THE ECOLOGY OF AN HAWAIIAN CORAL REEF

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INTRODUCTION

Whatever may have been the origin of a living coral reef it is not to be assumed that its formative period has been one of constant and progressive activity. Corals and other organisms inhabiting a reef may, at times, experience conditions facilitating rapid development and again be subjected to influences resulting in retardation of growth and partial or complete destruction. Power of adaptation, sometimes extending to wide ranges of physical and chemical changes, is especially necessary in the life of such organisms as coral colonies if they are capable of successfully maintaining themselves. Failure of adjustment to an environment which is constantly changing soon results in the extermination of fixed forms and, in time, in the depopulation of a coral reef.

Under stress of unusual natural phenomena the destruction or near destruction of living organisms inhabiting large areas of a coral reef may occur through a long period of time, or with sudden devastation. Raised reefs, typical of many islands of the Pacific, whether due to slow or rapid physical changes, represent the total extermination of corals and other organisms once thriving on a submerged platform. Guppy (10)[1] refers to the welling up of "dark water" which destroyed corals and other organisms over an area of about one-half the lagoon of Cocos-Keeling Island in 1876. Mayor[2] (16) reports the near extermination of corals on the reefs off the harbor of Suva, Fiji, in two years' time due to the action of fresh water, silt, and sewage. The same observer, in 1920, noted that thousands of coral colonies were killed on the Samoan reefs as a result of a heavy rainfall which occurred during an exceptionally low tide. The destructive action of hurricanes and typhoons on coral reefs has been observed on the Great Barrier Reef and elsewhere in the Pacific. Wake Island is a good example of the effect of forces of this nature. Especially along the south and southwest shores of this island the outer edge of the reef platform has, in many

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[1] Numbers in parentheses following proper names refer to literature cited at the end of the paper.

[2] In 1918 Dr. A. G. Mayer changed the spelling of his name to Mayor. Both names as they occur in this paper refer to the same contributor.

places, been torn to pieces and huge blocks of coral have been carried far up on the land area. There are evidences that the sea has, in times past, swept entirely over the island with terrific force.

Besides these unusual conditions to which they may be occasionally subjected, shallow water corals are constantly required to adapt themselves to the changing chemical composition of the sea water which surrounds them; to seasonal and daily variations of temperature and light intensity; and to wave and tidal activities. Reef-forming corals are, furthermore, continuously competing with and submitting to the ravages of numerous organisms such as algae, sponges, worms, bryozoans, and mollusks, some of which are recognized as responsible agents of coral destruction.

That environmental conditions on many sections of the Hawaiian reefs are unfavorable to the vigorous growth of corals is evident. When compared with more tropical localities in the South Pacific or even with Palmyra and Wake islands in the North Pacific, the inferior development of shallow water corals about the Hawaiian islands is especially noticeable.

Dana (7) attributed the flourishing growth of reef-forming corals within the torrid zone to the favorable temperature. His view was that the waters of the Hawaiian reefs, situated in a sub-torrid locality, represent an environment less advantageous to the development of shallow water corals than do the slightly warmer waters of regions in closer proximity to the equator.

On the reefs which largely surround the island of Oahu the variability in the distribution and growth of corals is a noticeable feature. While the species and varieties of corals are approximately identical and equal in number on the windward and leeward sides of the island, they are represented by larger, more numerous, and more vigorous colonies on the northern or windward side. Kaneohe Bay, on the windward coast, is recognized as one of the most favorable localities for the development of shallow water corals. Nearly all the reef-forming genera known in the Hawaiian islands are represented in certain areas of this bay and many species grow luxuriantly. At other localities along the windward coast of Oahu, such as Kaaawa, Kahana Bay, Punaluu, and Kawela Bay, the reefs are populated by thrifty colonies of such genera as *Porites, Pocillopora, Montipora, Pavona, Favia,* and *Leptastrea.* Although, for the most part, the same species of corals occur on the leeward shores of Oahu, they are more stunted in growth and there is a more general paucity of the massive forms of *Porites,* which are recognized as important reef builders.

In the development of corals, striking differences may be noted not only between localities separated geographically and ecologically, but also within a small section of any reef platform supporting living corals. In a general way, species are selective in the choice of their habitats. Some species

in the distribution and growth of corals is a noticeable feature. While the

thrive best near the outer edge of the reef, others approach the shore line, still others are apparently adapted to conditions in the middle areas. Some species are about equally distributed over large areas from near the shore to the outer reaches of the reef platform.

For such a fixed form as a coral colony, the boundaries of the habitat in which it develops and grows to maturity are the maximum and minimum limits of endurance which the organism in the performance of its natural functions presents to the combined factors composing its environment. It may be assumed that the physiological responses of living organisms to physical and chemical stimuli which reach them through the medium of the surrounding ocean water are determining factors in the growth and distribution of corals throughout any given section of a reef.

Vaughan (26) has outlined environmental conditions considered favorable to vigorous coral growth as follows: depth of water, down to about 45 m.; firm bottom with no silty deposits; good circulation of water; good food supply; strong light; minimum annual temperature not below 18°C.; salinity between about 27 and 38 per cent.

No portion of the Waikiki reef platform on which my observations have been made is covered even during a very high tide by more than approximately 10 feet of water. Much silt and shifting bottom material characterizes the Hawaiian reefs. The circulation of water on Waikiki reef may be considered good on the seaward half of the platform. During low tides, however, the near shore water may, for periods of an hour or two, undergo but slight circulation. The food supply for corals on Waikiki reef is apparently variable. Daily catches with a tow net throughout a year, on the surface about 150 feet from the shore, showed a rich animal plankton on some days while on other days the hauls were practically free from minute animal organisms. Conditions of sunlight, temperature, and salinity may be considered favorable to the vigorous growth of corals over a considerable area of the Hawaiian reefs, including most of the Waikiki section.

Besides the living coral colonies, among the general characteristics of an Hawaiian reef may be mentioned an abundance of nullipores, or lime-secreting algae, which usually have a wide range over the reef platform. A large amount of debris is also a common feature of most sections of Hawaiian reefs. This debris, consisting chiefly of fragments of nullipores and dead coral colonies pited and eroded by the action of worms, echinoderms, mollusks, and other agencies, is scattered about over the reef and gradually washed shoreward or slowly covered by sand and silt. Species of red, brown and green soft algae are plentiful on most Hawaiian reefs. Although for the most part small, these algae are responsible to a very large degree for the destruction of coral colonies. Few species of corals are able to

but slight circulation. The food supply for corals on Waikiki reef is ap-

long resist both internal and external attacks of algae. Especially are species of *Porites* readily smothered by external growths of red and brown algae, and rarely on the Hawaiian reefs are members of this genus free from attacks of forms of filamentous boring algae. In certain sections of Hawaiian reefs, the outer edge of the platform is raised above the level of the inshore areas and, therefore, exposed at low tides. This elevated reef edge, or lithothamnium ridge as it is sometimes called, is composed of rocks of coral formation usually coated by lime-secreting algae. Deep caverns have been eroded between these irregular elevated platforms making an approach to the edge of the reef somewhat hazardous even when the surf is not breaking over the exposed surface.

Although the Hawaiian reefs are populated by corals having Indo-Pacific affinities, they are also characterized by an apparent total absence of members of the genus *Acropora* which is widely distributed through the South Pacific and is well represented in the North Pacific at Wake Island and also at Johnston Island, 750 miles from Oahu. On Hawaiian reefs few alcyonarians are to be found and no hydroid corals such as *Millepora* and *Stylaster* have been reported although they exist at Johnston Island. In order to account for the absence of certain species of coral in Hawaiian waters, Vaughan (21) has suggested that possibly the larvae of some corals cannot be transported long distances.

According to Vaughan, 14 genera of madreporarian corals are recognized about the Hawaiian islands down to a depth of 25 fathoms. Of these the following are more or less common representatives of the reef platform from the shore line to its outer edge: *Porites, Pocillopora, Montipora, Cyphastrea, Pavona, Leptastrea, Favia, Stephanaria, Fungia,* and *Dendrophyllia.*

In order to make some specific contributions to the general ecology of Hawaiian shallow water corals and, if possible, to correlate the local distribution of corals with their comparative resistance to certain important environmental factors, the investigation reported in this paper was undertaken.

To a considerable extent my experiments have paralleled the ecological studies of reefs and shoal water corals conducted by Vaughan and Mayer at the Dry Tortugas and the Bahamas, and by Mayer at Murray Island and Samoa. Therefore, at least some comparisons can be made between results obtained in Hawaii and those obtained at other localities both in the Atlantic and the Pacific.

As a basis for intensive ecological study of Hawaiian corals a section of Waikiki reef on the south shore of Oahu was selected. This section, which may be considered a typical one for leeward Oahu, is very conveniently located with reference to the Marine Biological Laboratory of

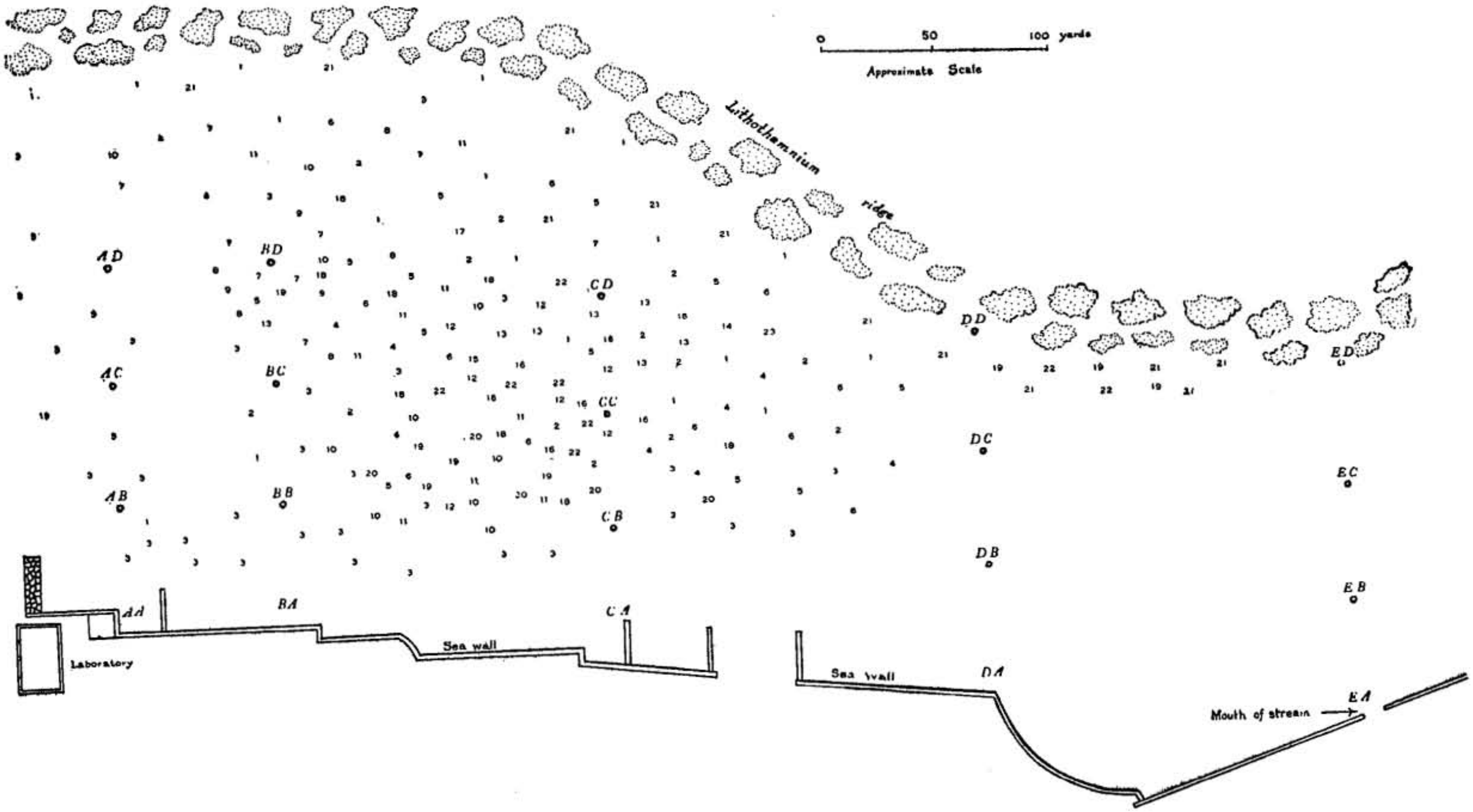

FIGURE 1.—Map of a section of Wakiki Beach showing general distribution of corals. AA, AB, and other paired letters indicate stations of observation. The numbers show the location of the species of corals as follows: 1, *Pocillopora meandrina* var. *nobilis* Verrill; 2, *Pocillopora ligulata* Dana; 3, *Pocillopora cespitosa* Dana; 4, *Porites evermanni* Vaughan; 5, *Porites lobata* f. *lacera* Vaughan; 6, *Porites lobata* f. *infundibulum* Vaughan; 7, *Porites lobata* f. *centralis* s. f. *alpha* Vaughan; 8, *Porites lobata* f. *centralis* s. f. *beta* Vaughan; 9, *Porites lobata* f. *centralis* s. f. *gamma* Vaughan; 10, *Porites compressa* f. *granimurata* Vaughan; 11, *Porites compressa* f. *angustisepta* Vaughan; 12, *Montipora verrucosa* (Lamarck); 13, *Montipora flabellata* Studer; 14, *Montipora patula* Verrill; 15, *Montipora verrilli* Vaughan; 16, *Pavona varians* Verrill; 17, *Pavona duerdeni* Vaughan; 18, *Cyphastrea ocellina* (Dana); 19, *Stephanaria stellata* Verrill; 20, *Stephanaria brighami* Vaughan; 21, *Favia hawaiiensis* Vaughan; 22, *Leptastrea agassizi* Vaughan; 23, *Fungia scutaria* Lamarck.

the University of Hawaii where most of the experimental work recorded in this paper was carried on.

The southern (southeastern) boundary of the section of the reef covered by the survey is a straight line extending from the laboratory to the edge of the reef, and its northern (northwestern) limit is a line joining the reef with the coast at a point near the mouth of the small stream that flows into the ocean at the boundary of Kapiolani Park. The land side of the reef is protected by a sea wall which, with the exception of one short break, extends the entire length of the section—approximately 600 yards. The average width of the reef platform in this area is about 250 yards, being widest at the southern boundary. The reef platform on its outer side is limited by a lithothamnium ridge, the disconnected portions of which are exposed for several hours during a moderately low tide. (See map, fig. 1.) Previous to the construction of the Waikiki drainage canal (about three years ago), the small stream opening near the northern boundary of this section of the reef drained a large area extending to the upper limits of Manoa Valley. During periods of heavy rainfall, usually in the winter months, it carried immense volumes of silt-laden fresh water outward over the reef platform. At such times the turbidity of the water over the section of reef surveyed reached a high degree, a week or more being required for the water to regain normal clearness. Since the opening of the Waikiki drainage canal, however, most of the run off from Manoa Valley enters the larger channel which has its outlet about a mile north of the laboratory. The small stream which previously carried large amounts of fresh water over the reef, now discharges but little water and its influence on organisms in the vicinity of its mouth is accordingly much less.

Twenty-three species, varieties, and forms of corals inhabiting the section of Waikiki reef shown in figure 1, were made the basis of the experimental work. This number probably does not include all the forms in the section surveyed but was considered sufficient for the comparative studies undertaken. A large proportion of the twenty-three species, varieties and forms are well represented on Waikiki reef. But only one colony of each of the following species was studied in the section of reef under consideration: *Pavona duerdeni* Vaughan, *Montipora verrilli* Vaughan, *Montipora patula* Verrill, and only a small group of *Fungia scutaria* Lamarck.

In constructing the map (fig. 1) no attempt was made to represent the total number of colonies but rather to indicate the range of distribution and the dominant locality of a species.

For convenience in the presentation of data, varieties and forms are considered on a par with and are frequently referred to as species.

over the section of reef surveyed reached a high degree, a week or more

RESPONSE OF CORALS TO TEMPERATURE

NATURAL ECOLOGICAL CONDITIONS

The effect of temperature on the metabolism and behavior of organisms and its importance as a factor in regulating their distribution have long been subjects of investigation. In recent years the attention of many workers has been focused upon the analysis and evaluation of the various stimuli comprising the environment of aquatic animals both in fresh water and in the sea. Among these stimuli temperature is recognized as very important.

