PIONEER INTERTIDAL POPULATION AND THE RELATED GENERAL VERTICAL DISTRIBUTION OF MARINE ALGAE IN HAWAII [1)]

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On the island of Hawaii lava flows have run down the slopes of the active volcanoes and into the sea in both prehistoric and historic times. The events leading to establishment of their marine algal populations have been followed closely on several 1955 flows [2)] (Fig. 1) with comparative observations being made on nearby prehistoric shores. The nature of the observations made and the major conclusions are reported here for these events, which seem to have been nearly ideal demonstrations of a number of major ecological phenomena. Likewise the opportunity is seized to describe the general vertical distribution pattern of the mature algal communities in this tropical part of the world, something that has not been done previously in this detail.

Without going into the possible tide level relationships of the different apparently dominant species (Fig. 2), generally *Ahnfeltia concinna* (*19682* [3)]) is the highest-growing conspicuous macroscopic alga on a prehistoric steep basalt shore in Hawaii. This species forms a yellow bunchy cover on the rocks with individual fronds often 25 centimeters long. At a distance it reminds one [4)] familiar with North Atlantic coasts of the similarly located yellow-brown stands of *Fucus* or *Pelvetia*. Such horizontally extensive populations with sharply defined upward and downward limits and seen one above the other are called zones. In a place where wave action dominates tidal action, as generally true in Hawaii, there are usually but 3 major intertidal zones. Note the variation in their standing crops with elevation and their often-sharp upper and lower limits in the successive zones as indicated in the 'blown up' part of Figure 3A.

The zone just below the *Ahnfeltia* is generally of about the same width as the *Ahnfeltia* zone itself. It is usually (between the parallel heavy lines in Fig. 2) one of several sorts: merely for the most part black rock; populated with *Ulva fasciata*; populated with *Ralfsia pangoensis* (*13201*) above and the *Ulva* below, or dominated by crustose corallines which seem to be largely *Porolithon onkodes*. Of course there are locations where there are mixtures of all three or other species. *Caulacanthus ustulatus* (*20074*) occurs here, too. Sometimes this zone is subdivided with the rock of the lower part coated with crustose coralline algae, the upper part with non-coralline algae. The corallines low

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2) The area of concern is near 19° 30′ N and 154° 30′ W.

3) Such numbers are the author's collection numbers and appear on the labels of the voucher specimens.

4) Dickie (1876: 454) also mentions this resemblance when writing of the algae collected on the island of Hawaii, at Hilo, by H. N. Moseley on the Challenger Expedition.

