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Behavior of Coral Planulae under Altered Saline and Thermal Conditions

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INTRODUCTION

Although it is possible to observe more than 20 species, varieties, and forms of stony corals on a typical reef of the Hawaiian Islands without advancing into water more than two or three feet deep, the planulae — representing the free swimming reproductive phase — of very few of them have been studied or even recognized. Of the corals about Oahu with which I am familiar, three species can be depended upon to yield planulae in considerable quantity or in sufficient numbers for experimental purposes. They are *Pocillopora damicornis* (Linnaeus), *Cyphastrea ocellina* (Dana), and *Dendrophyllia manni* (Verrill). Stray planulae of other species have occasionally been observed among an assortment of living corals but their source could not be determined. I have never taken coral planulae in the plankton over living colonies on Waikiki reef or in Kaneohe Bay where much towing has been done. Stephenson (12)[1] comments on the paucity of planulae in the tow on the Great Barrier Reef and suggests that the planulae may remain on the bottom and close to their source. It is a general observation, however, that planulae extruded from colonies under laboratory conditions tend to rise to the surface of the water and remain there for some time. Experiments indicate that this tendency to seek the surface occurs in total darkness as well as in subdued light. Twelve planulae of *Pocillopora damicornis,* immediately after extrusion, were placed in each of two cylinders 14.5 inches tall, filled with sea water. One cylinder was subjected to the subdued light of the

[1] Numbers in parentheses refer to Literature Cited, page 304.