Mayer (12) compared the responses to temperature of various marine animals inhabiting cold waters with those of warmer seas and emphasized the fact that animals of tropical waters are commonly living within 5°C. of their optimum temperature and usually within from 10°C. to 15°C. of their upper death temperature. Brues (3) has shown that the slight range is applicable to fresh water organisms normally enduring high temperatures. He found most of the animal forms in the thermal springs of Yellowstone National Park living at temperatures of 40°C. to 42°C. or precariously near their maximum temperature endurance. Orton (18) cites correlations between the temperature of sea water and the spawning seasons of marine animals and concludes that thermal conditions are of primary influence in the distribution of these forms. Nelson (17) has pointed out a very definite relation between the temperature of water and the rate of spawning of oysters on the New Jersey coast, and Chidester (5) has expressed the opinion that variations in temperature are more powerful factors in the behavior of fish than are variations in salinity.

It was concluded by Mayer (15) that, in general, the responses of different species of corals to temperature are correlated with their habitats on the reef platform. This investigator also pointed out that natural selection has apparently not operated in such a manner as to render corals of a tropical reef, such as Murray Island, more resistant to high temperatures than corresponding genera of the sub-tropical Florida reefs. Nor do the reef-forming corals of the Florida region resist low temperatures better than those of a more tropical locality.

The investigations relative to the responses of Hawaiian corals to thermal stimuli were carried on with a view of determining the comparative resistance of the Hawaiian species to varying degrees of temperature; to correlate, if possible, such responses with the habitats of the species on the reef; and to determine the range of temperature within which each species is capable of feeding.

Thermal limitations of feeding responses represent critical temperatures and are very important in the life of such organisms as coral colonies. If the temperature of the sea water were increased or decreased to such an extent that the feeding responses of the coral polyps were inhibited for a sufficient period, the animals would die of starvation, if not as a result of the changed thermal conditions.

The range of temperature to which Hawaiian corals are normally subjected is not a wide one. On Waikiki reef the annual extreme variation of the sea water is approximately 10°C.

Table 1 is a condensed record of the diurnal temperatures of the surface water of Waikiki reef. The readings were taken on an average about 28 times a month, but in the table only the maximum and minimum temperatures for each month are indicated.

It should be remembered that the afternoon temperatures of the surface water on a reef are higher than those of the morning on account of the accumulated solar heat which is released by the water during the night.

TABLE 1. MAXIMUM AND MINIMUM TEMPERATURES OF SURFACE WATER ON WAIKIKI REEF, FEBRUARY 1, 1921-JANUARY 31, 1922.

The temperatures recorded for each month are the highest and lowest of daily readings between 8 a. m. and 8 p. m., 100 feet from the shore nearest station AB. (See fig. 1.)

Month 1921	Highest temp. °C.	Day of Month	Hour	Lowest temp. °C.	Day of Month	Hour
Feb.	25.2	25	1:30 p.m.	22.1	2	2:15 p.m.
Mar.	26.6	17	2 p.m.	23.4	10	2 p.m.
Apr.	27.3	18	1:30 p.m.	23.5	10	2:30 p.m.
May	26.7	19	1:45 p.m.	23.5	24	8 p.m.
June	27.7	12	1:30 p.m.	25.6	3	12:15 p.m.
July	28	28	12:30 p.m.	25.9	5	9:45 a.m.
Aug.	28.4	25	12:15 p.m.	25.4	2	9 a.m.
Sept.	29	13	2:30 p.m.	25.9	5	9:30 a.m.
Oct.	28	19	3:45 p.m.	24.7	31	8:30 a.m.
Nov.	27	18	5 p.m.	23.5	12	9:30 a.m.
Dec.	26	2	5 p.m.	22	27	4:30 p.m.
1922						
Jan.	25	17	3 p.m.	21.5	13	9 a.m.

ON WAIKIKI REEF, FEBRUARY 1, 1921-JANUARY 31, 1922

For this reason the minimum temperatures recorded in Table 1 for the months of February, March, April, May, June, and December are two or three degrees higher than a reading earlier in the day would have indicated. Afternoon readings only were taken during those months. It is obvious, however, that approximately 10°C. may represent the variation between maximum and minimum temperatures of the surface water of Waikiki reef 100 feet from the shore, during a given year.

Although the annual temperature of the water on Waikiki reef at 100 feet from the shore may range through 10°C. the extreme variation experienced by a large proportion of the corals is much less. Few species of corals exist on the section of reef surveyed within 100 feet of the shore line. Most of them are beyond the 150 foot line and as the water deepens from the shore toward the outer edge of the reef the extreme variations of temperature both diurnal and annual become less marked. Therefore, most of the corals of this section of reef are living under fairly constant thermal conditions. A few species, however, approach the shore quite closely: *Pocillopora cespitosa* was found within 40 feet of the shore; *Stephanaria stellata,* within 60 feet; and *Montipora verrucosa* and *Porites compressa* forma *centralis* subforma *granimurata,* about 80 feet from the shore. During an extremely low tide the species which exist near the shore line, although never wholly exposed to the air, are covered by but a few inches of water. When low tides occur at night these coral colonies are subjected to a minimum temperature but when low water occurs in the late afternoon they must endure, during the summer months, a temperature which approaches or even slightly exceeds 30°C.

Records of variation in the temperature of the sea water from the shore line outward toward the edge of the reef were taken at intervals during the year 1925. Stations BA, BB, BC, and BD (fig. 1) were used as points of comparison. As shown in Table 2, the temperature of the sea water at an early morning low tide usually increases from the shore outward, while the reverse is true when low tide occurs about noon or during the afternoon. A variation amounting to as much as 5°C. may at times exist between the temperatures of stations BA and BD.

The salt water circulation of the Marine Biological Laboratory is a part of the general system used by the aquarium. An automatically controlled pump draws the water through the intake which is about 30 feet from the shore and forces it into a large wooden tank from which source the aquarium and laboratory are independently supplied by gravity. That the salt water circulated through the laboratory is not deleterious to the life of corals is shown by the fact that planulae in it readily develop, become fixed, and grow into colonies, and that adult colonies live continuously if the circulation is properly adjusted. The temperature of the laboratory salt

TABLE 2. TEMPERATURE OF SEA WATER ON WAIKIKI REEF, AT LOW TIDE, FROM SHORE LINE TOWARD EDGE OF REEF.

Based on readings at intervals during 1925. Temperature records in °C. Stations as in figure 1.

		Stations			
Date 1925	Hour	BA	BB	BC	BD
Jan. 17	2:30 p. m.	26.3°	25.8°	24.5°	24.5°
Jan. 21	8:30 a. m.	22.3°	22.7°	22.9°	23.4°
Feb. 27	12 m.	30.4°	26.5°	26.3°	25.3°
Feb. 28	3:30 p. m.	29.1°	26. °	25.9°	25.3°
Mar. 23	8:15 a. m.	24.5°	24.°	23.9°	23.9°
Apr. 19	7:30 a. m.	21.7°	22.8°	22.8°	23.°
May 11	11:30 a. m.	28.5°	24.9°	24.5°	24.°
July 4	6:30 a. m.	23.°	24.°	24.6°	24.7°
July 18	7:30 a. m.	25.°	25.9°	26.°	25.9°
Aug. 17	8 a. m.	24.°	24.7°	25.2°	25.7°
Sept. 2	8:30 a. m.	24.3°	24.8°	25.4°	25.7°
Nov. 18	1 p. m.	26.5°	25.6°	25.5°	25.4°
Nov. 21	2:30 p. m.	26.1°	25.7°	25.7°	25.6°
Nov. 27	8:30 a. m.	22.2°	22.9°	23.2°	23.5°
Dec. 5	2:30 p. m.	27.5°	26.°	25.7°	25.5°
Dec. 17	12 m.	26.1°	25.2°	25.1°	25.1°
Dec. 28	9 a. m.	23.2°	23.8°	23.8°	23.9°

water, owing to its passage through about 350 feet of iron pipe in addition to the supply tank, is, during the late morning and afternoon, cooler than that of the near short water of the reef. This variation on a warm afternoon may reach 4°C. During the night and early morning, however, the temperature of the laboratory water and that of the reef near the shore approach equality.

Records taken throughout the year 1925 indicate that during the day the salt water of the laboratory varies in temperature but slightly from that of the surface water on the reef between stations BC and BD, from 300 to 450 feet from the shore, which is a zone of good coral growth for this section of the reef. (See fig. 2.) The highest and lowest temperatures of the laboratory water are recorded in Table 3. In order to determine the thermal variation of the laboratory water during the night as well as

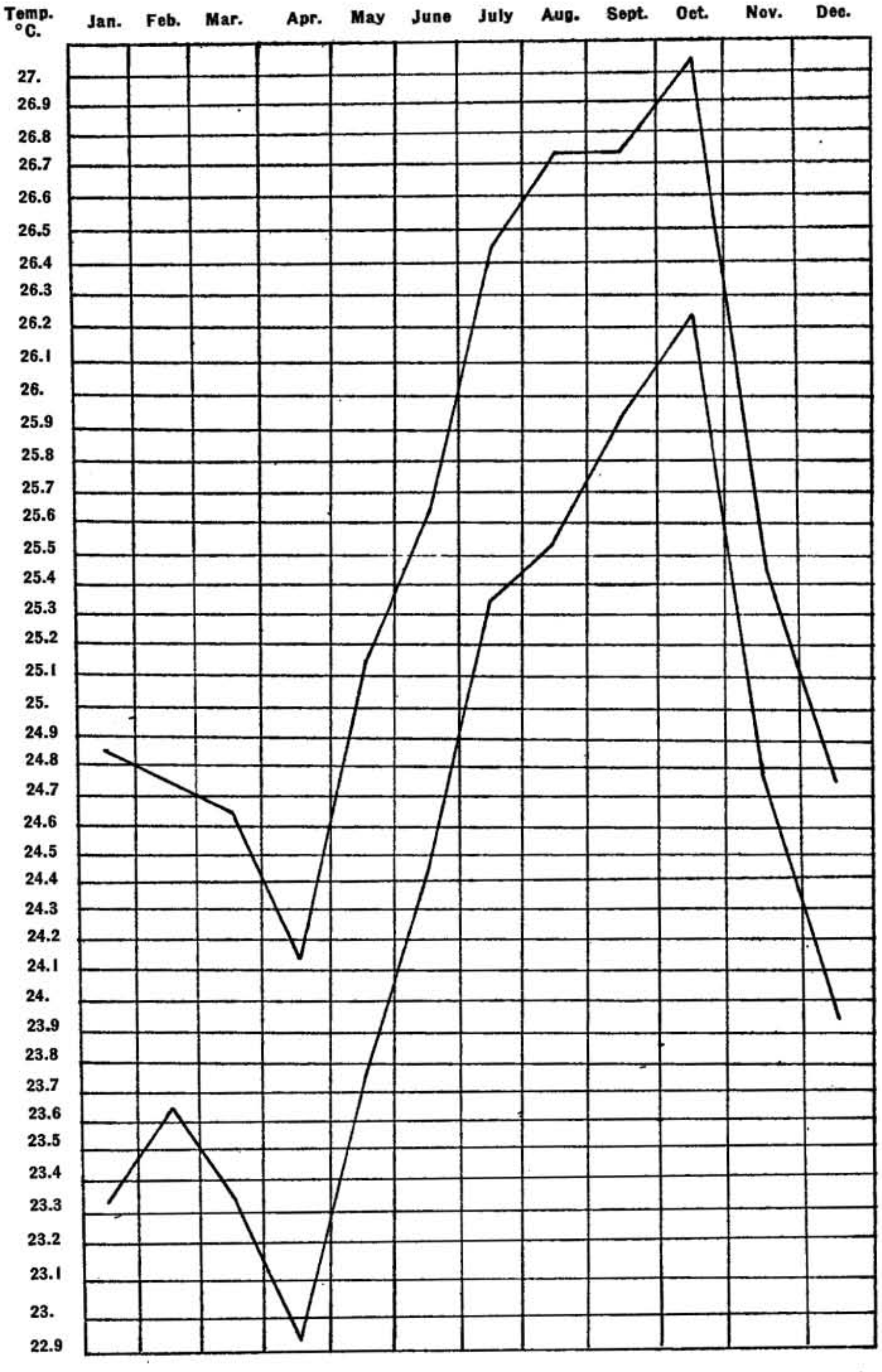

FIGURE 2.—Average temperature of circulating sea water of the Marine Biological Laboratory at Waikiki during 1925. Morning and afternoon temperatures, averaged from daily readings at intervals between 7 a.m. and 7 p.m., are recorded for each month. Lower curve, morning averages; and upper curve, afternoon averages.

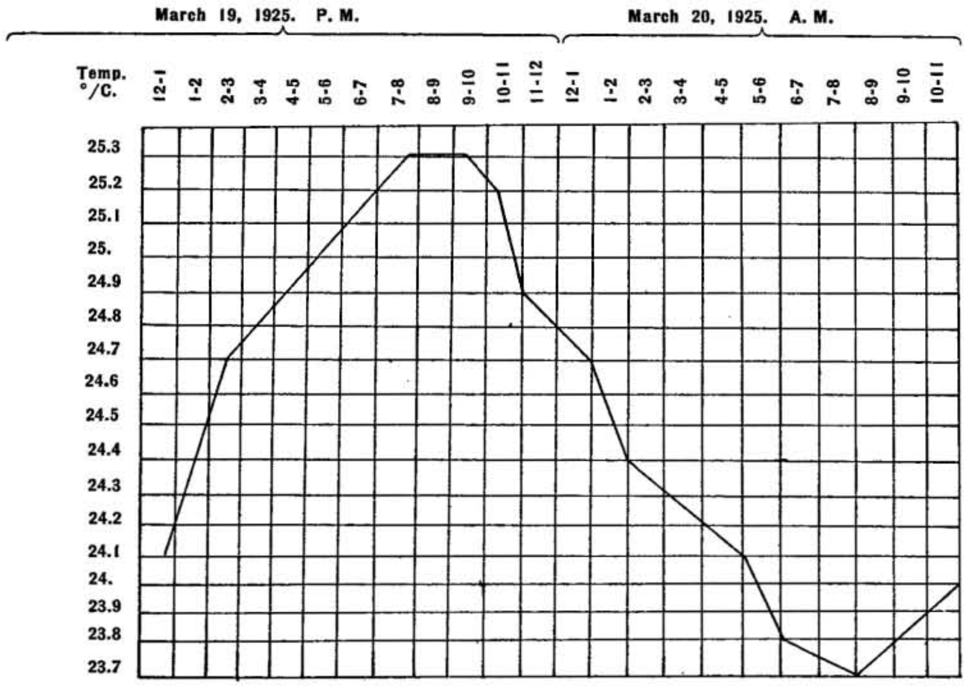

FIGURE 3.—Temperature of circulating sea water of the Marine Biological Laboratory at Waikiki during a 23 hour period from 12 m., March 19, to 11 a.m., March 20, 1925.

TABLE 3. MAXIMUM AND MINIMUM TEMPERATURES OF CIRCULATING SEA WATER OF THE MARINE BIOLOGICAL LABORATORY AT WAIKIKI, DURING 1925.

Of the numerous readings taken daily between 7 a. m. and 7 p. m. the highest and lowest for each month are given.

Month 1925	Lowest temp. °C.	Day of Month	Hour a. m.	Highest temp. °C.	Day of Month	Hour p. m.
Jan.	22.3	19	8:00	26.3	27	5:10
Feb.	23.1	9	8:07	26.4	28	5:40
Mar.	22.	13	8:30	25.7	2	4:20
Apr.	21.5	15	7:45	25.8	28	2:30
May	23.1	?	?	26.4	?	?
June	23.8	16	8:30	27.2	23	4:45
July	24.5	8	9:00	27.7	23	5:00
Aug.	24.6	3	7:00	27.9	25	5:00
Sept.	24.8	5	8:10	28.3	16	6:00
Oct.	25.1	12	7:15	27.9	24	4:45
Nov.	22.5	28	7:30	27.5	4	4:50
Dec.	22.4	26	8:30	26.	12	7:00

the day, temperature records were taken in the spring, summer and winter seasons of 1925 through periods ranging up to 24 consecutive hours. Figure 3, which is a record for March 19-20, indicates that the maximum temperature of the laboratory water was reached between the hours of 7 p. m. and 9 p. m. and the minimum at 8 a. m. The shore water falls below that of the laboratory in temperature during the night but rises above it in the daytime as is indicated in figure 4. Figure 5 shows that the temperatures of the laboratory water and the reef water near the shore were equal at about 9:15 a. m. on August 14, 1925, and that the shore water reached its maximum temperature at 4 p. m. It will be seen from figure 6 that the near shore reef water commonly does not exceed 3°C. in variation during a 24 hour period, while the difference between the maximum and minimum temperatures of the laboratory water during a similar period usually does not exceed 2°C.