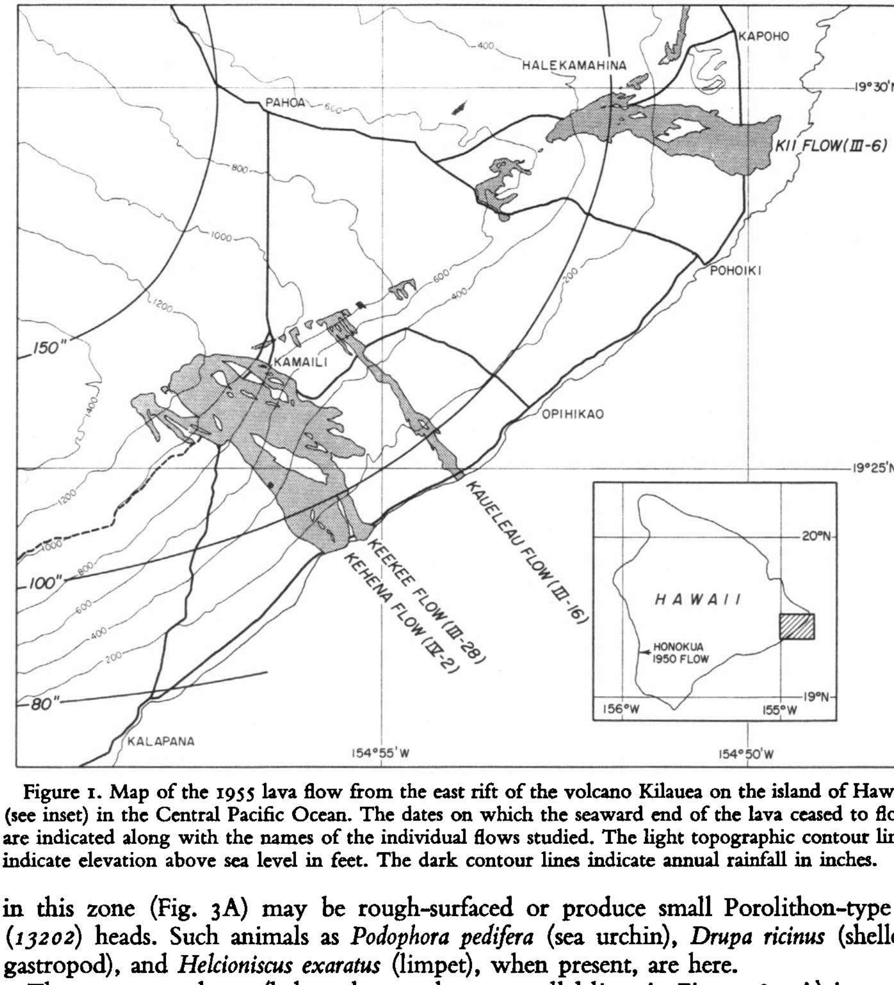


Figure 1. Map of the 1955 lava flow from the east rift of the volcano Kilauea on the island of Hawaii (see inset) in the Central Pacific Ocean. The dates on which the seaward end of the lava ceased to flow are indicated along with the names of the individual flows studied. The light topographic contour lines indicate elevation above sea level in feet. The dark contour lines indicate annual rainfall in inches.

in this zone (Fig. 3A) may be rough-surfaced or produce small Porolithon-type [5]) (*13202*) heads. Such animals as *Podophora pedifera* (sea urchin), *Drupa ricinus* (shelled gastropod), and *Helcioniscus exaratus* (limpet), when present, are here.

The next zone down (below the two heavy parallel lines in Figs. 2 & 3A) is comparatively as broad as or even broader than the two above together. It is underlain by smooth crustose coralline algae, often covered with a *Gelidium* (*13194*) and yet smaller species. At the lowest common level of the waves, the dense *Gelidium* cover rather abruptly terminates. When working on prehistoric shores the abrupt upper limit of this alga (Fig. 3A) provides a convenient level from which to measure vertical distribution; when under water the abrupt lower edge is similarly useful.

About 2 meters below the bottom of the *Gelidium* an algal stubble becomes dominant and is conspicuous for at least 5 meters on down. Conspicuous elements in this stubble are *Dictyota friabilis* (*13199*) and a *Griffithsia* (*13240*) as well as the small algae commonly found in the *Gelidium* communities and especially well developed in pools. *Pocilopora*,

[5]) The only saxicolous melobesioid coralline identified in this environment on the new solid substratum has been *Porolithon onkodes* (Heydrich) Foslie.