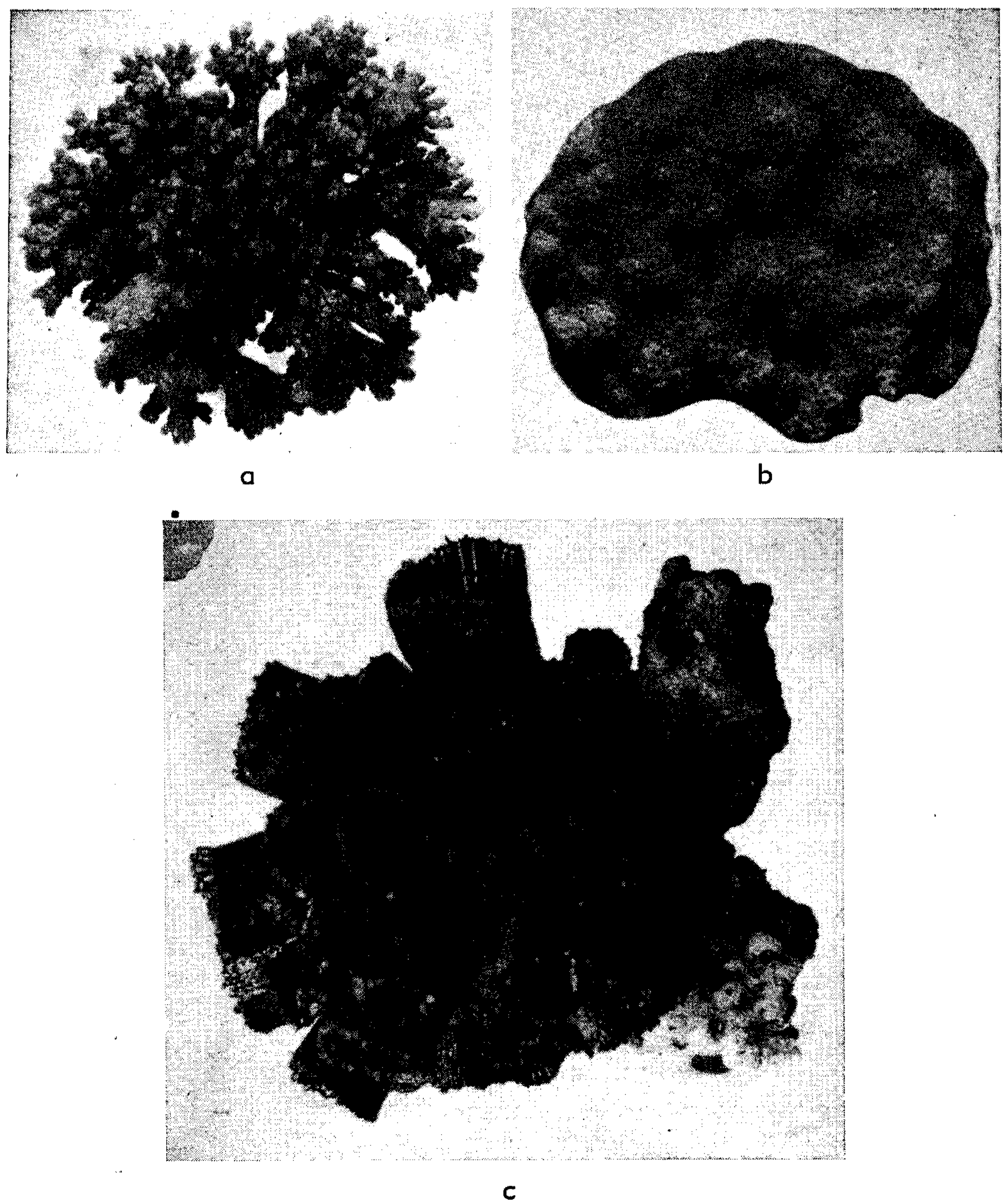

FIGURE 1.—**a**, *Pocillopora damicornis*; **b**, *Cyphastrea ocellina*; **c**, *Dendrophyllia manni*.

laboratory and the other to total darkness. The position of the planulae was noted after intervals of two and three hours. Readings at both periods were similar. In subdued light, 10 planulae were at the surface and two at the bottom. In darkness all planulae were at the surface. Positive thigmotaxis was indicated, as the organisms remained in contact with the glass surface instead of swimming freely through the water, but the influence of gravity was not greatly in evidence.

There have been occasions, however, under natural conditions, when coral planulae appeared on or near the surface of the ocean. Kawaguti (8) found great quantities of planulae of an *Acropora* in the plankton on the coast of Taiwan in the month of July, two days after full moon.

On many of the shallow reefs of Oahu *Pocillopora damicornis* (*P. cespitosa* Dana of some authors) is one of the most familiar corals. The colony consists of a finely branched clump, rarely exceeding 6 inches in diameter and usually considerably less (fig. 1, *a*). On Waikiki reef it grows within 40 feet of the shore where the colonies are small and stunted indicating unfavorable ecological conditions, which it doubtless must tolerate in such localities. The most luxuriant growths of the species I have seen are on reefs in Kaneohe Bay. The bathymetric distribution of the species, as given by Vaughan (13), is 1 to 25 fathoms.

The planula of *P. damicornis* is club-shaped, large ones being about 1.5 mm. in length. The aboral end, which precedes when the organism is in motion, is usually somewhat broader than the oral end. Algal cells crowding the interseptal areas are responsible for the brown longitudinal stripes by which the planula may be recognized (fig. 2, *a*).

In a previous paper (6) I stated that this coral had been observed to extrude planulae under laboratory conditions during the month of January. Since that time (1929), further investigation indicates that the release of planulae from *P. damicornis* in Hawaii may occur during all months of the year. Hada (7) states that in the Palau Islands the planulae of *P. cespitosa* are probably extruded throughout the year but apparently more actively during December than the other months of observation. On the Great Barrier Reef Stephenson (12) found the extrusion of planulae from *Pocillopora bulbosa* to be intermittent, the emission occurring at the time of new moon in the summer months and during full moon in the winter months.

In Hawaii the spawning of *P. damicornis* has not positively been associated with the phases of the moon, although more extended observation is necessary before a conclusion is reached. Planulae of this species, however, are almost always obtained by bringing well-developed colonies, or parts of them, into the laboratory and submerging them in a container of standing sea water. As the planulae are released, usually one planula from a polyp, they rise to the surface of the water showing positive phototaxis.

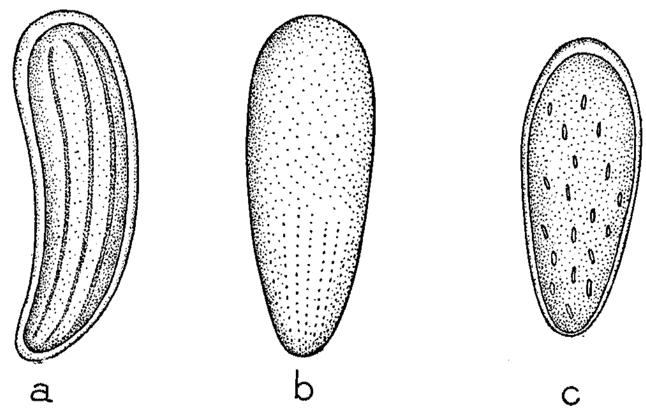

FIGURE 2.—**a**, planula of *Pocillopora damicornis;* **b**, planula of *Dendrophyllia manni;* **c**, planula of *Cyphastrea ocellina.*