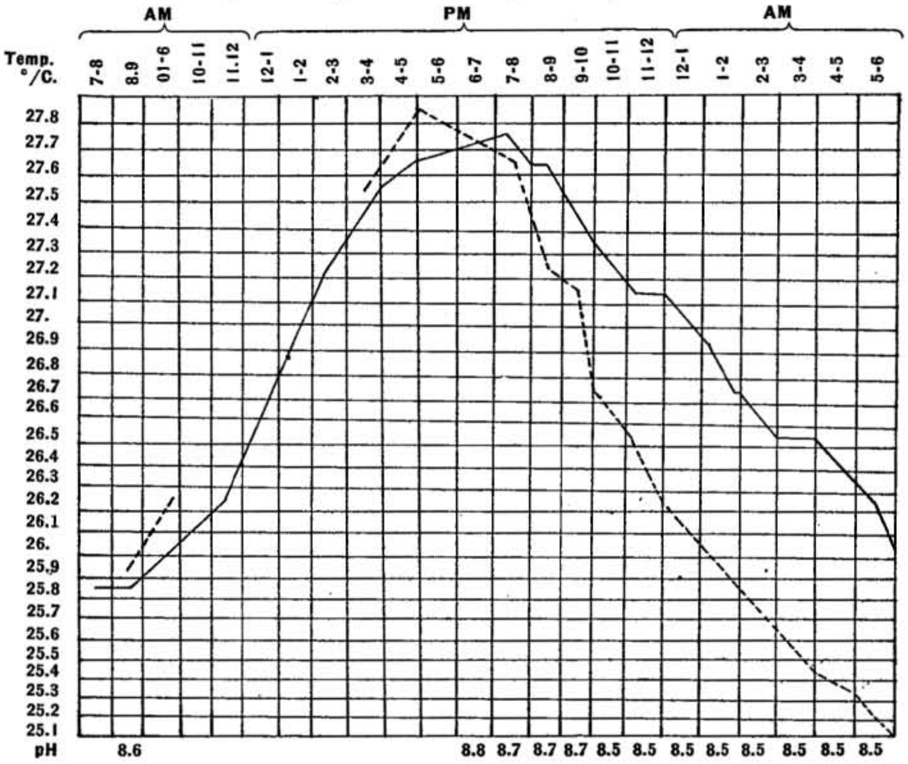

FIGURE 4.—Temperature records of circulating sea water of the Marine Biological Laboratory at Waikiki and the water of Waikiki reef during a 23 hour period from 7 a.m., August 6, to 6 a.m., August 7, 1925. Laboratory water represented by full line, reef water, near station AA (fig. 1), by dotted line. Temperature of reef water omitted between 10 a. m. and 3:30 p.m. pH values of reef water, at given temperatures, indicated on lower line.

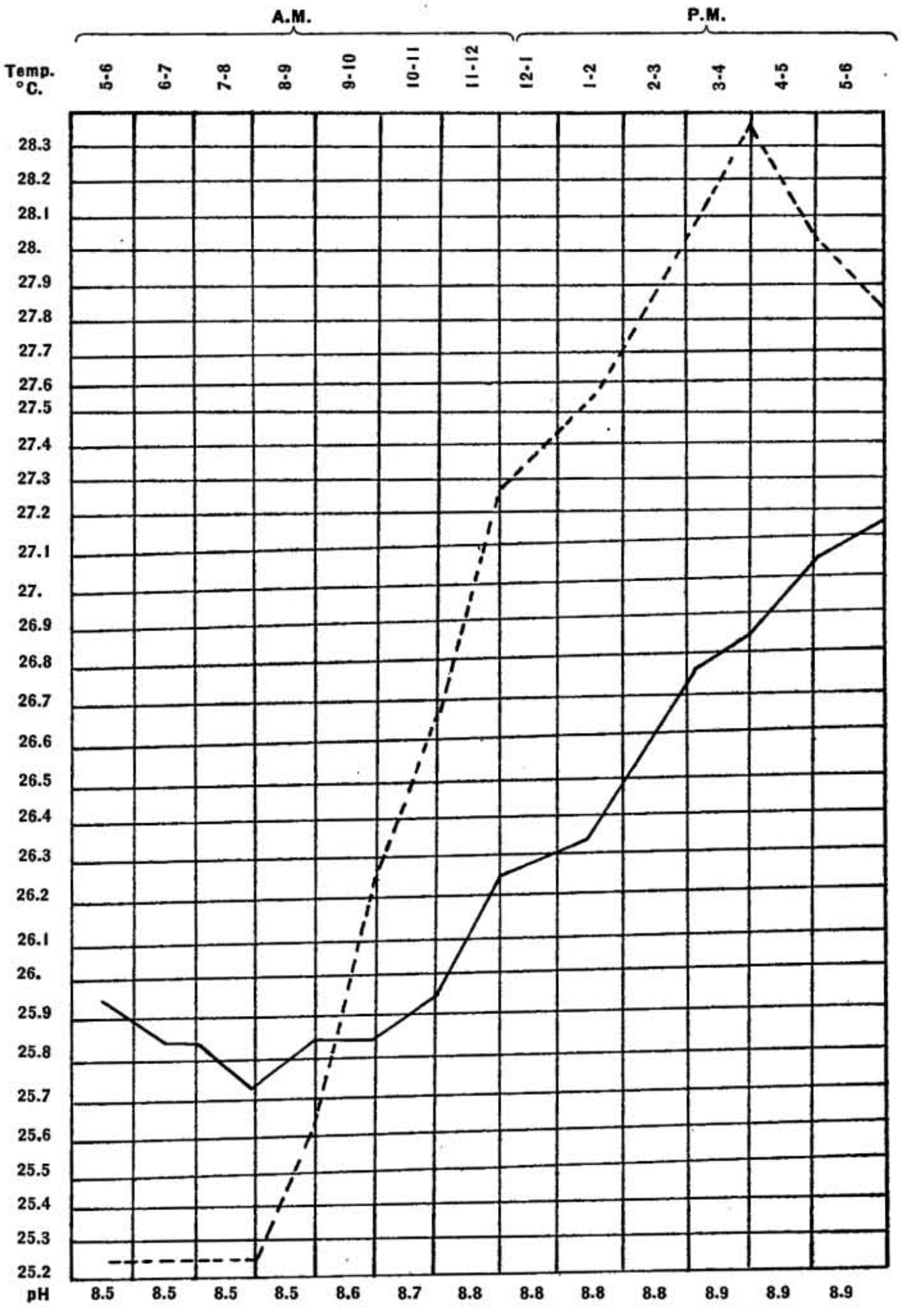

FIGURE 5.—Temperature of circulating sea water of the Marine Biological Laboratory at Waikiki and the water of Waikiki reef during a 13 hour period from 5 a.m. to 6 p.m., August 14, 1925. Laboratory water indicated by full line, reef water, near station AA (fig. 1), by dotted line. pH values of reef water, at given temperatures, on lower line.

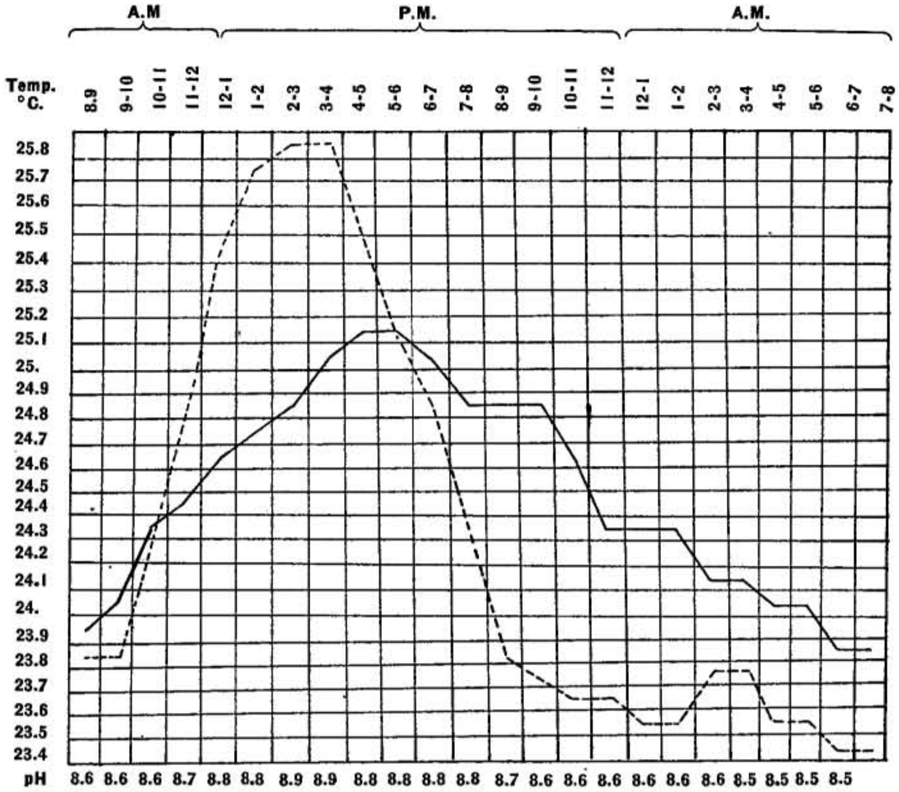

FIGURE 6.—Temperature of circulating sea water of the Marine Biological Laboratory and the water of Waikiki reef during a 24 hour period from 8 a.m., December 29, to 8 a.m., December 30, 1925. Laboratory water represented by full line; reef water, near station AA (fig. 1), by dotted line. pH values of reef water, at given temperatures, indicated on lower line.

TABLE 4. COMPARATIVE RESISTANCE OF HAWAIIAN CORALS TO A SLOW RISE OF TEMPERATURE (2°C. PER HOUR) TO 34°C., TO 35°C. AND TO 38°C.—40°C.

At 34°C. and 35°C., which experiments were distinct from each other and from that ranging from 38°C. to 40°C., the temperature was maintained for 1 hour, while there was a steady rise from normal temperature to 38°C. and continuing to 40°C. D = specimen dead, A = alive at the end of the specified period.

Corals	34° C.	35° C.				38° C.	38.5° C.	39° C.	40° C.
	60 min.	15 min.	30 min.	45 min.	60 min.				
Pocillopora meandrina var. nobilis	D	A	D			D			
Pocillopora ligulata	A	A	A	D		D			
Pocillopora cespitosa	A	A	A	A	D	D			
Porites evermanni	A	D				D			
Porites lobata forma lacera	D	D				D			
Porites lobata forma centralis subforma alpha	A	D							
Porites lobata forma centralis subforma beta	A	D							
Porites lobata forma centralis subforma gamma	?	D							
Porites compressa forma granimurata	A	D				D			
Porites compressa forma angustisepta	D	D				D			
Montipora verrucosa	D	D				D			
Montipora flabellata	A	A	D			A	A	D	
Montipora verrilli	A	A	A	D					
Montipora patula	A	D							
Pavona varians	A	A	A	A	D	D			
Pavona duerdeni	A	A	A	A	?				
Cyphastrea ocellina	D	D				D			
Stephanaria stellata	A	A	A	A	A	D			
Stephanaria brighami	A	A	D			A	A	A	D
Favia hawaiiensis	A	A	A	A	A	A	A	A	D
Leptastrea agassizi	A	A	A	A	A				
Fungia scutaria	A	A	A	A	A	?	?	D	

RESISTANCE TO INCREASING TEMPERATURE

After learning the temperature conditions under which the corals of Waikiki reef normally exist and the thermal variations to which they are usually subjected, it seemed desirable to determine their comparative resistance to increasing and decreasing temperatures even to the extreme levels of their endurance. In testing the resistance to rising temperatures, three forms of laboratory experiments were employed. In one set of experiments the sea water in a shallow container in which the corals were placed was raised, usually by electricity, to the temperature desired and maintained at that degree for definite periods. At regular intervals specimens of corals were removed and placed in a strong current of sea water and their condition determined on the following day or at some later period.

As Mayer (15) pointed out in experiments of this nature, the time element is a very important one. I can support his view that marine animals resist a higher degree if the temperature of the water is raised quickly than if it is raised slowly. In all of my thermal experiments, except where otherwise noted, the temperature of the sea water was increased or decreased at the rate of 2°C. per hour. As this was the rate employed by Mayer (15) in his investigations at Murray Island, some comparison may be made between the results obtained on the Great Barrier Reef and in Hawaii. Another important factor in experiments of this kind is the accurate determination of the condition of the specimens after being subjected to abnormal thermal or other influences. With species of *Pocillopora* it readily can be determined whether the specimens are dead or alive, but with other forms it is much more difficult. *Fungia scutaria* and *Stephanaria stellata* are examples of species which after an experiment may, to all appearances, be dead but on being restored to a strong current of sea water may revive if sufficient time is allowed. It is my experience that *Fungia scutaria* may require at least seven days to even begin to show evidences of recovery after being subjected to certain abnormal conditions, and that *Stephanaria stellata* may require as long or even longer time.

Another method used in testing the comparative resistance of corals to high temperatures was the raising of sea water quickly to a desired degree and plunging the specimens into it, the temperature being maintained for definite periods. The corals were removed at regular intervals, replaced in a strong current of sea water and examined later to note the effect of the sudden thermal change. Comparative resistance to increasing temperature was also tested by a slow and steady heating of sea water containing specimens of corals, and recording the maximum point of endurance for each species.

That different coral colonies of the same species show individual variations in their responses to stimuli is a conclusion drawn from a long series of experiments of this kind. I am not prepared to definitely state, at the present time, whether or not corals follow the general law as announced by Child (4), namely, that the young are more susceptible than older individuals to intensive stimuli if the stimulus is sufficient to kill without acclimatization and that the reverse is true if the stimulus is weak enough to permit some degree of adjustment. Andrews (1) has concluded from experimental work with marine animals that the young die more quickly than older individuals when subjected to abnormal conditions such as fresh water and high temperature of such intensity as to kill quickly, but that the young show a greater capacity for acclimatization when these conditions are less severe. The same investigator showed the reverse to be true when fresh water animals were exposed to conditions of increased acidity, the older individuals dying first, because they possess a smaller alkaline reserve. Some corals probably reach a senescent stage when physiological responses and general functions become modified as compared with younger periods. Vaughan (25) has concluded that colonies of some species may reach maturity and maximum size within a period of a few years after which old age may be considered as having set in. He observed a decrease in the rate of growth in *Maeandra areolata* (Linnaeus) after a length of about 60 mm. had been reached. Guppy (10) reports that certain branching acropores may reach their full height in 15 years, and that *Montipora digitata* grows to a height of 18 inches in 4 years, then begins to die.

In my investigations, specimens of coral colonies of moderate size were used, neither extremely young or old, the age factor probably having less influence in modifying results than the relative health and vigor of the individuals used. The experiments, however, were repeated frequently enough with a sufficient duplication of specimens to reduce the individual variation factor to a minimum. Wherever appearing in the tables the letter A indicates that the species which it follows was alive at the end of the stated period and subsequently recovered when returned to normal conditions. D. indicates that the species was dead.

Table 4 shows that approximately 70 per cent of the corals on Waikiki reef used in this experiment are capable of enduring 34°C. for a least one hour and that among the least resistant are *Pocillopora meandrina* var. *nobilis,* at least two species of *Porites, Montipora verrucosa,* and *Cyphastrea ocellina.* However if the sea water is slowly raised to 35°C., about 50 per cent of the corals are able to endure this temperature for 15 minutes, 36 per cent survive these conditions for 30 minutes, 32 per cent for 45 minutes, and 18 per cent for at least one hour.

Just as Mayer (15) found on the Great Barrier Reef certain species of corals highly resistant to changes of temperature living close together with species extremely sensitive to similar stimuli, so on Waikiki reef the ability of a species to endure high temperatures does not always indicate it to be a near shore form.