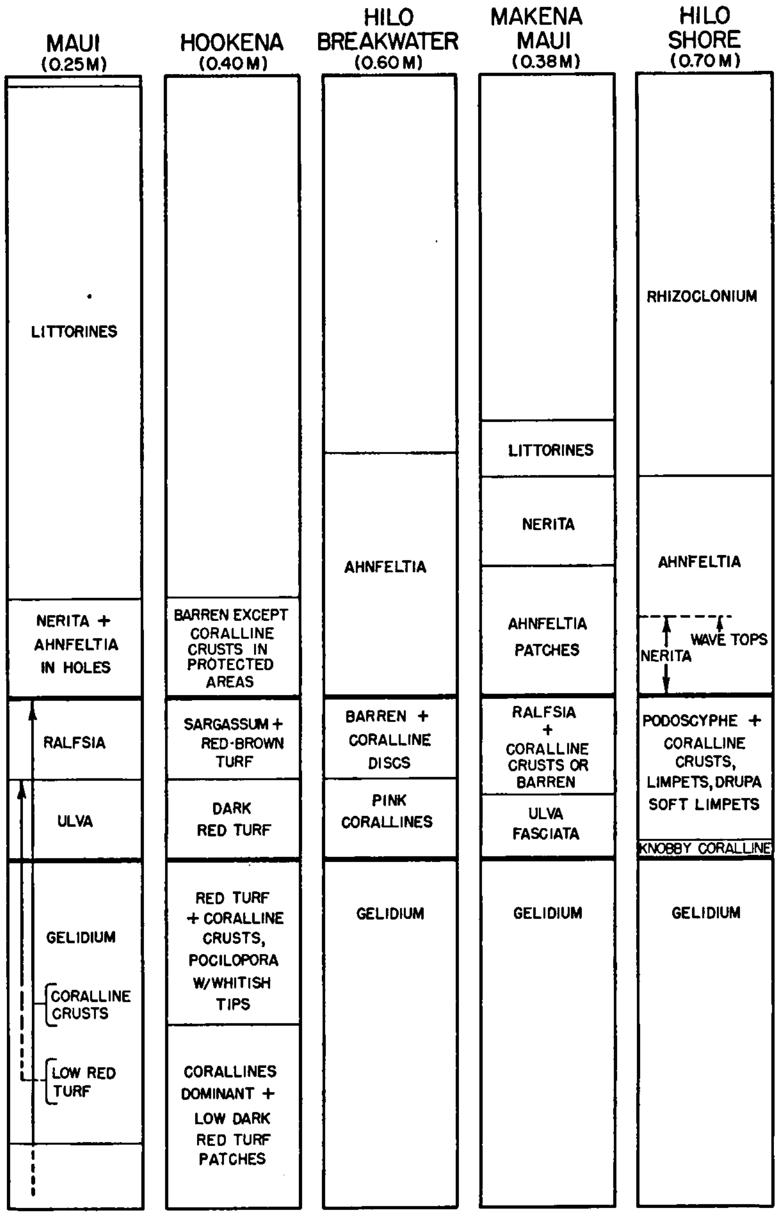
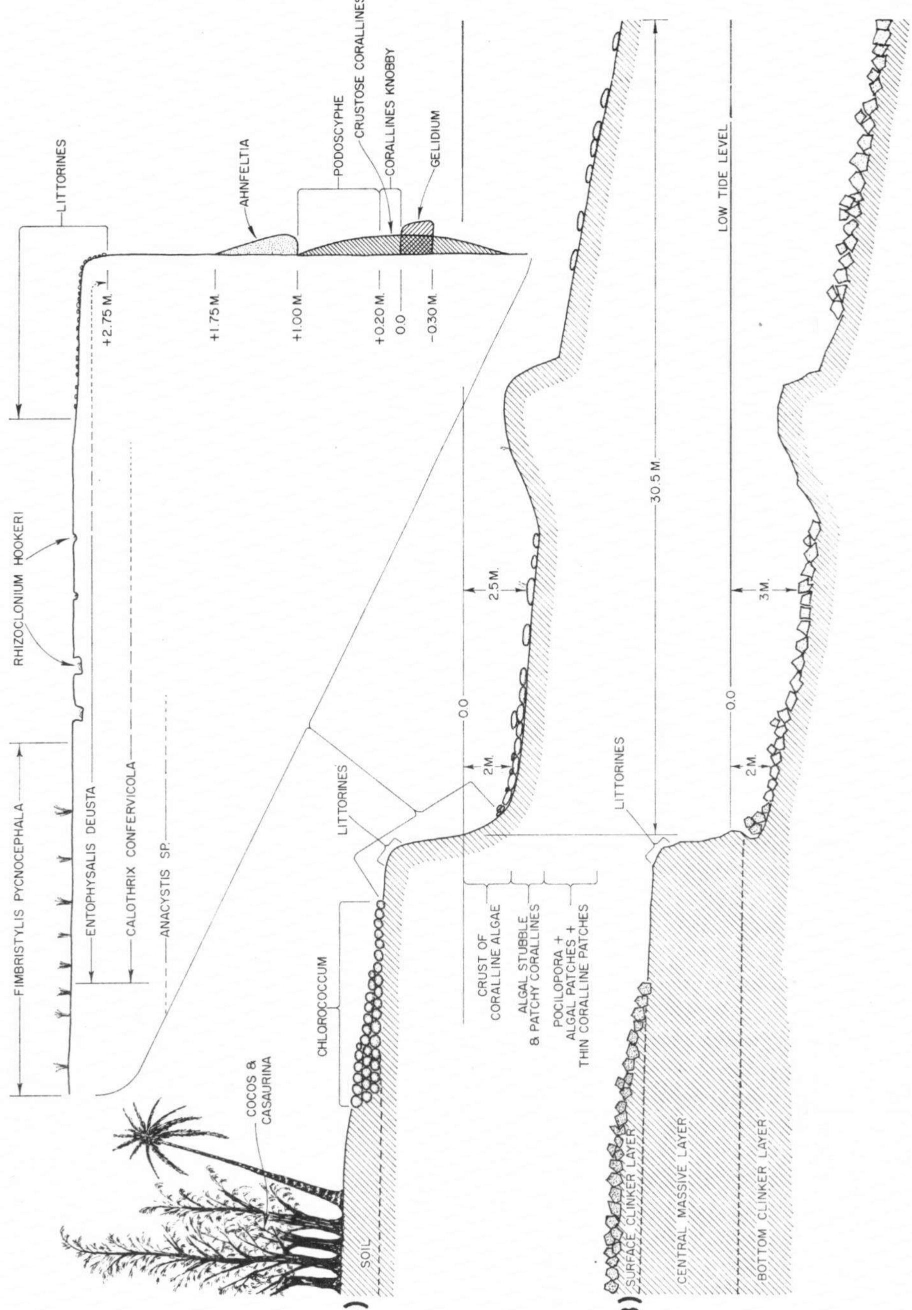