Typical colonies of *Cyphastrea ocellina* consist of thin encrusting layers from which are developed blunt knobs or lobes resulting in a very irregular surface (fig. 1, *b*). The colonies assume the contour of the surface which serves as a support, and may attain a length or breadth of 5 or 6 inches on local reefs, but most of them are smaller. The species is abundant in Hanauma Bay, common in Kaneohe Bay, on Waikiki reef, and at other localities about Oahu. In some localities, it approaches within 30 feet of the shore and its bathymetric distribution is 1 to 25 fathoms.

A large, mature planula of *Cyphastrea ocellina* slightly exceeds 1 mm. in length, its general form resembling that of the planula of *P. damicornis,* but the algal cells scattered throughout the endoderm are not distinctly arranged in longitudinal stripes as they are in that species. Distinctive markings of the planula of *Cyphastrea* consist of minute, fusiform, pearl-white bodies in the endoderm, scattered throughout or crowded nearer the oral end (fig. 2, *c*). These refractive bodies, of doubtful nature, maintain their entity under abnormal conditions. In the absence of light the chlorophyl of the algal cells may disappear but the pearl-white bodies remain distinctly outlined.

Normal emanation of planulae from *Cyphastrea* probably occurs in Hawaii throughout the year. Their extrusion has been observed under laboratory conditions during the months of January, February, April, June, September, October, November, and December. Observations were not made during the other months. Apparently phases of the moon have no influence in the production of planulae of this species. During November extrusion occurred on the 7th, 17th, 24th and 29th of the month.

A sudden or gradual increase of temperature of the water surrounding colonies of *Cyphastrea* often results in rapid emission of planulae. Colonies not normally producing planulae may extrude them when the temperature is gradually raised from normal to 35° C., their appearance often beginning about 31.6° C. Plunging colonies into water at temperatures ranging from 33° C. to 35° C. usually produces similar results. That these abnormal conditions force the extrusion of planulae is indicated by the appearance of numerous small and immature forms among those of regular size. Rapid emanation of planulae has also occurred in this species when colonies were placed in a dilute solution of sea water (one part sea water to one part fresh water).

The third coral, *Dendrophyllia manni,* planulae of which are considered in this paper, develops into a more or less spherical clump of corallites (calicles) radiating from a central nucleus (fig. 1, *c*). As growth takes place the corallites diverge from each other, large ones reaching a height of 20 mm. and a diameter of 12 mm. The entire colony may include 50 or more corallites in various stages of development, and reach a diameter of 3 or 4 inches. About Oahu the species is abundant in Kaneohe Bay, where it flourishes along the edges of reefs, where there is good circulation of water, at depths of a fathom or less. Colonies cling to the irregular, vertical face of a reef or are established under ledges where the light is subdued. The species has also been taken on Waikiki reef but apparently is rare on the leeward side of the island.

Living colonies of *Dendrophyllia manni* are very striking in appearance as each of the large corallites encloses a polyp of bright orange color. Unlike polyps of the two preceding species, those of *Dendrophyllia* lack algal cells in their tissues.

Large planulae of this species attain a length of about 2 mm. In form (fig. 2, *b*) they are quite similar to those of *P. damicornis*. The homogeneous color, like the parent polyp, renders the planula very conspicuous. There seems to be an irregular periodic spawning season for this species, ranging from late summer into early winter. During one year extrusion of planulae was observed about the middle of August, and during other years it began in late October continuing into the following January with the peak in November. Observation of colonies in the laboratory throughout the year indicates an infertile period extending through most of the winter, spring and summer months.

During the peak of the spawning season, large numbers of planulae are developed from a colony and from a single polyp. They may be extruded from polyps in streams, resulting in the release of several hundred in a few minutes. By inserting a pipette in the mouth of a polyp, quantities of planulae may be extracted. A polyp may become exhausted in its production of planulae, but after a rest of several days again enters into a reproductive phase. I have not observed any lunar influence in the development of planulae in this species. Planulae have been extruded from colonies daily throughout the month of November.