Of all the species on Waikiki reef *Pocillopora cespitosa,* though not the most resistant to increasing temperature, approaches nearest the shore line. It is the typical species within 100 feet of the water's edge and on the flat portion of the reef between stations AA and BA (fig. 1) it may be found within 40 feet of the shore. During an extremely low tide many colonies of this species are barely covered by water and are forced to endure the greatest extremes of temperature when low water occurs on a hot summer afternoon or at night during the cooler months of the year. On May 10, 1924, the sea water barely covering colonies of *Pocillopora cespitosa,* 50 feet from the shore, registered 31.6°C. and at 80 feet from the shore *Porites compressa* forma *centralis* subforma *granimurata* and *Montipora verrucosa* were bathed in water which reached 30.7°C. On this section of the reef *Montipora verrucosa* thrives best about 300 feet from the shore but a few colonies approach within 80 feet. This species is one of the most sensitive of Hawaiian corals to variations in temperature and in the near shore area is living within a very few degrees of its upper death point. On the other hand, of the species most resistant to increasing temperatures (Table 4), none may be considered a near shore form unless it be species of *Stephanaria,* which occasionally are found at 50 feet from the shore but are best developed between stations BB and CB at about 200 feet from the water's edge. The only group of *Fungia scutaria* observed on this section of the reef was approximately 450 feet from the shore and covered by about 5 feet of water at low tide. *Leptastrea agassizi,* although well distributed over the reef, is most abundant and best developed between 300 and 400 feet from the shore. *Favia hawaiiensis* also occurs as poorly developed, scattered colonies over many portions of the reef, but not within the near shore area, being best developed well out toward the lithothamnium ridge.

Table 4 also summarizes the results of an experiment to determine the maximum limitation of resistance of Hawaiian corals to high temperature sea water. It seems that when the temperature reaches 38°C. only four species remained alive and two of these, *Montipora flabellata* and *Fungia scutaria,* were eliminated at 39°C., and the other two, *Favia hawaiiensis* and *Leptastrea agassizi,* were dead when 40°C. was reached. It again may be observed that the species of coral most capable of enduring high temperatures are not, at least in the section surveyed, typical of near shore areas but thrive best halfway out on the reef platform or beyond, and that some of them are confined to these localities. It is obvious that if the water in contact with the corals on Waikiki reef should at any time reach 40°C., all species would be destroyed, and the same result would follow at a much lower temperature if a constant temperature were maintained for a period of a few hours. That the sea water on the reefs of Hawaii, in localities where corals predominate, may reach such high temperatures, under normal conditions, is inconceivable.

The results of endurance of Hawaiian corals to rising temperature extending over a period of 24 hours are set forth in Table 5 which shows that the 16 species used in the experiment all survive at 32°C. for 3 hours, except *Pocillopora meandrina* var. *nobilis* apparently the most sensitive of the corals tested. Although a few colonies have become established within 100 feet of the shore and scattered heads are found between 150 and 300

TABLE 5. COMPARATIVE RESISTANCE OF 16 SPECIES OF HAWAIIAN CORALS TO A SLOW RISE OF TEMPERATURE (2°C. PER HOUR) TO 32°C. AND MAINTAINED AT THAT LEVEL FOR 24 HOURS.

D = specimen dead, A = alive at the end of the specified period.

Corals	32° C.					
	3 hrs.	5 hrs.	8 hrs.	10 hrs.	18 hrs.	24 hrs.
Pocillopora meandrina var. nobilis	D					
Pocillopora ligulata	A	D				
Pocillopora cespitosa	A	D				
Porites lobata forma lacera	A	D				
Porites lobata forma centralis subforma alpha	A	A	D			
Porites lobata forma centralis subforma beta	A	A	D			
Porites compressa forma granimurata	A	A	D			
Porites compressa forma angustisepta	A	A	D			
Montipora verrucosa	A	D				
Montipora flabellata	A	A	A	A	A	D
Montipora patula	A	A	D			
Pavona varians	A	A	A	A	D	
Cyphastrea ocellina	A	A	D			
Stephanaria stellata	A	A	A	A	A	D
Favia hawaiiensis	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A

feet from the water's edge, this species is best developed far out on the reef. Should the temperature of the sea water on Waikiki reef rise to 32°C. and be maintained at that level for 8 hours, approximately two-thirds of the species of corals would be destroyed, and at the end of 24 hours probably not more than two species would survive.

All of my experiments relating to the responses of corals to increased temperature confirm Mayer's (12) observation that tropical animals are living within a very close margin of safety with respect to their high death points. A range of 10°C. is probably wide enough to include all Hawaiian reef-forming corals and at Waikiki some species are living considerably within this estimate.

Table 6, which summarizes the results of the sudden subjection of Hawaiian corals to increased temperature, shows that all species used in this experiment survived the abrupt change from normal temperature to 35°C. for a period of 15 minutes, but few survive the sudden rise to 38°C. for the same length of time. By comparing Table 4 and Table 6 it will be seen that for almost all species the endurance is greater if the change is sudden than if it is gradual. This also confirms Mayer's (15) observations.

All temperature experiments with Hawaiian corals show clearly that *Favia hawaiiensis* and *Leptastrea agassizi* possess a higher degree of resistance to increasing temperature than do other species and have a higher death point.

Corals and other organisms may be subjected either simultaneously or successively to at least two unusual conditions: an unusually low tide might occur during a period of high temperature simultaneously with or immediately preceding or following a dilution of the reef water by a deluge of rain or inflow of fresh water; or corals might be partially or completely covered by silt followed by excessively high temperatures.

In order to determine the effect of successively subjecting Hawaiian corals to these two unusual conditions, the experiment summarized in Table 7 was made. By comparing these results with Table 6, it will be seen that in most of the species the resistance to heating has been lessened by the previous exposure to dilute sea water. The three species surviving one hour (Table 7) were all considerably injured, *Favia hawaiiensis* being the least affected.

Mayer (15) covered corals with silt for a period of several hours then tested their resistance to increased temperature while they were still buried. As a result, some species showed no lessened resistance to rising temperature. He suggested that burial under silt put some corals in a condition resembling hibernation in which the vital processes are greatly reduced

Corals and other organisms may be subjected either simultaneously or

TABLE 6. RESISTANCE OF 21 HAWAIIAN CORALS WHEN SUDDENLY SUBJECTED TO TEMPERATURES OF 35°C. AND 38°C. MAINTAINED AT THOSE LEVELS FOR 60 AND 45 MINUTES RESPECTIVELY.

D = specimen dead, A = alive at the end of the specified period.

Corals	35° C.				38° C.		
	15 min.	30 min.	45 min.	60 min.	15 min.	30 min.	45 min.
Pocillopora meandrina var. nobilis	A	D			D		
Pocillopora ligulata	A	A	A	D	D		
Pocillopora cespitosa	A	A	A	D	D		
Porites evermanni	A	A	A	D	D		
Porites lobata forma lacera	A	A	A	D	D		
Porites lobata forma centralis subforma alpha	A	A	A	D	D		
Porites lobata forma centralis subforma beta	A	A	A	A	D		
Porites lobata forma centralis subforma gamma	A	A	?	?	D		
Porites compressa forma granimurata	A	A	A	A	D		
Porites compressa forma angustisepta	A	A	A	A	D		
Montipora verrucosa	A	A	A	D	D		
Montipora flabellata	A	A	A	D	D		
Montipora patula	A	A	A	D	D		
Pavona varians	A	A	A	A	A	D	
Pavona duerdeni	A	A	A	A	D		
Cyphastrea ocellina	A	A	D		D		
Stephanaria stellata	A	A	A	A	A	D	
Stephanaria brighami	A	A	A	A	A	D	
Favia hawaiiensis	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	D
Fungia scutaria	A	A	A	A	D		

and thereby not easily affected by heating. Mayer found, however, that corals living in clear water far out on the reef showed a decreased resistance to heat while buried. He concluded that their metabolism was more constant and not capable of the same degree of variation as near shore corals. Being buried under several inches of silt doubtless lessens the amount of available oxygen. It is known that corals and other coelenterates are capable of suspending metabolism in a medium with little oxygen. Mayer (14) reports that corals lived for more than 11 hours under an air pump which reduced oxygen to less than 5 per cent of that of normal sea water.

TABLE 7. COMPARATIVE RESISTANCE OF 13 HAWAIIAN CORALS TO A SUDDEN EXPOSURE TO A TEMPERATURE OF 35°C. IMMEDIATELY FOLLOWING 12 HOURS SUBJECTION TO A 50 PER CENT SOLUTION OF SEA WATER (1 PART SEA WATER, 1 PART FRESH WATER).

D = specimen dead, A = alive at end of specified period.

Corals	35° C.		
	30 min.	60 min.	
Pocillopora meandrina var. nobilis	D		
Pocillopora cespitosa	D		
Porites evermanni	D		
Porites lobata forma centralis subforma beta	D		
Porites compressa forma granimurata	D		
Porites compressa forma angustisepta	D		
Montipora verrucosa	D		
Montipora flabellata	D		
Pavona varians	A	A	
Cyphastrea ocellina	D		
Stephanaria stellata	A	D	
Favia hawaiiensis	A	A	
Leptastrea agassizi	A	A	

My experiments paralleling those of Mayer (15) are recorded in Table 8. By comparing Table 8 with Table 6 it will be seen that the resistance of certain species to heating is lessened by previous burial under silt, but that *Montipora flabellata* shows an increased endurance by such treatment. The two species least affected, *Favia hawaiiensis* and *Leptastrea agassizi*, are more capable of enduring many adverse conditions than are most Hawaiian shallow water corals. Neither of them is a near shore form.

While accepting in general Mayer's inferences, I am led to believe that the resistance of certain species of corals to silt when buried is due, in part at least, to the ability of the mucus of their cuticular surfaces to mechanically prevent the silt particles from pressing closely upon them.

The strength and vigor of the polyps of *Favia* and *Leptastrea* enable them to remain uninjured when buried under silt while the coenenchyma between the polyps may be entirely destroyed.

TABLE 8. COMPARATIVE RESISTANCE OF 12 HAWAIIAN CORALS TO A SUDDEN EXPOSURE FOR 60 MINUTES TO 35°C., IMMEDIATELY FOLLOWING A BURIAL OF 13 HOURS UNDER SILT.

Corals were heated while still under silt. D = specimen dead, A = alive at end of specified period.

	35° C.	
Corals	60 min.	
Pocillopora meandrina var. nobilis	D	
Pocillopora cespitosa	D	
Porites evermanni	D	
Porites lobata forma centralis subforma beta	D	
Porites compressa forma granimurata	D	
Porites compressa forma angustisepta	D	
Montipora verrucosa	D	
Montipora flabellata	A	
Pavona varians	A	
Cyphastrea ocellina	D	
Favia hawaiiensis	A	
Leptastrea agassizi	A	

RESISTANCE TO DECREASING TEMPERATURE

That living organisms are more capable of enduring a gradual reduction of temperature than a gradual increase of temperature is well known. Pfeffer (20) says: "It is easy to understand that, owing to the depressant effect of low temperatures upon metabolism, they should take longer to produce a fatal effect than high ones, which steadily accellerate respiration."

To reach a conclusion regarding the comparative endurance of corals to a moderately reduced temperature experiments recorded in Table 9 were conducted. With a constant temperature of 15°C., at the end of 8 hours no injury to any of the corals was apparent and at the end of 18 hours only one species, *Porites evermanni,* was dead. Four species failed to recover at the end of 23 hours. Most of those surviving showed little injury as a result of being subjected to approximately 10°C. below the normal temperature. Table 9 also shows that about 70 per cent of the species tested are capable of surviving for at least 15 minutes and that 50 per cent endure 10°C. for one hour or longer.

In order to determine the comparative lower temperature limits of endurance of Hawaiian corals, 16 species were subjected to a slow cooling at the rate of 2°C. per hour. The record shows that approximately 50 per cent of the species tested survived a reduction to 5.5°C. approximately 20°C. below the normal environment. (See Table 9.)

TABLE 9. RESISTANCE OF HAWAIIAN CORALS TO A SLOW REDUCTION OF TEMPERATURE (2°C. PER HOUR) FROM NORMAL TO 15°C., TO 10°C. AND TO 5.5°C.

Temperature was maintained at 15°C. for 23 hours and at 10°C. for 1 hour. A = specimen alive, D = dead at end of the specified period.

Corals	15° C.			10° C.				5.5° C.
	8 hrs.	18 hrs.	23 hrs.	30 min.	15 min.	45 min.	60 min.	
Pocillopora meandrina var. nobilis	A	A	D	A	A	A	A	A
Pocillopora ligulata	A	A	A	A	A	A	A	A
Pocillopora cespitosa	A	A	A	A	A	D		A
Porites evermanni	A	D		D				D
Porites lobata forma lacera	A	A	A	A	A	D		D
Porites lobata forma centralis subforma alpha	A	A	A	D				
Porites lobata forma centralis subforma beta	A	A	D	D				A
Porites compressa forma granimurata	A	A	D	D				D
Porites compressa forma angustisepta	A	A	A	A	D			D
Montipora verrucosa	A	A	A	A	A	A	A	D
Montipora flabellata	A	A	A	A	A	A	D	D
Montipora patula	A	A	D	A	A	A	A	D
Pavona varians	A	A	A	A	A	A	A	D
Stephanaria stellata	A	A	A	D				A
Cyphastrea ocellina	A	A	A	A	A	A	A	A
Favia hawaiiensis	A	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A	A

Porites evermanni

The reaction of corals on Waikiki reef to sudden reductions in temperature is recorded in Table 10. When plunged into sea water at 10°C., all species of corals tested endured for at least one hour, approximately 50 per cent of the species endured 5°C. for 15 minutes, and about 25 per cent for one hour. When plunged directly into sea water reduced to 2.5°C., only 7 of the 21 species used in the experiment survived for a period of 15 minutes and only 1 recovered after being subjected to this low temperature for one hour. The table shows that *Pocillopora meandrina* var. *nobilis* is the most resistant to sudden cooling, and of all the species on Waikiki reef is the only one capable of enduring for one hour or more an abrupt reduction in temperature to a level varying from 0°C. to 0.5°C.

The species of *Porites,* taking the genus as a whole, are among the most sensitive of Hawaiian corals to low temperatures. *Pavona varians,* which is quite resistant to increasing temperatures, also dies quickly when slowly cooled to 10°C. But a number of species which are highly sensitive to rising temperatures are fairly resistant to cold, for example *Pocillopora* and *Cyphastrea ocellina.* Among those species which best endure temperatures ranging down to at least 5°C., are also some corals which are the most highly resistant to temperatures up to 40°C. The species *Favia hawaiiensis* and *Leptastrea agassizi* are living within a wider margin of safety than many other corals on Waikiki reef. My observations show that *Favia* has a slightly greater resistance to high temperatures while *Leptastrea* endures cold better. *Stephanaria stellata* may exist within almost as wide a range of thermal conditions as *Favia* or *Leptastrea.* The species *Montipora flabellata,* although enduring fairly high temperatures (Table 4), is much more sensitive to cooling down to 5°C. than is *Favia hawaiiensis, Leptastrea agassizi,* or *Stephanaria stellata.*

It is evident that Hawaiian reef-forming corals are in little danger of extermination by the natural cooling of the sea water. Even during the coolest months of the year the near shore waters seldom fall below 20°C. and at a distance of 300 feet from the shore on Waikiki reef in a more favorable growth zone the temperature of the water washing the coral colonies probably never descends to 20°C.

Mayer (15) concluded that a sustained exposure to 18.5°C. would destroy most of the shallow water corals of the Floridian reefs, and Vaughan (26) expressed the opinion that 18.15°C. is about the minimum temperature at which a coral reef will survive.

Experiments to determine the resistance of planulae of *Cyphastrea ocellina* to variations in temperature showed that almost without exception swarms of planulae of this species are readily obtained by the simple process of raising the temperature of the sea water surrounding the adult colony to 35°C. At times the planulae appear at 32° or 33°, and occasionally the

TABLE 10. RESISTANCE OF 21 HAWAIIAN CORALS TO A SUDDEN DECREASE FROM NORMAL TEMPERATURE TO 10°C., TO 5°C., TO 2.5°C. AND TO 0- 0.5°C.

Results at the end of 1 hour at 10°C. are shown and at the termination of 15, 30, 45 and 60 minutes for each of the lower temperatures. A = specimen alive, D = dead at the end of the specified period.

Corals	10° C.	5° C.				2.5° C.				0-0.5° C.			
	1 hr.	15 min.	30 min	45 min	60 min.	15 min.	30 min	45 min	60 min.	15 min.	30 min.	45 min.	60 min.
Pocillopora meandrina var. nobilis	A	A	A	A	A	A	A	A	A	A	A	A	A
Pocillopora ligulata	A	A	A	A	A	A	A	D		A	A	D	
Pocillopora cespitosa	A	A	A	D		A	A	D		D			
Porites evermanni	A	D				D				D			
Porites lobata forma lacera	A	D				D				D			
Porites lobata forma centralis subforma alpha	A	D				D				D			
Porites lobata forma centralis subforma beta	A	D				D				D			
Porites lobata forma centralis subforma gamma	A	D				?				?			
Porites compressa forma granimurata	A	A	D			D				D			
Porites compressa forma angustisepta	A	A	D			D				D			
Montipora verrucosa	A	D				D				D			
Montipora flabellata	A	D				D				D			
Montipora verrilli	A	D				D				D			
Montipora patula	A	D				D				D			
Pavona varians	A	A	A	D		A	D			D			
Cyphastrea ocellina	A	A	A	D		D				D			
Stephanaria stellata	A	A	A	A	A	A	D			D			
Stephanaria brighami	A	A	A	A	A	A	A	A	A	D			
Favia hawaiiensis	A	A	A	A	A	D							
Leptastrea agassizi	A	A	A	A	A	A	A	D		D			
Fungia scutaria	A	A	A	A	D	D				D			

temperature has been maintained at 35°C. for 45 minutes before they are released from the polyps. It is not contended, however, that rising temperature is the sole cause of the swarming of planulae in *Cyphastrea ocellina*. Extensive work in progress on the development and growth of Hawaiian corals indicates that increasing temperature is but one of a number of unusual conditions which may bring about the swarming of planulae.