Figure 2. The vertical distribution patterns common to mature Hawaiian shore areas for three places on the island of Hawaii and two places on the nearby island of Maui. The distance in meters given at the top of each strip is the distance between the two horizontal dark lines across it and, thus, provides a scale for that strip. The necessity for different scales in this area where the tidal phenomena are relatively uniform is correlated with differing degrees of wave action.



Caption at foot of facing page.

the only conspicuous coelenterate coral seen, appears regularly at about 3 meters below low tide level with the individual heads perhaps 3 meters apart down to the -8 meter level.

No really sharp limits below the bottom of the *Gelidium* have been observed in Hawaii. From the results of dredging it appears that the algal standing crop may actually increase once depths below those affected by wave action are reached. The crustose corallines extend on below the *Gelidium*-covered zone (Figs. 2 & 3A), often completely covering all consolidated rock surfaces down to a depth of 1 to 1.5 meters below low tide line. They extend much further down (certainly beyond -100 meters) but as a gradually thinner cover, becoming yet thinner and covering the surface less completely as greater depths are reached. Preliminary explorations in a small research submarine to depths of -160 meters and the results from dredging indicate the species are not greatly different from those nearer the surface though some, such as *Codium phasmaticum*, appear to be more abundant in deeper water and others, such as *Codium mammilosum*, are restricted to subtidal levels. In the greatest depths most remaining species are merely more delicate and further apart.

The observations on the 1955 lava where it went into the sea were made not only to provide a record of events but to provide a series of special observations to test certain hypotheses concerning the development of intertidal populations. These hypotheses are, largely, concerned with the separation and distinction of succession and periodicity, the events in zonation, the regulation of climax formation, and classification of the different algae and other organisms according to the part they play in the populating process. Testing, observation, and experimentation elsewhere (Northcraft, 1948; Fahey & Doty, 1949; Fahey, 1953) have been concerned with surfaces such as concrete, old rock, or wood brought to the sea for the first time, denuded surfaces, and (e.g., Williams, 1965) glass slides.

In the intertidal regions of the Hawaiian Islands there are historic lava flows dated from about 1750 down to the present. None of them has quite the same population on it as is to be found on the adjacent, probably much older, undated or prehistoric lava shores. This is a problem for, in studies elsewhere, intertidal observation has led us to expect five or six years for the climax situation to become established. Indeed, perhaps because of the few years involved, some have said that in the case of intertidal populations there was 'direct development' of the mature or climax population. Fahey reviewed (1953) this situation briefly.

The initial hypotheses were that this phenomenon of slow development toward a climax situation was related to the chemical or physical composition of the lava. These hypotheses were unsupported or negated by a few simple experiments and measurements. For example, chunks from recent and old lava flows of different dates, composition, and physical surface were seated in concrete blocks, sometimes enclosed in wooden forms, and exposed in the sea. It was found that the pioneer and secondary populants that did appear during the course of the experiment developed about the same on all surfaces exposed, including the wood and concrete. The chemical, physical, and age differences seemed to have no influence.

Figure 3. Profiles through shores on the island of Hawaii from the levels that are definitely terrestrial to those that are about 6 meters below low tide line. The vertical distributional features of the populations are drawn to scale but not the horizontal and geological details. (A) Represents a mature shore near Hilo with insets to show in greater detail the distributions of various intertidal and near-shore populations. (B) Represents an idealized section through a shore formed by the erosion of a lava flow perhaps one year old as described in the text for the 1955 Kehena and Kaueleau flows.

Chemically the hot lava, being cooled in contact with sea water (Macdonald, 1959) at the Kaueleau site, was not altered. Samples of the water washing the rocks shortly after they had begun to develop algal populations had about the same phosphate content as samples of water from offshore or that washing the prehistoric shores. Again, chemical differences were not found to substantiate the chemical difference hypothesis.