Coral colonies increase in size by budding, but a species is distributed by means of sexually produced planulae which escape through the oral aperture of the parent polyp. Following a period of free existence the planula may settle and become affixed by the aboral end, thus beginning a new colony. The dispersal of corals, therefore, depends upon the success of the planulae in maintaining themselves under such varied ecological conditions as they may meet in the sea, and upon the place of attachment being favorable to the future development of a colony. Although provided with locomotor cilia on the external surface, the movements of planulae are weak, resulting in their being carried by currents, perhaps for considerable distances from their origin. The response of planulae to light, temperature, currents, salinity, and other physical and chemical factors doubtless accounts for the presence or absence of coral colonies in a given locality.

Careful studies have been made by a number of investigators of the postlarval development of corals, but less attention has been given to the behavior of planulae during their free existence and to their responses to the ecological factors of their environment. Kawaguti (9) recently discussed the phototaxis, geotaxis, rheotaxis, and thigmotaxis of the planulae of four corals, one of which (*Pocillopora damicornis*) is considered in this paper. He concluded that the distribution of corals possessing zooxanthellae was largely determined by the positive phototaxis and negative geotaxis of their planulae. Abe (1), in observations on the behavior of planulae, noted that those of *Fungia* showed a reverse in phototaxis about 24 hours after extrusion, changing from a positive to a negative response. I recorded (6) a similar change in planulae of *Dendrophyllia* which possess no zooxanthellae.

This paper deals with the responses and behavior of planulae of three Hawaiian shoal water corals when subjected to controlled variations of salinity and temperatures. It may be assumed that organisms of this nature are capable of physiological adjustments permitting them to survive a considerable stress of environment. It is not assumed, however, that planulae are commonly forced to meet or endure the extremes of variation included in the following experiments. It is, rather, an attempt to fix, in some degree, a range of endurance.

RESISTANCE OF PLANULAE TO FRESH WATER AND DILUTE SEA WATER

It is quite probable that coral planulae may, at times, come into contact with various degrees of dilute sea water on shallow reefs. Doubtless torrential rains, especially during periods of low tide, seriously affect marine organisms at or near the surface of the water. I determined (5) that colonies of *Pocillopora damicornis* (*P. cespitosa*) will live 31 hours but not 49 hours in a mixture of sea water and fresh water in a ratio of 3: 1, and that *Cyphastrea ocellina* will survive four days but not seven days in a similar solution. According to Child (3), young organisms acclimate themselves more quickly than older ones to adverse conditions if the change is not a lethal one, but the young are more susceptible if the altered condition is quickly fatal.

Planulae of the three corals under consideration were suddenly subjected to fresh water for periods ranging from 30 seconds to and including 12 minutes. The contact with fresh water results in an immediate cessation of movement with a sharp contraction into a flattened body or a shortening of the organism with irregularity of contour (figs. 3, *a;* 4, *a;* 5, *a*). On return to sea water, if the planula is still living, a gradual elongation of the body occurs and the contour becomes more regular (figs. 3, *b;* 4, *b;* 5, *b*). Movement may be resumed before expansion of the planula is completed. An exposure of 30 seconds to fresh water apparently has no serious effect on planulae of *Cyphastrea,* as activity was resumed within four minutes after being returned to sea water, and the recovery was almost as rapid following a contact with fresh water of two and a half minutes (table 1). The planulae of *Pocillopora* and *Dendrophyllia,* however, were more permanently affected by an exposure of 30 seconds to fresh water, both requiring 24 hours for the restoration of activity. An exposure of one minute to fresh water proved fatal to planulae of *Pocillopora,* and two and a half minutes constituted a lethal exposure for those of *Dendrophyllia.* A contact of 12 minutes was fatal to the planulae of *Cyphastrea* (table 1). I determined (5) that colonies of *Pocillopora* and *Cyphastrea* did not survive a 30-minute contact with fresh water (shorter periods not recorded).