In order to compare the resistance to thermal variations of the planulae and the adult of *Cyphastrea ocellina* both planulae and adults were carried together in experiments. On raising the temperature of sea water from 22.1°C. to 40°C. at the rate of 8° an hour, the planulae survived without serious injury although a contraction of the bodies occurred at 37.5°C. but the adult colonies died before 40°C. was reached. Planulae of this species, however, are not able to endure one hour at 40°C. When the sea water containing planulae is raised at the rate of 8° an hour from normal temperature to 35°C. and maintained for one hour all planulae survive. They survive 30 minutes at 36°C. but 45 minutes prove fatal.

To test their resistance to sudden rising temperature the planulae of *Cyphastrea ocellina* on being released from the polyps were transferred directly from 32°C. to varying degrees of increased temperature. No inhibition of movement was observed up to 42°C. At 42° movements were retarded and slight contraction occurred. On being suddenly transferred from 32°C to 42.5°C. the planulae died immediately.

On reducing the temperature of sea water containing planulae of *Cyphastrea ocellina* from 24.5°C. to 5°C. in 1 hour and 30 minutes and maintaining it at that point for 45 minutes all movement of the planulae ceased. On restoring them to salt water at normal temperature the planulae apparently recovered and resumed activity after 3 hours. This revived condition was, however, only temporary; 24 hours later the planulae assumed highly lobulated forms and soon disintegrated and died. When the temperature was reduced to 8°C. at the rate of approximately 13°C. an hour, the planulae apparently survived a period of 30 minutes but disintegrated and died the next day. Similar after effects followed a subjection of planulae to 10°C. for a period of 30 minutes. This shriveling and eventual disintegration of planulae following apparent restoration of normal functions invariably resulted from a sustained temperature of 10°C. or lower. Cohn, according to Pfeffer (20), has found that some plants appear fresh and living when exposed to fatally high temperatures, but die as an after effect of the exposure even under the best external conditions.

Starting with planulae of *Cyphastrea ocellina* at 33°C. at which temperature they showed normal movements, they were suddenly transferred to varying degrees of reduced temperature. A reduction to 19°C. resulted in no contraction and no retardation of movement. A fall to 16.5°C. caused a contraction of the planulae but no slowing up of their movements. A drop in temperature to 13°C. resulted in a sharp contraction of the planulae and an immediate and complete cessation of movement. The temperature was then reduced to 12°C. for 5 minutes after which the planulae were suddenly transferred to 22°C. Movement of the planulae was resumed almost at once with the bodies contracted but normal form was gradually assumed and no detrimental after effects were observed.

From the record of a large number of experiments it appears that the planulae of *Cyphastrea ocellina* endure somewhat higher temperatures than do the adults, but are more sensitive than the adults to temperatures of 10°C. or lower. The explanation may be that the planulae possess a much higher degree of acclimation to advancing temperature than do the adults.

TEMPERATURE AND FEEDING RESPONSES

Rising or falling temperatures of the sea water may bring about complete inhibition of the feeding responses of corals before their death points are reached. As heat or cold rigor is approached the tentacles of the polyps are rendered incapable of holding food brought within their reach and ingestion ceases. The real safety zone for any species is not, therefore, limited by the maximum and minimum degrees of thermal endurance but by the high and low temperature levels at which its feeding responses cease.

Mayer (15) found that most shallow water corals are unable to capture food when exposed to a temperature of 16°C. for one hour, and concluded that a sustained temperature of 18.5°C. would probably kill reef corals by starvation if not by cold.

In Table 11 is recorded the temperature range of the feeding responses of 14 species of Hawaiian reef corals. These feeding experiments were carried on under a binocular microscope, where necessary, with expanded colonies in containers of sea water subjected to a rise or decline of temperature at the rate of approximately 5°C. an hour. The polyps were artifically fed at intervals until the temperature was reached at which the tentacles failed to hold and the release of food previously ingested took place. In this and other experiments in which artificial feeding was a part, the food used consisted almost exclusively of fresh crab muscle which the corals took readily. The soft parts of bivalve mollusks also were used but were accepted by corals with less relish than crab meat. Immature eggs of crustaceans were readily ingested by corals.

It will be seen by comparing Table 11 with the temperature endurance records of Table 10 that, in general, those species which are extremely resistant to low temperatures continue to feed at lower levels than those more sensitive to cooling. This is especially true of *Pocillopora meandrina* var. *nobilis* and *Leptastrea agassizi.* There are, however, some exceptions. Some individuals of *Porites compressa* forma *angustisepta* continued feeding until the remarkably low temperature of 8.3°C. was reached. It may be concluded however, that if the temperature of the sea water washing the corals of the Hawaiian reefs should fall to 10°C. nearly all of the corals would cease feeding, and some would be incapable of taking food at 11.5°C. If the temperature of the reef water were raised to 33.5°C. a very large pro-

TABLE 11. TEMPERATURE RANGE OF FEEDING RESPONSES OF HAWAIIAN CORALS ON A GRADUAL RISE OR DECLINE OF APPROXIMATELY 5°C. PER HOUR.

Temperatures at which feeding responses were resumed after complete inhibition by heating or cooling are indicated in the third and fourth columns. Temperature records in °C.

Corals	Maximum feeding temp.	Minimum feeding temp.	Resumption after maximum inhibition	Resumption after minimum inhibition
Pocillopora meandrina var. nobilis	33.5°	9.7°	29°	20°
Pocillopora ligulata	32.5°	10.4°	?	20°
Pocillopora cespitosa	33.6°	10.4°	30.2°	20.2°
Porites evermanni	34°	11.4°	31.5°	20.8°
Porites lobata forma lacera	32.5°	11.4°	29.8°	22.2°
Porites lobata forma centralis subforma alpha	33.4°	10.3°	?	22°
Porites lobata forma centralis subforma beta	33.6°	11°	31°	20.6°
Porites compressa forma granimurata	33°	11.2°	31°	?
Porites compressa forma angustisepta	33°	8.3°	31°	16.3°
Montipora verrucosa	31.5°	10.5°	31°	?
Pavona varians	31.5°	?	?	?
Pavona duerdeni	32.5°	?	?	?
Cyphastrea ocellina	33.5°	?	?	?
Stephanaria stellata	33°	10°	?	17.3°
Favia hawaiiensis	35.5°	10.6°	32.5°	17°
Leptastrea agassizi	33.2°	7.9°	31.2°	?
Fungia scutaria	34°	11.5°	?	22°

portion of the corals would cease feeding at once. For some species 31.5°C. seems to be the limit.

To determine the relative lasting effects of heat and cold upon the feeding responses of corals, the temperature on reaching the high or low feeding points for a species was reversed and slowly reduced or increased and the point of resumption of feeding noted. (See Table 11.) On the reversal of temperature after the maximum feeding point had been reached, the species of corals tested usually resumed feeding following a cooling of from 2° to 5°C. However, after the minimum feeding temperature had been reached, on the rising mercury feeding was not resumed until from 6.5° to 10°C. had passed. It is obvious that corals will stand cooling much better than heating and that their feeding responses have a wider range below than above normal temperature. That their feeding activities are restored after heat paralysis at a much more rapid rate than after paralysis from cold is also shown by these experiments.

The temperature of the sea water surrounding 15 species of Hawaiian corals was raised slowly, approximately 2° per hour, from normal to 32°C. and maintained at that level for one hour. At the end of that period nearly all species were capable of feeding. On reducing the temperature from normal to 16°C. at the rate of 2° per hour, it was found that after a period of one hour 63 per cent of the species examined were incapable of feeding. The prolonged cooling at this temperature paralyzed the tentacles so that they failed to hold particles of food brought within their reach and when introduced to the mouths of polyps food fell off.

On slowly cooling corals to 16°C. and maintaining that temperature only 7 of 19 species were capable of capturing and ingesting food at the end of one hour. These results are in accord with those of Mayer (13, 15) based on experiments with the shallow water corals of Porto Rico and Dry Tortugas.

RESPONSE OF CORALS TO ALTERED SALINITY

RESISTANCE TO DECREASED SALINITY

Although a small number of organisms are capable of adjusting themselves to both fresh and salt water, corals apparently require for their optimum growth and development a medium having a degree of salinity averaging about that of normal sea water.

To determine the comparative resistance of Hawaiian corals when subjected to decreasing or increasing grades of salinity of sea water, a large number of laboratory experiments were conducted (Tables 12-20). Consideration was also given to correlations between these experiments and the ecology of the corals and their particular habitats on limited sections of local reefs.

In conducting experiments on salinity at Murray Island, Mayer (15) used fresh rain water. In my experiments tap water from the Honolulu city mains was used. For much of the time fresh rain water was not available. After carrying on carefully guarded, parallel experiments with both fresh rain water and tap water as dilutants, no appreciable difference in results could be detected.

An abrupt change from normal sea water to fresh water for a period of 30 minutes proved fatal to all but 3 of 21 species of corals tested (Table 12). Of these three species, *Fungia scutaria, Favia hawaiiensis,* and *Leptastrea agassizi,* endured fresh water for 2 hours, the coenenchyma then being macerated and almost wholly lost. On removal to sea water, *Fungia* showed signs of recovery after a period of 4 days. *Favia hawaiiensis* and *Leptastrea agassizi* are about equally resistant to fresh water. At the end of 3¼ hours both showed evidences of life but both were dead after a period of 4 hours.

The result of subjecting 23 species of Hawaiian corals to a 50 per cent solution of sea water is given in Table 13. The specific gravity of the solution as determined by Becker's chainomatic balance was about 1.0125 at 20°C; the NaCl content was determined as about 15.89 mg. per cc.

All of the species used in the experiment endured this solution for a period of 12 hours and nearly all were alive at the end of 15 hours. At the expiration of 30 hours, however, only 7 species survived and but 3 at the end of 53 hours. Most of the *Stephanaria* and *Favia hawaiiensis* died within 10 days. In one experiment, however, the two species of *Stephanaria* revived after 11 days, a period of 15 days in circulating sea water being required before evidences of recovery were noted. In another experiment *Favia hawaiiensis* revived after 25 days, which represents by far the greatest resistance of any Hawaiian species coming under my observation. My experiments indicate that *Pocillopora cespitosa* is, of all species on Waikiki reef, subjected to the greatest danger from dilute sea water. This species approaches within 40 feet of the shore line and has established itself nearer than any other to station AA where specific gravity readings indicate the salinity to be commonly lower than at other stations in this section of the reef. Although the shallow waters of the near shore areas are in danger of dilution from heavy rainfalls and from shore drainage, it is apparent that the waters of Waikiki reef at 40 feet from the shore, if they ever

TABLE 12. RESISTANCE OF HAWAIIAN CORALS ON SUDDEN SUBJECTION TO FRESH WATER.

D = specimen dead, A = alive at the end of the specific period.

Corals	30 min.	2 hrs	3¼ hrs.	4 hrs.
Pocillopora meandrina var. nobilis	D			
Pocillopora ligulata	D			
Pocillopora cespitosa	D			
Porites evermanni	D			
Porites lobata forma lacera	D			
Porites lobata forma infundibulum	D			
Porites lobata forma centralis subforma alpha	D			
Porites lobata forma centralis subforma beta	D			
Porites compressa forma granimurata	D			
Porites compressa forma angustisepta	D			
Montipora verrucosa	D			
Montipora flabellata	D			
Montipora verrilli	D			
Montipora patula	D			
Stephanaria stellata	D			
Stephanaria brighami	D			
Cyphastrea ocellina	D			
Pavona varians	D			
Favia hawaiiensis	A	A	A	D
Leptastrea agassizi	A	A	A	D
Fungia scutaria	A	A	?	

reach a 50 per cent dilution are not maintained at that low salinity for continuous periods of 30 hours. The constant wave and tidal activities offset the possible danger from dilution.

The optimum natural locality for all species of corals in this section of Waikiki reef is beyond 150 feet from the shore. That a number of species,

TABLE 13. COMPARATIVE RESISTANCE OF 23 SPECIES OF HAWAIIAN CORALS TO A 50 PER CENT SOLUTION OF SEA WATER.

The solution is 1 part sea water to 1 part fresh water, changed daily. A = specimen alive, D = dead at end of specified period.

Corals	12 hrs.	15 hrs.	23 hrs.	26 hrs.	30 hrs.	39 hrs.	53 hrs.	5 da.	6 da.
Pocillopora meandrina var. nobilis	A	A	D						
Pocillopora ligulata	A	A	D						
Pocillopora cespitosa	A	A	A	A	A	D			
Porites evermanni	A	A	A	D					
Porites lobata forma lacera	A	D							
Porites lobata forma infundibulum	A	D							
Porites lobata forma centralis subforma alpha	A	D							
Porites lobata forma centralis subforma beta	A	A	D						
Porites lobata forma centralis subforma gamma	A	A	D						
Porites compressa forma granimurata	A	A	D						
Porites compressa forma angustisepta	A	A	A	D					
Montipora verrucosa	A	A	A	D					
Montipora flabellata	A	A	A	A	A	D			
Montipora verrilli	A	A	D						
Montipora patula	A	A	A	D					
Pavona varians	A	A	A	A	A	D			
Pavona duerdeni	A	A	A	?					
Cyphastrea ocellina	A	A	D						
Stephanaria stellata	A	A	A	A	A	A	A	A	D
Stephanaria brighami	A	A	A	A	A	A	A	A	D
Favia hawiiensis	A	A	A	A	A	A	A	A	D
Leptastrea agassizi	A	A	A	A	A	A	D		
Fungia scutaria	A	A	A	A	D				

however, are capable of adapting themselves to near shore conditions has been shown by transporting corals from far out on the reef to localities near the beach.

Of the six species which, as shown in Table 13, have equal resistance with *Pocillopora cespitosa* to a 50 per cent solution of sea water none is typically a near shore form. *Stephanaria stellata* and *Stephanaria brighami,* although occasionally taken about 60 feet from shore, are best developed beyond 150 feet. The other four species which show relatively high resistance are typically of the middle zone of the reef, or from 300 to 400 feet from the shore. That these species are less sensitive to dilute sea water than others living in the same locality or even farther out on the reef can, I believe, only be explained by physiological differences.

When subjected to a standard solution (2 parts sea water, to 1 part fresh water; specific gravity, 1.0164 at 20°C.; NaCl content 22.33 mg. per cc.), a large percentage of the Hawaiian corals tested are not readily adjusted. (See Table 14.) After a period of 31 hours, 50 per cent of the species failed to recover; among them were all of the *Porites, Pocillopora meandrina* var. *nobilis, Pocillopora ligulata,* and *Montipora verrucosa.* It will be observed that *Pocillopora cespitosa* is somewhat more resistant to this dilution than are the other two species of the genus. At the end of 49 hours but 7 species remained alive, while 4 species so accommodated themselves to the altered conditions that they lived for 4 months with little or no apparent injury. On one occasion *Leptastrea agassizi* and *Favia hawaiiensis* survived a period of 6 months in a 66 2/3 per cent solution of sea water. They were, however, seriously injured at the end of the experiment, probably due to insufficient nourishment. It is remarkable that the 4 most highly resistant species, as indicated in Table 14, are capable of living without injury for a period of 4 months in a dilution, amounting to approximately two parts of sea water to one part of fresh water, practically void of living organisms in the form of animal plankton which normally furnish food for corals. The discovery by Boschma (2) that Anthozoa are able to digest the Zooxanthellae contained in the endoderm may explain the endurance of corals in a medium with little food. The work of Parker (19) on *Paramecium bursaria* also supports the view that infesting algae, under certain conditions, may be ingested by the host. There is no doubt that animal plankton is the normal food of corals, if not the sole food as Vaughan (23) has concluded. However, my experiments on the self supporting power of certain corals leads to the belief that corals may draw upon the algae inhabiting their tissues for nourishment if the normal food supply is absent. Not only are certain species of corals able to live for several months in sea water diluted 33 1/3 per cent and practically without animal plankton, but I have kept *Fungia scutaria, Stephanaria* *brighami,* and *Leptastrea agassizi* alive for more than three months in sea water which had been passed through filter paper thereby removing all animal plankton upon which corals probably normally feed. The corals during this period being kept shaded but in strong, diffused light developed a deep brown color which indicated a rich supply of infesting algae. *Fungia* and *Stephanaria* showed some injurious effects during the first month in the thinning of the coenenchyma but later were restored to normal condition. When the experiment was terminated all three species were apparently healthy and vigorous.