The 1955 lava flows ran into the sea along a shore (Fig. 1) where there was very little sand. Shortly after the flows had cooled, extensive beaches of black sand were seen extending along the shores to the left and right of the new lava flows. Uniform samples of the water washing the intertidal surfaces were taken from near the 1955 flows and from near the much older undated flows. These revealed a measurably larger amount of sand and sediment in the water from the new flow areas. Rigg (1914) and Dawson (1954: 10) both comment on the denuding action of such volcanic pumice and sand on nearby populations. In our case, no such observation of the removal of old nearby populations was made. With time, as determined by successive observation, this sand moved off or away (initially often moving inland) from these first formed beaches. As it has moved away so have the algal populations become established and stable.

Not finding chemical nature or sand erosion a factor, a different hypothesis finally arose after following the populations on these 1955 intertidal lava flow surfaces for some time. This is to the effect that the substratum must be so stabilized that it will remain effectively constant for at least the five or six years we expect it takes a climax population to appear. Here a small dated flow that has not yet worn back to the general coast line does not bear a sere-wise mature population. Surely large flows, like the flow nearby which went into the sea in 1961, will form permanent contour modifications that will be populated with a climax population in some years. The 1750 flow on the island of Maui should be studied in this regard. Erosion of the 1955 lava shores was rapid and, in some cases, several meters of the new lava surface were removed in but a few months. In passing, it may be noted that the Honokua 1950 lava flow (see inset in Fig. 1) at Hookena was so worn back, in late 1955, that in many places the massive basalt face of the prehistoric flow under it was again exposed to the sea and on it was a well established algal population. We note too that the breakwater around the harbor at Hilo thirty odd miles away and which was made of large stones in recent years now bears a more mature population than one would expect if it were a lava flow of similar age and exposure.

Stability of the shore is not restricted to the solid rock of the massive part of a lava flow (Fig. 3). As indicated by the contrast between Figures 3A and 3B, there is a change in the boulders on the euphotic sea bottom with time as well. Not only did the rocks in the sea fronting the Kehena flow become smaller, more closely packed, and more rounded, they also became more completely populated, largely by crustose algae. Early visits to the area were marked by recorded notes of the frequency with which stones were seen thrown by wave action beyond the splash of the water itself. Likewise, moving stones were often seen while skin and SCUBA diving. The author observed stones, adjudged to be of 7 to 12 centimeter dimensions, in the turbulent water at 0.3 to 0.7 meters off the bottom during a period of unusually rough seas while swimming under the larger breaking waves after having been washed off the study area. Observations have not been made in the water at this place under just such conditions during the last few years, but the impression is that the closely packed stones on the bottom are fewer, more uniformly dense, of rounded contour, more mechanically stable in form, and not moving as freely as they did during the first two years of the study. Again, the populations on them developed as the available surfaces became more stable.

In June, 1955, one of the dominant algae on the 1955 lavas was *Liagora maxima* [6]). It was present both on prehistoric lava near the 1955 Keekee flow (*12801*) and on the 1955 Kehena flow (*12802* & *12806*). This alga was much less evident in November (*13032*) and in December, 1955, than it had been earlier in June and August, and by February and March, 1956, none was seen at all. However, in May and in July, 1956, it was again abundant (*13235*). This we regard as an manifestation of seasonal progression or periodicity rather than as pioneer colonization without ecesis.

Our study has been rewarding in connection with observations that bear on the problem of distinguishing seral progression. As illustrated in Figure 4, the first macroscopic populants on the newly cooled lava were fine green filaments later shown to be *Enteromorpha*. Specifically they were not identifiable further than to genus. These populations were very hard to reach consistently for measurement or collection.

A subsequent and more consistent study was possible when portions of the flow surface broke away and disappeared. In these cases, one of which is illustrated as the record B in Figure 4, regardless of time of year or vertical position in the intertidal region, the same *Enteromorpha* appears as a fine, hair-like, rather uniform coating on such 'fresh' surfaces. Certainly this catastrophic phenomenon induces a subclimax in consideration of the whole area, yet on the particular fresh lava surface just exposed the *Enteromorpha* is a pioneer. In time the *Enteromorpha* matures into isolated tufts of mature thalli (*13149*) that may eventually become somewhat brownish with the development of epiphytic diatoms. Then it disappears as succession takes place.

