations to seasonal aspects of the tides.

In general, few algae are found on tropical intertidal shores, due largely to the intense insolation (Biebl, 1962; Krishnamurthy, 1967). Except on shaded and constantly splashed shores, there is so little that it appears that nobody has made the effort to measure it. An exception is Lawson's (1957) work in Ghana. He found higher intertidal densities during the winter months (southern hemisphere); although he refers to the existence of unpublished data of his own, no published studies of tropical standing crops of algae in terms of mass per unit of area have come to the author's attention.

MATERIALS AND METHODS

To be able to describe their variations in Hawaii, the standing crops of frondose algae on the reef flat in front of the War Memorial Natatorium in Waikiki, Honolulu, were measured seven times during the 17-month period of December 1966, through April 1968. Observations were made using 100 or more samples from 45-cm rings thrown in a randomly stratified manner within a rectangular sample area of 240 m from a sea wall to the algal ridge of the reef segment being studied. Wet weights, after a freshwater rinse, were measured and, after drying at about 45 °C, dry weight values were obtained. The results were calculated in terms of the mean weight/m^2 of reef surface. While there were, indeed, slight variations in technique, none of them is thought to have been significant in the final data as reduced to determine the nature of any seasonality and the degree and relative responsibility of light, wave action and temperature as causal factors.

In view of the rate of growth of seaweeds, it appears necessary to search among the weeks antecedent to that of crop measurement for the factors which control its size. In the present study such factors in relation to crop size and environment were sought statistically through use of linear correlation and regression. The correlation and regression values were calculated for crop size against each of the three environmental factors, light, wave size and temperature, separately for each of the six previous weeks and for the week contemporary with the harvest. From the seven sample harvests of the whole 3.36 ha reef area studied, the values used were g/m^2 wet and dry mean weight.

Information on environmental variables was obtained from the U. S. Weather Bureau, the Environmental Science Services Administration and List's (1966) Tables. All were assembled and treated both graphically (Fig. 1) and statistically (Figs 2 and 3).

RESULTS

The wet standing crop averages 2.3 kg/m^2 and varies from 1.3 to 3.1 kg/m^2 (Doty, 1969) over the period investigated. There is an increase in the negative regression of standing crop with light (Fig. 2) as sampling time is approached. Concurrently the correlation with light (Fig. 3) increases. That these changes are real, although with low confidence levels, would seem to be attested by the steadiness of the change in these values as a function of time. Light values recorded at the site were not used due to the vagaries in the record, but, in general, they changed seasonally in the same way as those in List's (1966) Tables which were used.

The negative regression values of wet weight on wave action (Fig. 2) tend to increase for the second through the third antecedent weeks but are low or positive for other periods. Correlations between wave height and wet standing crop (Fig. 3) are closer as the third antecedent week is reached and then decline as one goes further back in time. Although the statistical values do not change as regularly with time, as do those of light, this may be due to the use of observations from Makapuu, which is a few miles away from the harvesting site and has a somewhat

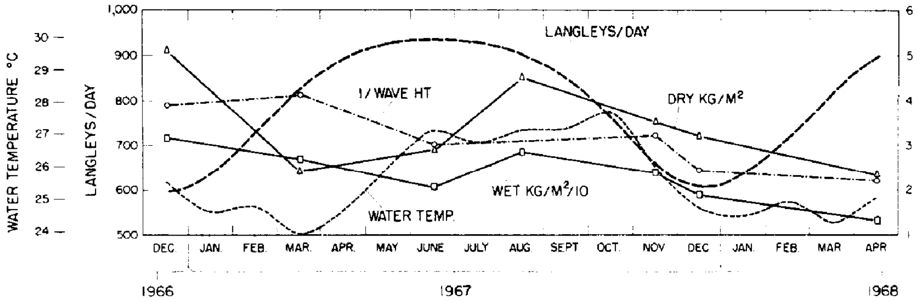
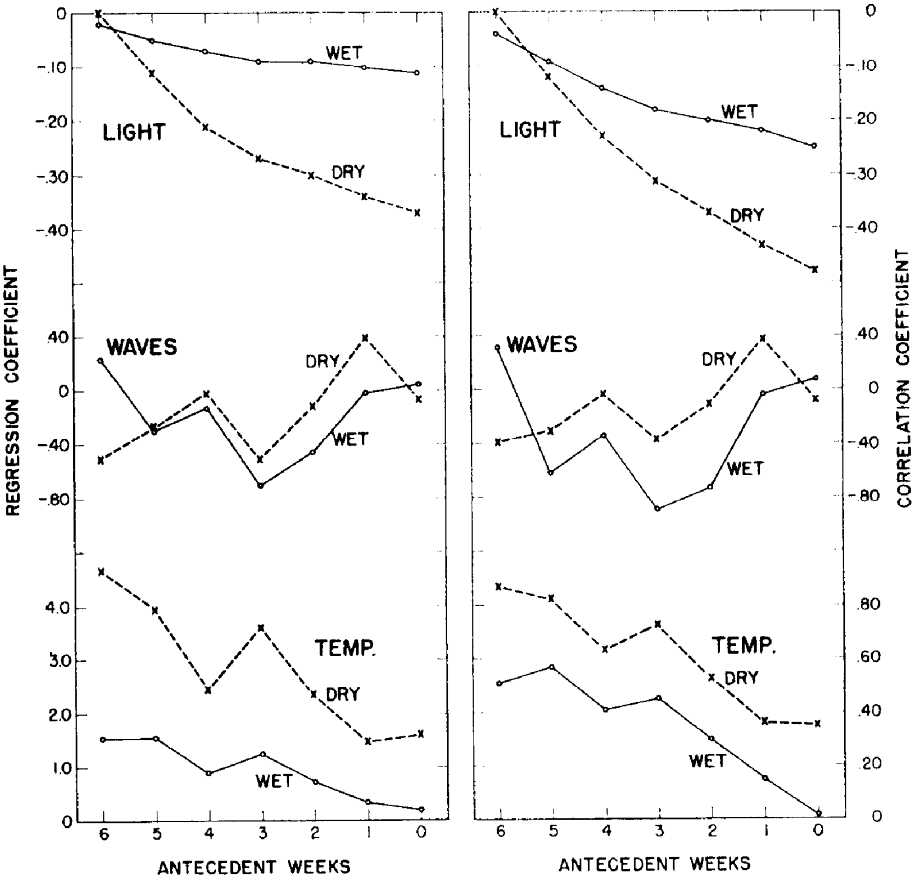