TABLE 14. COMPARATIVE RESISTANCE OF 21 HAWAIIAN CORALS TO A 66 2/3 PER CENT SOLUTION OF SEA WATER.

The solution is 2 parts sea water to 1 part fresh water, changed daily. D = specimen dead, A = alive at end of specified period.

Corals	31 hrs.	49 hrs.	70 hrs.	100 hrs.	7 da.	30 da.	4 mo.
Pocillopora meandrina var. nobilis	D						
Pocillopora ligulata	D						
Pocillopora cespitosa	A	D					
Porites evermanni	D						
Porites lobata forma lacera	D						
Porites lobata forma infundibulum	D						
Porites lobata forma centralis subforma alpha	D						
Porites lobata forma centralis subforma beta	D						
Porites lobata forma centralis subforma gamma	D						
Porites compressa forma granimurata	D						
Porites compressa forma angustisepta	D						
Montipora verrucosa	D						
Montipora flabellata	A	A	A	A	A	D	
Montipora verrilli	A	A	A	A	D		
Montipora patula	A	D					
Stephanaria stellata	A	A	A	A	A	A	A
Cyphastrea ocellina	A	A	A	D			
Pavona varians	A	A	A	A	D		
Favia hawaiiensis	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A
Fungia scutaria	A	A	A	A	A	A	A

On comparing Tables 13 and 14 it will be seen that an increase in solution of sea water from 50 per cent to 66 2/3 per cent increases but slightly the length of life of a considerable number of species. Its effect, however, as shown by the increased endurance of *Stephanaria stellata, Favia hawaiiensis, Leptastrea agassizi,* and *Fungia scutaria* is most notable.

An increase in salinity to a 75 per cent solution of sea water (3 parts sea water, 1 part fresh water; specific gravity about 1.0178 at 20°C.; NaCl about 23.96 mg. per cc.) has a beneficial effect upon certain species. (Compare Tables 14 and 15.) Although this salinity level is too low for a continued existence of the *Pocillopora,* the *Porites,* certain of the *Montipora* and *Cyphastrea ocellina,* the lives of *Montipora flabellata* and *Pavona varians* are prolonged to 55 days and 4 months respectively. Of the 5 species surviving at the end of 4 months, *Pavona varians* was by far the most seriously injured and could have endured but little longer. The 4 species which were capable of resisting a 66 2/3 per cent solution of sea water for at least 4 months endured a 75 per cent solution for the same period with little or no injury. On introducing food to the more resistant species at intervals during the course of the experiment, it was found that the feeding responses were normal and, doubtless, each of the four species, *Stephanaria stellata, Favia hawaiiensis, Leptastrea agassizi,* and *Fungia scutaria,* is capable of accommodating itself to this dilution of sea water for an indefinite period provided sufficient food is available. Vaughan (24) found at the Dry Tortugas, Florida, that a reduction of salinity from normal to 27.87 had no effect on 16 species of corals for 48 hours, but on subjecting them to a salinity of 18.28 for 24 hours all but 3 were killed or injured.

That living organisms may acclimate themselves to unusually adverse conditions by a process of slow adjustment is well known. During the course of my investigations a number of experiments were conducted to determine the relative endurance of corals to grades of salinity lower than normal reached by slow adjustment as compared with their resistance to the same salinity levels reached by abrupt changes. (See Tables 16 and 17.)

In these tests five species of corals which are capable of endurig a 75 per cent solution of salt water (3 parts salt water, 1 part fresh water) for 4 months without serious injury were, at the end of this period, transferred to a 50 per cent solution (1 part salt water, 1 part fresh water) for 1 month. Those surviving this period were then transferred to a 33 1/3 per cent solution (1 part salt water, 2 parts fresh water) or to a 25 per cent solution (1 part salt water, 3 parts fresh water) until they were no longer able to resist the altered conditions. By comparing these results (Table 16) with the records of resistance of the same species to similar grades of salinity when subjected to them without intermediate steps, the increased resistance due to the graduated reduction is shown. (See Table 17.) Thus the resistance

them to a salinity of 18.28 for 24 hours all but 3 were killed or injured

TABLE 15. COMPARATIVE RESISTANCE OF 21 HAWAIIAN CORALS TO A 75 PER CENT SOLUTION OF SEA WATER.

The solution is 3 parts sea water to 1 part fresh water, changed daily. D = specimen dead, A = alive at end of specified period.

Corals	31 hrs.	49 hrs.	70 hrs.	100 hrs.	7 da.	30 da.	55 da.	4 mos.
Pocillopora meandrina var. nobilis								
Pocillopora ligulata	D							
Pocillopora cespitosa	A	D						
Porites evermanni	D							
Porites lobata forma lacera	D							
Porites lobata forma infundibulum	A	D						
Porites lobata forma centralis subforma alpha	D							
Porites lobata forma centralis subforma beta	A	D						
Porites lobata forma centralis subforma gamma	D							
Porites compressa forma granimurata	A	A	D					
Porites compressa forma angustisepta	A	A	A	D				
Montipora verrucosa	A	A	D					
Montipora flabellata	A	A	A	A	A	A	D	
Montipora verrilli	A	A	A	D				
Montipora patula	D							
Stephanaria stellata	A	A	A	A	A	A	A	A
Cyphastrea ocellina	A	A	A	A	D			
Pavona varians	A	A	A	A	A	A	A	A
Favia hawaiiensis	A	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A	A
Fungia scutaria	A	A	A	A	A	A	A	A

of *Stephanaria stellata* to a 50 per cent solution is seen to be increased about 6 times by the slow reduction process over that of direct subjection, and the resistance of this species to the lower grades of salinity is also increased several fold. The resistance of the other species is correspondingly increased by the gradual reduction method. *Pavona varians,* after enduring a 75 per cent solution 4 months, lives for about 20 days when transferred to a 50 per cent solution, but when placed directly in a 50 per cent solution this species commonly dies within 2 days. The tables show no difference in the resistance of *Stephanaria stellata* to 33 1/3 per cent and 25 per cent solutions, either as a result of the slow reduction or of the direct subjection method, but *Leptastrea agassizi* is somewhat more sensitive

TABLE 16. RESISTANCE OF FIVE HAWAIIAN CORALS WHEN SUBJECTED BY GRADUATED STEPS TO LOW DEGREES OF SALINITY REPRESENTED BY 33 1/3 PER CENT AND 25 PER CENT SOLUTIONS OF SEA WATER.

The time indicated in each column is the length of subjection to the percentage of solution. The arrows show the course of transferrence of each species. A = specimen alive, D = dead at end of specified period.

Corals	75%	50%	33⅓%				25%			
	4 mo.	1 mo.	2 da.	3 da.	4 da.	6 da.	2 da.	3 da.	4 da.	6 da.
Stephanaria stellata	A—>	A—>	A	A	A	D				
" "	A—>	A	—	—	—	->	A	A	A	D
Leptastrea agassizi	A—>	A	—	—	—	->	A	D		
Favia hawaiiensis	A—>	A—>	A	A	A	D				
Fungia scutaria	A—>	A	—	—	—	—>	A	D		
Pavona varians	A—>	D								

TABLE 17. RESISTANCE OF THE SPECIES LISTED IN TABLE 16 WHEN TRANSFERRED FROM NORMAL SEA WATER DIRECTLY INTO 50 PER CENT, 33 1/3 PER CENT AND 25 PER CENT SOLUTIONS OF SEA WATER, WATER CHANGED DAILY.

A = specimen alive, D = dead at end of specified period.

Corals	50%				33⅓%			25%	
	1 da.	2 da.	5 da.	6 da.	1 da.	2 da.	3 da.	1 da.	2 da.
Stephanaria stellata	A	A	A	D	A	D		A	D
Leptastrea agassizi	A	D			A	D		D	
Favia hawaiiensis	A	A	A	D	A	A	D	A	D
Fungia scutaria	A	D							
Pavona varians	A	D			D			D	

Pavona varians A—> D

to a 25 per cent solution when introduced directly to it than when transferred by gradual steps, and *Favia hawaiiensi* shows increased resistance to a 33 1/3 per cent solution by the process of acclimatization.

RESISTANCE TO INCREASED SALINITY

Studies of resistance of organisms to increased salinity have been made by various investigators. Clarke (6) has summarized the evidence supporting the view that the sea is becoming more concentrated through increasing amounts of salts carried into it through land erosion. Goldfarb's work (9) indicates that some marine animals are capable of enduring a wide range of salinity. He showed that *Cassiopea* lived in solutions ranging from 40 per cent to 153 per cent sea water, and regenerated in solutions from 50 per cent to 133 per cent, while the optimum solution for regeneration was 95 per cent solution of sea water. This investigator also found that the optimum solution for regeneration in *Eudendrium* was 85 per cent sea water, and Loeb (11) reported that *Tubularia* regenerated best in a 65 per cent solution.

To test the resistance of Hawaiian corals to increased salinity the experiments summarized in Tables 18 to 20 were conducted. In these experiments two methods of obtaining increased concentrations of sea water were employed. One was the process of evaporation, adding the residue from a known volume of normal sea water to volumes of normal sea water in such proportions as were required to increase the salinity to the per cent desired. In the other method salts were added directly to normal sea water in proper amounts, assuming that the salts of sea water are of constant proportion. Solutions of about 110 per cent, 125 per cent and 150 per cent were prepared daily and during the time the corals were subjected to them, the solutions were changed once every 24 hours. Identical results followed the use of concentrated solutions obtained by these two methods. I fully realize the inaccuracy of these methods and look upon the percentages of concentration indicated as approximations only. However, the comparative resistance of Hawaiian corals to these concentrated solutions is of some interest.

The *Pocillopora* proved the most sensitive to the concentration of 110 per cent (Table 18). All the *Porites* lived at least 8 days and *Porites evermanni* endured almost 3 weeks. The species *Montipora flabellata,* the most resistant of the genus to many altered conditions, died within 4 days; *Cyphastrea ocellina* endured for about 30 days; and *Stephanaria stellata, Favia hawaiiensis,* and *Leptastrea agassizi,* which in other ways show remarkable accommodation to environmental changes, existed for approximately 3 months. At the end of this period all were somewhat affected, the most serious in-jury being to *Leptastrea agassizi* which lost much of the coenenchyma.

In sea water of higher concentration (approximately 125 per cent) the species of *Pocillopora* are typically the most sensitive (Table 19). At the end of 3 days but 3 species survived, these being the same species which proved most resistant to water of 110 per cent concentration. *Stephanaria stellata, Favia hawaiiensis,* and *Leptastrea agassizi* recovered after having been subjected to a solution of sea water of approximately 125 per cent for 20 days, all, however, being considerably injured. Twenty-two days exceeds the limit of endurance for most *Stephanaria* and commonly represents the limit for both *Favia* and *Leptastrea.*

A solution of sea water of about 150 per cent proved fatal within 24 hours to nearly all species of Hawaiian corals tested. (See Table 19.) Four species, *Pavona varians, Leptastrea agassizi, Stephanaria stellata,* and *Stephanaria brighami* at times showed evidences of life at the end of 24

TABLE 18. COMPARATIVE RESISTANCE OF 16 HAWAIIAN CORALS TO SEA WATER AT A CONCENTRATION OF ABOUT 110 PER CENT.

Water changed daily. A = specimen alive, D= dead at end of specified period.

Corals	24 hrs.	39 hrs.	48 hrs.	72 hrs.	4 da.	9 da.	10 da.	14 da.	21 da.	50 da.	84 da.
Pocillopora meandrina var. nobilis	A	D									
Pocillopora cespitosa	A	A	D								
Porites evermanni	A	A	A	A	A	A	A	A	D		
Porites lobata forma lacera	A	A	A	A	A	D					
Porites lobata forma infundibulum	A	A	A	A	A	?					
Porites lobata forma centralis subforma alpha	A	A	A	A	A	?					
Porites lobata forma centralis subforma beta	A	A	A	A	A	D					
Porites compressa forma granimurata	A	A	A	A	A	D					
Porites compressa forma angustisepta	A	A	A	A	A	A	A	D			
Montipora verrucosa	A	A	A	D							
Montipora flabellata	A	A	A	A	D						
Pavona varians	A	A	A	A	A	A	D				
Stephanaria stellata	A	A	A	A	A	A	A	A	A	A	A
Cyphastrea ocellina	A	A	A	A	A	A	A	A	A	D	
Favia hawaiiensis	A	A	A	A	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A	A	A	A	A

TABLE 19. COMPARATIVE RESISTANCE OF 16 HAWAIIAN CORALS TO SEA WATER AT A CONCENTRATION OF ABOUT 125 PER CENT.

Water changed daily. D = specimen dead, A = alive at end of specified period.

Corals	24 hrs.	39 hrs.	45 hrs.	53 hrs.	72 hrs.	6 da.	17 da.	22 da.
Pocillopora meandrina var. nobilis	D							
Pocillopora cespitosa	D							
Porites evermanni	A	A	D					
Porites lobata forma lacera	A	A	D					
Porites lobata forma infundibulum	A	A	D					
Porites lobata forma centralis subforma alpha	A	A	A	A	D			
Porites lobata forma centralis subforma beta	A	A	D					
Porites compressa forma granimurata	A	D						
Porites compressa forma angustisepta	A	D						
Montipora verrucosa	A	D						
Montipora flabellata	A	A	A	D				
Pavona varians	A	A	A	D				
Stephanaria stellata	A	A	A	A	A	A	A	D
Cyphastrea ocellina	A	A	A	A	D			
Favia hawaiiensis	A	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A	A

hours, but on being returned to normal sea water only the species of *Stephanaria* eventually recovered.

My experiments with altered salinity seem to show that a limited number of Hawaiian corals may be capable of living, under laboratory conditions, for at least three months in solutions of sea water ranging from 66 2/3 per cent to about 110 per cent. Certain species are apparently more readily acclimated to limited dilutions of sea water than to concentrations of a similar degree.

By a series of experiments the resistance of the planulae of *Cyphastrea ocellina* to low salinity was compared with that of the adult of the same species. When the planulae were transferred directly from normal salt water to fresh water, the organisms immediately contracted sharply, ciliary movements ceased and death occurred. On being restored to salt water the ectosarc disintegrates leaving highly lobulated, lifeless forms remaining. When planulae were subjected to a 50 per cent solution of sea water they contracted and ciliary movements were inhibited for a period of about 15 minutes, after which the normal form and activity were resumed. It has been shown (Table 13) that most *Cyphastrea ocellina* in the adult form die within 24 hours when subjected to a 50 per cent solution of sea water. The planulae of this species, however, were maintained alive in a 50 per cent solution of sea water for a period of 25 days, with the water changed daily. During the course of the experiment about 10 per cent of the planulae settled and became fixed but in none of them was more than a faint trace of skeletal formation observed. On several occasions active planulae have been removed from the mouths of adult polyps of *Cyphastrea ocellina* which had been killed in a 50 per cent solution of sea water, the planulae being uninjured by a solution which was fatal to the adults. There would seem to be a remarkable degree of acclimation on the part of the planulae rendering them capable of resisting this low salinity 25 times as long as the adults. The ability of planulae to resist adverse conditions may be an important factor in the dispersal of certain species of corals.

To correlate the results of laboratory experiments with conditions as they actually exist under natural surroundings is not an easy task, and I fully realize the difficulty in even approximating the value of salinity as a factor in regulating the selection of habitats by corals on a reef platform where wave and tidal action must be considered.

However, the specific gravity and salinity determinations of a large number of water samples taken from both Waikiki reef and windward

TABLE 20. COMPARATIVE RESISTANCE OF 14 HAWAIIAN CORALS TO SEA WATER AT A CONCENTRATION OF ABOUT 150 PER CENT.

Water changed daily. D = specimen dead, A = alive at end of specified period.