Ectocarpus breviarticulatus (*12798*, *12803*) can be expected to appear (Fig. 4C) shortly after the *Enteromorpha* has appeared and with it but also alone at still higher intertidal levels. This was seen to happen at several sites. While the *Ectocarpus* at first may be diffusely spread over the surfaces, intermixed with the hair-like coating of *Enteromorpha*, it also becomes restricted to small tufts. The tufts become fewer and larger as time goes on. In age the lower tufts of *Ectocarpus* may become intermixed with a *Cladophora*, the tufts of which, other than for color, are quite similar macroscopically.

While the *Ectocarpus*, all the time it remains, is the highest macroscopic alga, a blue-green coating began to appear conspicuously on the rocks above the *Ectocarpus* in December, 1955, six months after the flow had cooled.

The series of events illustrated in Figure 4 was progressive. The blue-green algal population gradually became more dense and could be readily detected in its lower reaches even when dry. At first it was seen as a blue-green sheen only when wet. Concurrently *Littorina pintada* became progressively more abundant. Lower down the same events were true for the high-growing limpet, *Helcioniscus exaratus*. *Ralfsia pangoensis* and the crustose corallines appeared as small spots over a wide vertical range, became larger, tended to completely cover the surface in a smaller vertical range, and became fertile. The corallines often developed erumpent edges where adjacent crusts closed together. The early populants *Ectocarpus*, *Chnoospora minima* (*13102*, *13237*), and the various Chlorophyta were gone by 1958 (Fig. 4K) except on an occasional spot where a chunk of lava had recently broken away.

As time goes on, the pioneers became replaced by other algae and zonation (Fig. 4) became evident and more stable as longer-lived organisms appeared. We have gained the impression that with excessive abrasion during storms, many of the zoned organisms are removed. In fact, so many may be removed irregularly and replaced by pioneers

[6]) The verification of the determination of this species by Dr. Isabella Aiona Abbott is gratefully acknowledged.