Fig. 1. Time course of frondose benthic algal standing crop and related environmental factors as measured on the reef flat at Waikiki in Honolulu, Hawaii.



Figs. 2, 3. The statistical relationships between environmental factors and the size of the frondose benthic algal crop as they change as a function of time in relation to time antecedent to the crop measurement. The values used in Fig. 1 are those used for calculating regression, Fig. 2 (left), and correlation coefficients, Fig. 3 (right). The week labeled "0" is the week most nearly antecedent to the last day of each of the seven 4- to 5-day measurement periods.

different exposure to the wind. Again, however, there is a general trend indicating a higher effect of waves toward the third antecedent week where the correlation (Fig. 3) is significant at the 1 % level. The wave action to dry weight relationship is, however, quite different. The average correlation with these dry weight values is very low ($r = 0.37$) and so erratic (Fig. 3) as to be not significant.

The relationship with temperature (Figs 2 and 3) is different from that either for light or wave height. Here, the effect of temperature decreases from at least the fifth week. Again the regularity of the changes with time inspires confidence, though the small changes in regressions and the correlations, while significant at the 1 % and 5 % levels for dry weight at the sixth and fifth antecedent weeks respectively, are not impressive by themselves.

Discussion

Little seasonality is apparent (Fig. 1) in the total standing crop, yet seasonal variation exists in light energy and temperature. Something other than these seasonally regular factors would seem, therefore, to dominate control of standing crop size.

It would seem to be natural for the relationship to light to decrease with time as it does. That it is higher in more nearly contemporary time may be thought of as due to its being the factor primarily responsible for producing dry weight. The other two factors acting to reduce the dry matter in this crop must act secondarily and, thus, further back in antecedent time. Accepting the graphs as trend lines for linear relationships, one would predict that light conditions beyond three weeks before the harvest measurement would have less than a 10 % influence on the the dry matter in the standing crop. Since many of the algae concerned produce sizable crops in deeper water beyond the reef, the negative regression here is not surprising.

The inverse relationship between crop size and wave height is not surprising since storm waves destroy the standing crop. It is well known that the beach may bear considerable cast seaweed after a storm. A good correlation between average wave size, observed three weeks before the measurement period, and crop size may indicate the length of time required by the algae to grow tall enough for their crop to be reduced by the average storm: wet weight is the crop measurement of concern here. The fact that a lower correlation exists with dry weight would seem to indicate that the more succulent growth was removed by storms. Perhaps after three weeks, new growth is able to resist the average storm waves more successfully.

The influence of temperature would seem to be yet more remote among the antecedent events. Whereas light promotes the productivity of basic photosynthetic material, it is temperature sensitive processes related to respiration that are most closely related to differentiation, *i.e.*, the conversion of basic materials to new or more photosynthetic tissue. It does seem logical that the dry weight increase in secondary deposition or accumulation would be further back in antecedent time than the production and enlargement of new cells which is a more immediate result of photosynthesis.

It must be noted that for convenience the seven harvest periods were for the most part spring tide periods. This means that during the immediately antecedent weeks there were fewer extreme deviations from mean sea level than during the harvest period. The tidal variation is from a range of 1.7 to 2.9 ft between the highest and lowest tide for any of the weeks involved, and less than 5 % of the area investigated is ever exposed to air, albeit momentarily. No suggestions can be made with respect to the possible effects of lower low water exposure of seaweeds in summer during the sunny parts of the day, or at night during the winter other than to comment that considerable killing of seaweeds by insolation was seen during one of the harvest periods. In addition, during high tides waves run across the reef flat, but they are normally stopped by the reef margin at low tide. If such factors are major and regular influences, they could explain some of the variation in standing crop that cannot now be explained. Meanwhile it appears that tides as seasonal influences have little effect on the standing crop on subtidal reef flats as opposed to their influence on the intertidal tropical populations as Lawson (1957) has demonstrated. The present results are different from those of Lawson since we are dealing with a different habitat and with mass in contrast to population density.

In conclusion one could expect that on other shores there is a chronological separation of the major causal factors determining standing crop of benthic algae. Also, from the general size of the regression values during their variation over antecedent weeks before harvesting, one would predict light and temperature to have less effect than wave action on crop size. It appears that the more random rather than seasonal occurrence of storms is a greater influence on the size of the harvestable standing crop of frondose marine algae in non-monsoonal areas such as Hawaii than are the regular seasonal factors.

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