Corals	24 hrs.	Corals	24 hrs.
Pocillopora meandrina var. nobilis	D	Porites compressa forma angustisepta	D
Pocillopora cespitosa	D	Montipora verrucosa	D
Porites evermanni	D	Pavona varians	D
Porites lobata forma lacera	D	Cyphastrea ocellina	D
Porites lobata forma infundibulum	D	Stephanaria stellata	A
Porites lobata forma centralis sub-forma alpha	D	Stephanaria brighami	A
Porites compressa forma granimurata	D	Leptastrea agassizi	D

Oahu prove that the near shore waters about this island are, in places at least, considerably diluted. On May 8, 1925 water from station AA Waikiki reef, during a low tide, showed a NaCl content of 26.18 mg. per cc. In Kawela Bay, windward Oahu, on June 7, 1925, the NaCl content at the inner border of the coral zone was 25.37 mg. per cc., while near the shore where no corals grow it was 20.03 mg. per cc. These samples were taken at low tide. Frequent use of Becker's chainomatic balance indicated an almost constant, appreciably lower specific gravity for the near shore stations on Waikiki reef than for those farther seaward.

Table 21 shows that the NaCl content at the near shore stations is usually lower than that of stations farther out. Salinity at station AA is usually lower than at station BA probably because AA is near the outlet from the aquarium and laboratory.

Some of the probable causes of the apparent dilution of the shore waters of Waikiki reef may be briefly stated. A small stream near the northern boundary of the area surveyed until recently has discharged vast amounts of fresh water silt over the reef. (See p. 8.) The diluted water and the silt, acting in conjunction, are probably responsible for the fact that living corals are not now found within a radius of approximately 400 feet of the mouth of the stream. At the southern extremity of the area, near the Marine Biological Laboratory, is the outlet for the overflow from the aquarium and the laboratory. As it passes through the buildings the sea water is diluted, being mixed with the waste from several fresh water

TABLE 21. COMPARISON OF TEMPERATURE AND NaCl CONTENT BETWEEN SHORE AND OFF SHORE WATER. RECORDS AT LOW TIDE.

Position of stations shown in figure 1.

Station	Date	Hour	Water Temp. °C.	Air Temp. °C.	NaCl mg. per cc.
AA	Jan. 17, '25	3:30 p.m.	26.	23.7	30.17
AD	" "	"	24.5	22.3	33.86
AA	Jan. 21, '25	8:45 a.m.	22.2	22.2	32.29
AD	" "	"	23.	22.5	33.34
AA	May 8, '25	8:30 a.m.	26.6	26.3	26.18
AD	" "	"	24.	25.	32.47
BA	Jan. 17, '25	2:30 p.m.	26.3	24.8	32.76
BD	" "	"	24.5	22.5	34.41
BA	Jan. 21, '25	8:30 a.m.	22.3	22.7	32.60
BD	" "	"	23.4	22.	33.00
BA	May 8, '25	8:30 a.m.	28.5	25.8	32.43
BD	" "	"	24.	24.5	32.52

tanks and pipes. A constant stream of this dilute water, approximately 2 inches in diameter, flows into the reef water at the outlet.

Chemical analyses of the reef water at this outlet after having been mixed with the overflow from the aquarium and laboratory indicate a low salinity. Records during January, May, and June, 1925, show a range in NaCl content of from 29.42 mg. per cc. to 29.61 mg. per cc. Water samples taken at the same time from station AB, 150 feet from the outlet, indicated a range in NaCl of from 32.16 mg. per cc. to 33.46 mg. per cc. As shown in Table 21, the NaCl content of sea water at station AB does not range much lower than that at station AD, which is 450 feet from the shore and entirely without the influence of such fresh water as may be discharged along the shore from drainage outlets. This would seem to show that although the overflow from the aquarium dilutes the reef water in the immediate vicinity of the outlet and may alter the salinity of station AA, it has little influence at a distance of 150 feet.

Between the outlet and station AB numerous colonies of *Pocillopora cespitosa* and one or two colonies of *Pocillopora meandrina* var. *nobilis* have established themselves. Several colonies of *nobilis* set in concrete blocks have been growing for nearly two years within 60 feet of the aquarium outlet. Their growth, however, has been very slow.

Throughout the entire length of the surveyed section of the reef 18 drainage pipes have their outlets through the sea wall. Not all of these are now discharging fresh water onto the reef but they were placed for that purpose and represent surface drainage pipes, outlets from the laundry houses and cess pools of private residences located near the wall. These are no doubt contributing to a general reduction of salinity of the shore water. Farther southward along the coast of Oahu at a number of points fresh water springs mingle with the reef water sometimes bubbling up beneath the salt water at a little distance from the shore. No such springs occur in the section of Waikiki reef surveyed during these investigations.

On consulting the map of the reef (fig. 1) it will be seen that the greatest number of species of corals occurs between the lines of B and D stations, and beyond 150 feet from the shore. This represents the middle area of the reef somewhat removed from the possible influence of fresh water and silt from the direction of the shore. A denser population of the northern limits of this section of the reef has, doubtless, been inhibited during the past few years by the small stream at the northern boundary of the section, and the paucity of corals toward the southern extremity of this section of reef may, I believe, be accounted for, in part at least, by drifting sand. (See p. 51.) It is significant that in going outward on the reef platform from the mouth of the stream, the species of corals first to appear are those most highly resistant to both dilute salt water and silt.

Experiments show that *Favia hawaiiensis, Stephanaria stellata,* and *Leptastrea agassizi* are physiologically capable of enduring extreme conditions, similar, in some degree, to those met with in certain localities on the reef.

The records show that living corals cannot long maintain themselves in a 50 per cent dilution of sea water and that a dilution of 25 per cent is fatal to nearly 50 per cent of Hawaiian corals in two days (Table 15). It is very probable that except for very unusual circumstances even a dilution of 25 per cent is seldom or never reached over the larger area of this section of reef at a distance of 40 feet from the shore which is about the nearest approach of *Pocillopora cespitosa* to the water's edge. On Feb. 3, 1923, a tidal wave, or succession of tidal waves, laid Waikiki reef bare for approximately half its width, the recession of water occurring several times during a period of a few hours. Many colonies of corals were wholly exposed by these abnormal low tides each of which, however, did not last more than 15 or 20 minutes. Should a heavy downpour of rain occur during such unusual phenomena or during a very low normal tide, the reef corals of the near shore areas would doubtless seriously suffer.

RESPONSE OF CORALS TO SILT

When eroded material and fresh water are carried out over a reef together, both doubtless have detrimental effects upon certain marine organisms. But the influence of the silt is usually much more lasting than fresh water. Previous to the construction of the Waikiki drainage canal a high degree of turbidity of the water on Waikiki reef frequently lasted for more than a week after a heavy rainfall, the suspended material being kept in motion by the action of waves and tides until it finally settled with a smothering effect upon weak and low lying coral colonies. The actual burial of coral colonies by mud carried over reef platforms by fresh water streams or by drifting sand is not an unusual occurrence. That silt is a very important factor in the growth and distribution of corals is strongly advocated by Wood-Jones (27) who says: "Sedimentation is the most potent cause of coral death and the most important influence upon all phases of their existence."

Mayer (15) was led to the conclusion that the death of corals buried under silt was a process similar to that resulting from high temperature. He called attention to the correlation between resistance to high temperatures and to silt showing that corals sensitive to increasing heat were killed quickly when buried under mud, while species highly resistant to one of these conditions also showed greater endurance when subjected to the other.

In my laboratory experiments the specimens were buried in a wooden trough under four inches of sand and silt with a strong current of sea water circulating over them. The results shown in Table 22 when compared with those shown in Table 4 indicate a correlation in full accord with that announced by Mayer. It may be noted that the species of corals killed quickly by silt are the ones which die first when subjected to increasing temperatures. Of the 23 species used in my experiments, those of *Pocillopora, Porites,* and some of *Montipora* are the least resistant to silt when completely buried, usually dying within 24 hours. The species most enduring when buried, *Stephanaria stellata, Stephanaria brighami, Favia hawaiiensis, Leptastrea agassizi,* and *Fungia scutaria* are the ones which stand heating best. Although the species of *Stephanaria, Favia,* and *Leptastrea* are usually almost completely exhausted or dead after being under silt for 5 days, *Favia hawaiiensis* and *Leptastrea agassizi* in one experiment lived for 10 days. Of these two *Favia* was usually the least injured in all of the experiments with silt. My experiments show that *Favia* also stands heating slightly better than does *Leptastrea.* The species *Fungia scutaria* will live under silt for 75 hours showing, however, at the end of the period a considerable degree of injury. The species was not tested longer than 75 hours but would probably live for 4 days under these conditions.

There can be little doubt that silt carried by fresh water has in past years been a very influential agent in controlling the distribution of corals

TABLE 22. COMPARATIVE RESISTANCE OF 23 HAWAIIAN CORALS WHEN COMPLETELY BURIED UNDER 4 INCHES OF SAND AND SILT.

D = specimen dead, A = alive at end of specified period.

Corals	12 hrs.	17 hrs.	24 hrs.	28 hrs.	40 hrs.	48 hrs.	75 hrs.	96 hrs.	5 da.
Pocillopora meandrina var. nobilis	D	D							
Pocillopora ligulata	D								
Pocillopora cespitosa	A	A	D						
Porites evermanni	A	A	D						
Porites lobata forma lacera	A	A	D						
Porites lobata forma infundibulum	A	A	D						
Porites lobata forma centralis subforma alpha	A	A	D						
Porites lobata forma centralis subforma beta	A	?	D						
Porites lobata forma centralis subforma gamma	A	D							
Porites compressa forma granimurata	A	A	D						
Porites compressa forma angustisepta	A	D							
Montipora verrucosa	A	A	D						
Montipora flabellata	A	A	A	A	D				
Montipora verrilli	A	A	A	A	D				
Montipora patula	A	?	D						
Pavona varians	A	A	A	A	D				
Pavona duerdeni	A	A	A	A	A	A	D		
Stephanaria stellata	A	A	A	A	A	A	A	A	A
Stephanaria brighami	A	A	A	A	A	A	A	A	A
Cyphastrea ocellina	A	A	A	A	D				
Favia hawaiiensis	A	A	A	A	A	A	A	A	A
Leptastrea agassizi	A	A	A	A	A	A	A	A	D
Fungia scutaria	A	A	A	A	A	A	A	?	?

Porites lobata forma infundibulum | A | A | D

on the section of Waikiki reef surveyed, and probably has been in no small way responsible for the stunted growth of coral colonies over much of this area. The corals nearer the mouth of the small stream opening on this section of the reef are forms most resistant to both dilute sea water and to silt. The species *Stephanaria stellata, Stephanaria brighami, Favia hawaiiensis, Leptastrea agassizi,* and *Fungia scutaria* would especially be in frequent danger of smothering by silt if they were not highly resistant to its influence; they live low on the reef platform in situations favorable for covering by settling particles of silt or by drifting sand.

As species of *Pocillopora* are destroyed very quickly on being buried under silt, it might be supposed that *Pocillopora cespitosa,* which approaches the shore nearer than any other species, would suffer most severely, but observation does not support this assumption. In fact, Mayor (16) found that as compared with many other species, those of *Pocillopora* are better able to protect themselves against silt in suspension. By means of the well developed cilia of the cuticular surface, they are capable of warding off fine particles of suspended mud and silt, but when completely covered they die quickly.

At the southern and seaward boundary of the section of Waikiki reef surveyed, the lithothamnium ridge is somewhat lower and more broken than elsewhere, permitting a stronger inward sweep of the sea. This, I believe, is responsible, in part at least, for the large amount of sand that has drifted over the southern area of the reef. Dredging operations in the construction of swimming pools near the southern extremity of this section have also increased the accumulation of sand which, in turn, is probably responsible for the general paucity of corals between stations AB and AD. The predominating species here, *Pocillopora cespitosa,* has gained a foothold on rocks above the reach of the shifting sand.

It is obvious that the influence of sand and silt has been greater near the extreme northern and southern boundaries than in the middle area of the section of reef surveyed, and in the middle area is to be found a larger variety and a more vigorous growth of corals.

RESPONSE OF CORALS TO DIRECT SUNLIGHT

A large number of experiments were conducted with a view of determining the comparative resistance of Hawaiian corals to sunlight while entirely out of water (Table 23). For these tests the corals were taken from the sea water, placed on a wire frame, and exposed to the direct rays of the sun. At intervals of 15 minutes the specimens were removed from the sunlight and restored to circulating sea water for later examination.

Because the degree of resistance of marine organisms to such a dehydration process as exposure to sunlight varies with the intensity of the accompanying heat and with the general humidity of the atmosphere, readings of the dry and wet bulbs of the recording instrument were taken during the course of the experiments.

All species survived 15 minutes under temperature and atmospheric conditions recorded in Table 23. Nearly 50 per cent of the species endured 30 minutes but only 4 were alive after a period of 45 minutes. Three species survived for 1 hour and *Favia hawaiiensis* and *Leptastrea agassizi* recovered after a period of 1 hour and 15 minutes. *Fungia scutaria,* though not tested for more than 1 hour, indicated a resistance equal to that of *Favia* and *Leptastrea. Stephanaria stellata,* which shows remarkable resistance to increased temperature when submerged under water, proved to be highly sensitive when subjected to the direct rays of the sun. Most individuals of this species died in 15 minutes but some lived for 30 minutes. After an exposure of 30 minutes to the sun some representatives of this species remained 5 days in circulating sea water before evidences of recovery were noted.

Doubtless there are many reefs on which coral colonies are partially exposed to the air and sun at very low tides. I have observed this on the reefs of Oahu, Wake, and Johnston islands. Vaughan (22) found that if the bases of some corals, especially those with spongy skeletons, are submerged in water the upper portion will endure the direct rays of the sun for a much longer period than when the entire colonies are exposed. These species are capable of drawing up water by capillarity, thereby preventing rapid evaporation from the tissues of the polyps. Regarding this my observations are in accord with the finding of others. For example, *Montipora verrucosa, Porites evermanni,* and *Porites lobata* forma *lacera* lived for 1½ hours exposed to the direct sunlight with an air temperature of 35.5°C. when the bases of the colonies were submerged in water. When wholly exposed to the air and strong sunlight, these species usually die in from 30 to 45 minutes.

TABLE 23. COMPARATIVE RESISTANCE OF 20 HAWAIIAN CORALS WHEN ENTIRELY OUT OF WATER AND EXPOSED TO THE DIRECT RAYS OF THE SUN.

Atmospheric conditions of temperature and moisture recorded at the end of the specified periods. Experiment beginning at 2:32 p. m. April 20, 1925. A = specimen alive, D = dead at end of indicated periods.

Corals	15 min. Dry bulb 96° F. Wet bulb 79°	30 min. Dry bulb 94° F. Wet bulb 78°	45 min. Dry bulb 96° F. Wet bulb 80°	60 min. Dry bulb 94° F. Wet bulb 78°
Pocillopora meandrina var. nobilis	A	A	D	
Pocillopora ligulata	A	A	D	
Pocillopora cespitosa	A	A	D	
Porites evermanni	A	D		
Porites lobata forma lacera	A	D		
Porites lobata forma infundibulum	A	D		
Porites lobata forma centralis subforma alpha	A	D		
Porites lobata forma centralis subforma beta	A	A	D	
Porites compressa forma granimurata	A	D		
Porites compressa forma angustisepta	A	D		
Montipora verrucosa	A	A	D	
Montipora flabellata	A	A	A	D
Montipora verrilli	A	D		
Montipora patula	A	D		
Pavona varians	A	D		
Cyphastrea ocellina	A	D		
Stephanaria stellata	A	A	D	
Favia hawaiiensis	A	A	A	A
Leptastrea agassizi	A	A	A	A
Fungia scutaria	A	A	A	A

subforma beta A A D

On some Hawaiian reefs the coral colonies are partially exposed to the air at extremely low tides, but none was observed on the section of Waikiki reef under consideration even with tides infrequently as low as -0.5. At such times, however, numerous colonies of *Pocillopora cespitosa* on the flats near shore are covered by not more than 2 or 3 inches of water. The species which approach within 100 feet of the shore grow low and close to the bottom so that very unusual conditions must exist if the water should entirely recede from them. During a tidal wave on February 3, 1923 when, in the course of about 4 hours, nearly one-half of the reef platform was uncovered several times, many coral colonies were exposed to the air and sun for from 15 to 20 minutes. No serious effect was observed on the living corals as a result of this unusual disturbance.

In Kawela Bay, windward Oahu, during a low tide of -0.5 on June 9, 1925, I observed many coral colonies, chiefly forms of *Porites lobata* and *Porites compressa,* exposed above the surface of the water to an extent of not less than three inches. This unusually low tide occurred on two successive mornings but early in the day before the sun was high. In addition, the bases of the colonies were submerged in water which assured their safety for a much longer period than if they were wholly exposed.