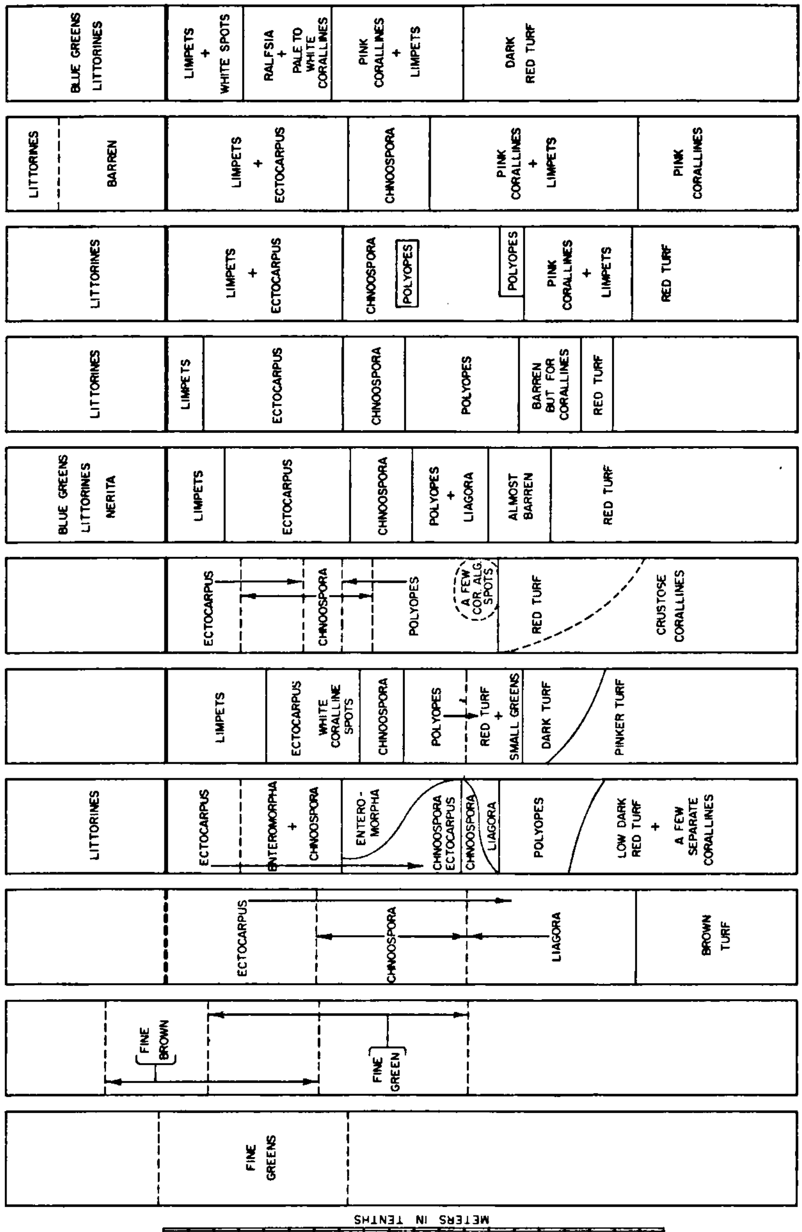


Figure 4. Population changes in time on a vertical 1955 lava surface extruded into the sea and observed as follows: A & C at Kaueleau (respectively), 21-VI-1955 and 15-VIII-1955; and at Kehena (respectively), B, 30-XII-1958; D, 21-XII-1955; E, 24-III-1956; F, 16-V-1956; G, 14-VII-1956; H, 18-VIII-1956; I, 10-XI-1956; J, 20-IV-1957; K, 30-XII-1958. The base line for measurement was the top of the particular population across which on the figure a dark horizontal line is drawn. This corresponded in general with a set of recognizable physical features of the shore but the physical features changed from time to time as erosion took place.

that zonation becomes obscured. It would seem this catastropich process is related to that which holds some areas in a subclimax condition semi-permanently but this is not, e.g., in the case illustrated in Figure 5, a phenomenon peculiar to new lava flows.

The finger-shaped point of rock some 7 meters broad and perhaps 4 meters thick which jutted into the sea some 20 meters and bore the surface repeatedly studied, photographed, and measured to provide most of Figure 4, almost completely disappeared between visits early in 1961. Perhaps this is related in part to removal of the bottom clinker layer (Fig. 3B) and undermining as the depth alongside increased. Even before that time, disclimatic events had disrupted the study and such climax genera as *Sargassum* never did develop there. Of this point there remains only an isolated islet perhaps 2 meters in diameter which is constantly washed over by the waves at high tide. Other sizeable protrusions and seaward faces of the 1955 lava flows were noted to have disappeared between visits. As a result, by 1966 the flow at Kehena was hardly an irregularity in the outline of the shore. Undoubtedly, this rapid wearing back of the flows to the general island contour is a major reason for the lack of bays in this youngest part of Hawaii.

In the series of phenomena observed through 1961, we feel there was demonstrated seral progression as *Sargassum echinocarpum* (*17021*), *S. obtusifolium* (*17022*), and the crustose coralline algae became well established (at Kaueleau, Fig. 1) only during the second year of observation of the 1955 flow surfaces. *Corallina sandwicensis* (*13236*) became present as dense fertile hemispheres at Kehena, as did occasional tufts of an *Alsidium* sp. (*13239*) and *Lophosiphonia villum* (*13233*) at their characteristic high elevations. This seral progression, while it had resulted in populations having some of the more conspicuous algae and animals of the climax situation, had not yet progressed very far either qualitatively or quantitatively. On more protected, less rapidly abraiding, areas and in pools the populations were much more advanced toward the climax situation and the standing crop was higher.

No one has yet been successful in determining the precise quantities of algae on such rough, nearly perpendicular, intertidal shores exposed to the full sweep of the surf as these shores in Hawaii, but simple comparative observations showed that though forms conspicuous in climax populations were present and fertile in 1961, e.g., crustose coralline algae, the cover is still not as dense as it is on prehistoric adjacent shores. Thus one would not say balance between the most advanced undisturbed communities and the environment had been achieved, i.e., a climax situation does not yet exist.

Certain qualities, e.g., the red algal species *Ahnfeltia concinna*, coelenterate corals, and the brown *Ralfsia pangoensis*, were absent during the first year of observation. Of these during the second year small patches of *Ralfsia* appeared. *Ahnfeltia* was first noted at the Kaueleau site in December, 1959, about four and a half years after the surface had cooled. These two qualities have been found sparsely developed on the surfaces of the 1950 Honokua flow (Fig. 1, inset) five years old at the time of observation. By April, 1962, tufts of *Ahnfeltia concinna* 7 to 8 cm tall were conspicuous on the 1955 Kaueleau lava flow study point. This alga, while not forming a band, was quite abundant here though not frequent elsewhere on the 1955 lava. Much of the flow surface inland from the study point had been removed during the seven years. The material removed was largely loose clinker material, but some of the clinkers or chunks of massive lava removed must have weighed at least a metric ton. This removal is slight in comparison to the complete removal of most of the study point at the Kehena site and which event closed the present study.