Unless a tide sufficiently low to completely uncover coral colonies occurs during the warmest period of the day there is no danger of the Hawaiian reefs becoming depopulated by exposure to direct sunlight. Tides as low or lower than -0.4 occurred 30 times at Honolulu during 1924, and 27 times in 1925. On two dates only during each of these years did the low tide occur at an hour of the day when there might have been injury done to coral colonies had they been completely exposed to the air.

RESPONSE OF CORALS TO AIR IN THE SHADE

Should tides sufficiently low to wholly uncover coral colonies on a reef occur at night or on cloudy days it is obvious that evaporation of water from the tissues would proceed at a lower rate than when exposed to direct sunlight. It is, therefore, to be expected that corals can resist exposure to air for a longer period when shaded than when receiving the direct rays of the sun about midday or in the early afternoon.

To test the comparative resistance of Hawaiian corals to a complete exposure to air but in the shade, 21 species were exposed for a period of 5 hours during which time the temperature of the air was recorded. (See Table 24.) It will be seen that nearly all the species lived for 3 hours out of water in the shade, that more than 70 per cent were alive at the end of 4 hours and that 9 species recovered after an exposure of 5 hours. As a group, the *Pocillopora* will endure 5 hours but not much longer, and this period is usually the limit for *Stephanaria stellata* and *Fungia scutaria,* while it is rather an exception for *Porites compressa* forma *angustisepta*. *Favia hawaiiensis* and *Leptastrea agassizi* are usually considerably injured by an exposure of 5 hours, but on one occasion both species exhibited slight evidences of life at the end of 9 hours.

The tenacity of life shown by corals when wholly exposed to air but in the shade clearly indicates that tides low enough to completely uncover near shore species, if occurring at night or on cloudy days, would have no injurious effect upon the Hawaiian coral population. *Pocillopora cespitosa* which, at least on Waikiki reef, would be most subject to such conditions due to its near shore approach, is capable of enduring 4 or even 5 hours of total exposure.

uncover near shore species, if occurring at night or on cloudy days

RESPONSE OF CORALS TO ABSENCE OF SUNLIGHT

It is well known that reef-forming corals are limited in their bathymetrical range to comparatively shallow water but the views expressed by various investigators relative to the depth limitation are not in agreement. About the Hawaiian islands this range is about 40 fathoms, although most of the species are probably best developed within 25 fathoms. Wood-

TABLE 24. COMPARATIVE RESISTANCE OF 21 HAWAIIAN CORALS WHEN ENTIRELY OUT OF WATER BUT IN THE SHADE.

Air temperature taken at the end of the period indicated. A = specimen alive, D = dead at the end of the specified period.

Corals	3 hrs. Temp. of air 26° C.	4 hrs. Temp. of air 26.3° C.	5 hrs. Temp. of air 25.2° C.
Pocillopora meandrina var. nobilis	A	A	A
Pocillopora ligulata	A	A	A
Pocillopora cespitosa	A	A	A
Porites evermanni	A	A	D
Porites lobata forma lacera	A	A	D
Porites lobata forma centralis subforma alpha	A	A	D
Porites lobata forma centralis subforma beta	A	A	D
Porites lobata forma centralis subforma gamma	D		
Porites compressa forma granimurata	A	A	D
Porites compressa forma angustisepta	A	A	A
Montipora verrucosa	A	A	D
Montipora flabellata	A	A	D
Montipora patula	A	A	D
Pavona varians	A	D	
Pavona duerdeni	A	D	
Cyphastrea ocellina	A	D	
Stephanaria stellata	A	A	A
Stephanaria brighami	A	D	
Favia hawaiiensis	A	A	A
Leptastrea agassizi	A	A	A
Fungia scutaria	A	A	A

Jones (27) is of the opinion that sedimentation is a most important factor in determining the bathymetrical range of shallow water corals. Dana's suggestion (7) that the depth range of reef-forming corals was limited by decreasing temperature is not supported by Mayor's observations at Samoa where he found a decided thinning out of coral colonies at a depth of 6 or 7 fathoms, while there was a difference of less than 1°C. between the surface water and that at a depth of 200 feet. Mayor (16) believed that diminishing light was responsible for the reduction in the number of corals even at a few fathoms below the surface. Gardiner (8) was of the opinion that light by its action on the commensal algae of the tissues of the corals limited their depth-range. Vaughan (21), while recognizing the value of light in this connection, expressed the view that other factors including pressure and food supply may also influence the depth limits of reef-forming corals.

The presence of Zooxanthellae, or unicellular algae, in the endoderm of reef-building corals has been construed by many investigators as a symbiotic relationship. Recent work by Boschma (2) on Anthozoa and by Parker (19) on *Paramecium bursaria* seems to indicate, however, that conditions may arise making possible the digestion of infesting algae by the host (p. 37). Although the real advantage in this association of algae with coral is somewhat obscure, the association does exist among shallow water corals almost without exception. A reduction of sunlight naturally inhibits the proper activities of the plants and also weakens the vigor of the corals. Such a relationship, therefore, is absent in deep water corals which exist below the penetration of light rays.

Both Vaughan (22, 24) and Mayor (16) have made observations on the detrimental effect of diminished light upon shallow water corals. Vaughan noted that few or no corals at Dry Tortugas grew attached to the more central piers at Ft. Jefferson where the light was very weak, and found that total darkness limited the life of the most resistant corals to about 43 days. Mayor (16) reports a considerable reduction both in the number and size of coral colonies of certain species living at depths below seven fathoms on the Samoan reefs and ascribes the paucity and slow growth of corals at those depths to a lessened light intensity.

My determinations of the comparative resistance of Hawaiian corals to the absence of light were made by placing 17 species in a specially constructed floating dark box anchored on the reef (Table 25). Species of *Pocillopora* and *Porites*, in general, show least resistance to the absence of light; 18 days was fatal to all species of *Pocillopora* and to all of the *Porites* with the exception of *Porites lobata* forma *lacera* which showed slight life at the end of that period. Four species, *Stephanaria stellata, Favia hawaiiensis, Leptastrea agassizi,* and *Fungia scutaria,* survived for 45

below the penetration of light rays.

days when the experiment was terminated. All were more or less injured by the loss of coenenchyma and were very much paler than at the beginning of the experiment. *Favia hawaiiensis* was bleached white and required a month in circulating sea water, in diffused light, before the green coloration, due to the presence of algae, began to make its appearance.

I have frequently observed that corals brought into the laboratory from the reef and placed in running sea water in shallow containers in strong, diffused light soon show a decided intensification of color indicating an increase in quantity of infesting algae.

Experiments were also conducted to determine the behavior of planulae of corals in total darkness. On one occasion planulae of *Cyphastrea ocellina* lived for 60 days in a small container with sea water changed daily. During this period the normal brown coloration was wholly lost, but the pearly-

TABLE 25. COMPARATIVE RESISTANCE OF 17 HAWAIIAN CORALS TO TOTAL DARKNESS,

Corals suspended in a light-proof box anchored on Waikiki reef. D = specimen dead, A = alive at end of specified period.

Corals	18 da.	33 da.	38 da.	45 da.
Pocillopora meandrina var nobilis	D			
Pocillopora ligulata	D			
Pocillopora cespitosa	D			
Porites evermanni	D			
Porites lobata forma lacera	A	D		
Porites lobata forma centralis subforma alpha	D			
Porites lobata forma centralis subforma beta	D			
Porites compressa forma granimurata	D			
Porites compressa forma angustisepta	D			
Montipora verrucosa	D			
Montipora flabellata	A	D		
Pavona varians	A	A	D	
Stephanaria stellata	A	A	A	A
Cyphastrea ocellina	A	D		
Favia hawaiiensis	A	A	A	A
Leptastrea agassizi	A	A	A	A
Fungia scutaria	A	A	A	A

white markings, characteristic of this planula, were still clearly defined. None of the planulae became fixed during this time and there was no evidence of the formation of tentacles, as frequently appears in this species while the organisms are still free swimming. A gradual reduction in the size of the planulae occurred until at the end of the experiment the survivors were not more than one-half as large as at the beginning.

Repeated tests with the planulae of this species under conditions of total darkness resulted in about 50 per cent of the total number becoming fixed and developing slight skeletal structures. With the sea water changed daily they lived for more than three months but gradually grew paler and finally died.

The planulae of *Dendrophyllia manni* under similar conditions of darkness apparently become fixed more readily than do those of *Cyphastrea ocellina.* In a number of parallel experiments 100 per cent of the planulae of *Dendrophyllia* became attached to the bottoms and sides of the glass containers within a period of 30 days. All deposited skeletons and grew into small polyps, some of which lived more than three months in total darkness with the sea water changed daily. The exclusion of light did not greatly reduce the orange color characteristic of both planulae and adults of this species, but after the first month of the fixed condition there was a noticeable thinning of the tissues of the polyps, probably due to insufficient nourishment.

SUMMARY AND CONCLUSIONS

1. The extreme variation in temperature to which the shallow water corals of Waikiki reef are subjected during the year is approximately 10°C. Near shore species may occasionally be subjected to temperatures as high as 31°C. or 32°C. for brief periods during very low tides. Rarely does the temperature of the near shore water washing living corals fall below 20°C.

2. Species of Hawaiian corals vary in their resistance to thermal changes. Should the temperature of the reef water slowly rise to 32°C. and be maintained at that point for 8 hours, more than half the species of corals would die; and if maintained for 24 hours probably not more than three species would survive. The Hawaiian shallow water corals are living within from 5°C. to 10°C. of their upper death points. Near shore species which are at times subjected to maximum temperatures are not, however, the most resistant to increasing heat.

3. Hawaiian corals show greater resistance to decreasing temperatures than to rising temperatures. They endure a relatively low thermal degree much longer than a correspondingly high degree. Should the temperature of the reef water be slowly reduced to 15°C. and maintained at that point for 23 hours, probably not more than 3 species would be exterminated. The species of *Pocillopora,* which are very sensitive to sudden heating, show remarkable endurance on rapidly falling temperatures. Other species such as *Leptastrea agassizi* and *Favia hawaiiensis,* which are highly resistant to increasing temperatures, also endure cold very well even when the thermal change takes place slowly. Of all the shallow water corals examined, my experiments indicate that *Leptastrea agassizi* and *Favia hawaiiensis* exist within by far the widest margin of safety with reference to temperature.

4. Rising and falling temperatures completely inhibit the feeding responses of Hawaiian shallow water corals within a few degrees of their death points. The feeding responses of the corals examined cease at rising temperatures of 31.5°C. to 35.5°C., and at falling temperatures of 11.5°C. to 7.9°C. On the reversal of temperatures, after the complete inhibition of the feeding responses, feeding is resumed much more quickly from a condition of heat paralysis than from that of cold rigor.

5. The planulae of *Cyphastrea ocellina* are more highly resistant to increasing temperatures than are the adults of that species, but are more sensitive to temperatures of 10°C. or lower. Planulae of this species, at least, are apparently acclimated to higher more readily than to lower degrees of temperature. The planulae, during the greater part of their free ex-

istence, swim at or near the surface of the water, which fact may be correlated with their ability to endure higher temperatures at this period of their life than during the adult stage.

6. An exposure of 30 minutes to fresh water is fatal to nearly all species of Hawaiian shallow water corals. Not more than three species survive such treatment for 2 hours and these usually die within 4 hours. A very large proportion of Hawaiian corals are able to endure a 50 per cent dilution of sea water for a period of 15 hours, and more than half the species will survive this reduced salinity for 23 hours. At least three species may live in a 50 per cent dilution of sea water for 5 days but usually all are dead at the end of 6 days. Fully one-half the species of Hawaiian corals survive 31 hours in a 66 2/3 per cent solution of sea water. At least 4 species which readily live 30 days in this reduced salinity accommodate themselves to such an extent that they endure it for a period of 4 months without serious injury. Two species, *Favia hawaiiensis* and *Leptastrea agassizi,* lived in this dilute sea water for 6 months, and, without doubt, would live indefinitely if sufficient food were available. Approximately 70 per cent of the shallow water corals examined endured a 75 per cent solution of sea water for 31 hours. At least 7 species will live 30 days in this solution and all but one of these will continue to endure it for 4 months or more without serious injury. By a process of gradual accommodation, a higher degree of resistance to lower grades of salinity is indicated in certain species.

7. Experiments with increased salinities show that a large proportion of Hawaiian corals are able to endure a solution of sea water of about 110 per cent for 96 hours. Three species lived in this concentration for 3 months without much injury. In a solution of sea water of about 125 per cent usually but 3 species of corals survive for 3 days, and 20 days is commonly the extreme limit of endurance of the most resistant forms. Of the species examined, *Favia hawaiiensis* and *Leptastrea agassizi,* are less sensitive than others to this degree of salinity. In a solution of sea water increased in salinity to about 150 per cent, only 2 species of corals lived at the end of 24 hours. My experiments with altered salinities seem to indicate that at least 3 or 4 species of Hawaiian corals are able to live for at least 3 months in solutions of sea water ranging from about 66 2/3 per cent to about 110 per cent. Corals accommodate themselves much more readily to limited dilutions of sea water than to concentrations of similar degrees. Planulae of *Cyphastrea ocellina* are capable of enduring a 50 per cent dilution of sea water for 25 times as long as the adult of that species.

8. Of the 23 species of Hawaiian corals buried under 4 inches of sand and silt all but 2 survived a period of 12 hours, *Pocillopora meandrina* var. *nobilis* and *Pocillopora ligulata* being the more sensitive. Less than 50 per

cent of the species, however, were able to endure this condition for 24 hours, and at the end of 5 days usually but 3 species were alive. Of those examined, some individuals of *Favia hawaiiensis* and *Leptastrea agassizi* survived after having been buried for 10 days. *Favia* is least injured by such treatment and of all the Hawaiian corals tested this species is also most resistant to heating.

9. Approximately 50 per cent of the Hawaiian reef corals die within 30 minutes if entirely removed from the sea water and exposed to the direct rays of the sun during the hottest part of the day. Of 20 common species usually but 3 survive these conditions for a period of 1 hour. When the bases of colonies of corals remain submerged in sea water, species with porous skeletons may live three times as long as when completely exposed to the sun's rays. About 40 per cent of the shallow water corals will survive a period of 5 hours if entirely removed from the sea water but kept in the shade.

10. Sunlight is apparently an important factor in the life of shallow water corals. Approximately 50 per cent of Hawaiian corals die in 18 days when exposed to total darkness on the reef with normal circulation of water and normal food supply. In a group of 17 species, 4 survived the absence of sunlight for a period of 45 days. Planulae of two species of Hawaiian corals tested became fixed in total darkness more or less readily. All the planulae of *Dendrophyllia manni* attached themselves within 30 days while only about 50 per cent of those of *Cyphastrea ocellina* responded in a similar way. Some resulting polyps of both species lived more than 3 months, with light excluded, but all gradually took on an unhealthy appearance and eventually died. Lack of food may have been a factor in these experiments which were carried on in a dark room with standing sea water changed daily.

11. The physical condition of the living coral colonies populating the platform of the Waikiki reef, and their present distribution over the reef are due, without doubt, to a combination of factors some of which are of more importance than others. The paucity of living corals along the northern extremity of this section of reef is doubtless due to the combined influence of fresh water and silt carried out over the reef in former years. Silt especially is probably responsible for much of the stunted condition of coral colonies over wide areas of this reef platform. The scarcity of corals in the southern area of this section may be accounted for, in large part at least, by the inward shifting of sand due to wave action, and also by the disturbance of the platform itself due to dredging operations. Dilution of near shore waters is constantly occurring especially in the southern extremity of the section due to the overflow from the aquarium, laboratory, and other drainage outlets. This dilution, however, has a very small influence on the

reef water. Although it may retard the advance of corals shoreward, it is probably not an important factor in their ecology at a distance of 150 feet from the shore.

12. Under normal conditions, even at extremely low tides, I have not observed coral colonies on this section of Waikiki reef to be wholly or partially exposed to the direct rays of the sun.

13. Wave action is an agent of no little significance in the destruction of fragile coral colonies especially on a reef such as Waikiki where there is an abundance of debris. Colonies of *Stephanaria* in this section of reef are almost always found to be detached from their supports and in a fragmented condition, as are also certain species of branching *Porites*. Species of *Pocillopora* are easily injured or destroyed by the shifting of their supports and the movement of debris.

14. Among the most destructive agents of coral colonies on Waikiki reef are sea weeds. They are responsible for the rapid and complete smothering of many species of living corals. Even the *Pocillopora* which are more resistant to the ravages of sea weeds than are many other forms are not wholly exempt. Boring algae, mollusks, worms, sponges, etc., are also of common occurrence in Hawaiian shallow water corals. Their presence, without doubt, weakens the skeletal structure of the coral thereby hastening its destruction even though no other detrimental effects may be produced.

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