It can be stated here that the idea of Fahey, Northcraft, and others, that the pioneer organisms, e.g., *Enteromorpha*, *Polysiphonia*, and *Ectocarpus*, may be occasional organisms in climax situations seems to be borne out by our observations. To this group we would add *Cladophora*. *Enteromorpha* after 1961 was restricted to but a few spots on some of the population-wise most advanced surfaces. It appears in abundance, however, as a pioneer coating over any new surface such as is formed when a piece of the flow is broken away by the waves. *Ectocarpus breviarticulatus*, on the other hand, may remain as a rather regularly predictable populant of the highest intertidal regions for a year or more even when, as at Kehena (Fig. 4), it is not being held as on the breakwater at Hilo (Fig. 5)

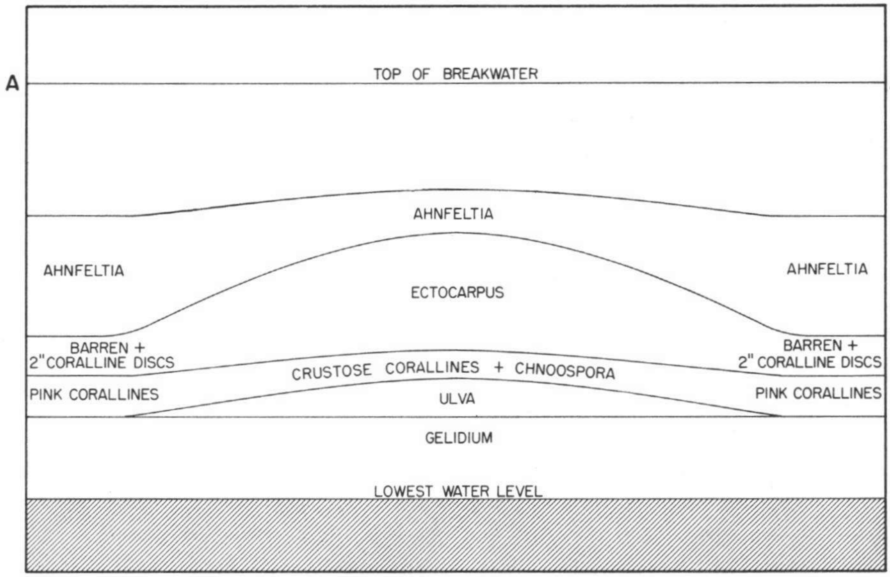


Figure 5. Proportionate diagram of algal vertical distribution on a scoured wave-exposed projecting angle of the breakwater at Hilo, Hawaii, in relation to the adjacent less scoured and less wave-exposed portions of the same breakwater. Scouring is maximal at the center and reduced toward both A and A'.

in a disclimax by scouring. It is much less conspicuous on older surfaces and absent for the most part on prehistoric flows where *Ahnfeltia concinna* is abundant in a position which would seem suitable for this *Ectocarpus* otherwise. It is to be noted that the more permanent crustose colonizers, e.g., *Ralfsia pangoensis* and the crustose corallines, appear as small spots and grow so as to occupy most of the surface. In doing so, they leave less and less space free such as that on which the frondose or short-lived earlier populants grew.

For comparison with the seral state of the Kehena study area, the vertical distribution of the populations (Fig. 2) on two Maui Island and two Hawaii Island prehistoric shores and on the large stable stones of the Hilo breakwater are shown. The Hilo shore sites depicted in Figures 2 and 3A were near each other and of similar exposure and form. The difference may be said to represent the seral development yet necessary before the climax is attained and the differing wave action. As determined elsewhere on artificially denuded or introduced stable surfaces this may require five or six years, but on Hawaiian lava flows it can be expected to require more than ten. Yet an initial remark in this paper, to the effect that the communities on historic flows (say, 100 years old) are generally different from those on adjacent prehistoric flows, would indicate this process, which in its pioneer phases is so quick, may be measured in its later phases in terms of a few centuries as in the case of terrestrial communities.

SUMMARY

The populations of the seaward intertidal ends of the 1955 lava flows in Hawaii were studied during the first few years of their development. Different seral phenomena were recognized such as pioneer colonization, succession, disclimax, and subclimax. The term climax is used as a practical term to denote existence of an equilibrium between the populations and the environment. Appearance of the climax situation seems to be related to stability of the substratum for a period at least as long as six to ten years, but even populations on surfaces as old as 100 years are different from some that are on adjacent prehistoric surfaces.

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