TABLE 1.—BEHAVIOR OF CORAL PLANULAE ON SUDDEN EXPOSURE TO FRESH WATER FOR SHORT PERIODS, THEN RETURN TO NORMAL SEA WATER

TIME EXPOSED (FRESH WATER)	POCILLOPORA DAMICORNIS (SEA WATER)	CYPHASTREA OCELLINA (SEA WATER)	DENDROPHYLLIA MANNI (SEA WATER)
30 seconds	active after 24 hours	activity after 2-4 minutes	activity after 24 hours
1 minute	no recovery	recovery in 3-4 minutes	recovery after 24 hours
2.5 minutes	no recovery	recovery in 3-5 minutes	no recovery
12 minutes	no recovery	no recovery	no recovery

In addition to cessation of movement and change of form, the most obvious effect upon the planula of exposure to fresh water is a loss of the ectodermal layer. Sloughing off of the outer cells may occur either while exposed to fresh water or after being returned to sea water. The ectoderm seems to be more quickly affected in planulae of *Pocillopora* and *Dendrophyllia* than in those of *Cyphastrea* (figs. 3-5). Under an oil immersion lens, elements of the removed material may be recognized as ectodermal cells, cilia, and nematocysts. Resumption of movement of planulae from which peripheral cells have been removed suggests that ciliated cells of the ectodermal layer may be regenerated within 24 hours (table 1).

On subjecting planulae to sea water of subnormal salinity, it is apparent that those of *Cyphastrea* are more resistant than others to the greater dilutions and that planulae of *Dendrophyllia* are the most sensitive (table 2). In a solution of one part sea water to two parts

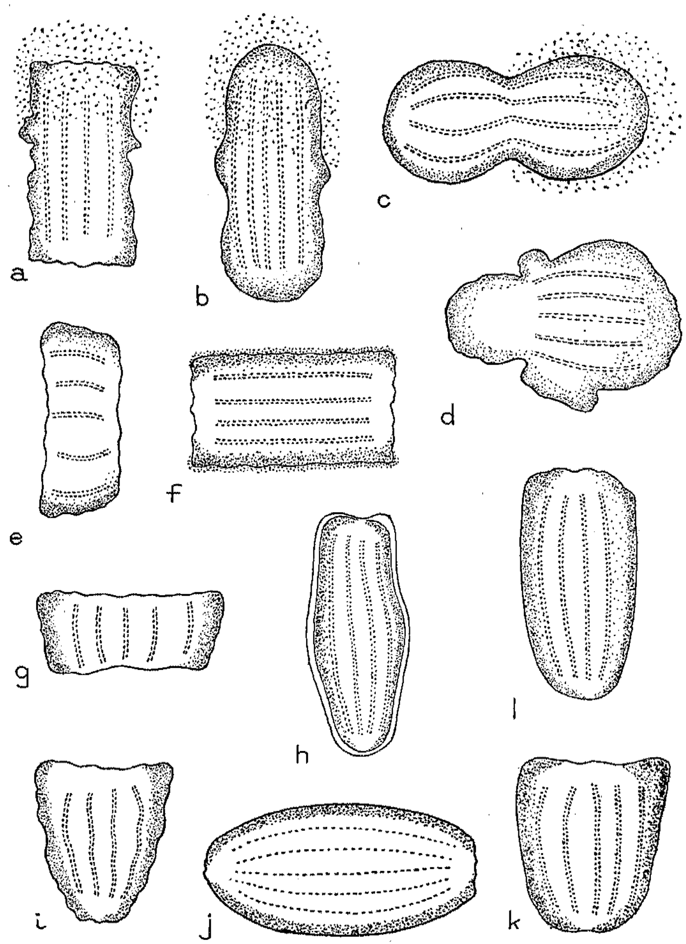

FIGURE 3.—Response of planulae of *Pocillopora damicornis* to fresh water and dilute sea water: **a,** after 30 seconds in fresh water, then two minutes in normal sea water (epidermis lost, no movement); **b,** 20 minutes after planula *a* is returned to normal sea water (appearance normal after 24 hours, movement slight, recovery probable); **c,** after one minute in fresh water then return to normal sea water (epidermis lost, no movement); **d,** 24 hours after planula *c* is returned to sea water (no recovery); **e,** immediate effect of exposure to solution of one part sea water to three parts fresh water (sharply contracted, cessation of movement); **f,** after exposure of 10 minutes to the solution (epidermis lost, no movement, disintegrates in eight hours); **g,** immediate effect of exposure to solution of one part sea water to one part fresh water (sharp contraction, cessation of movement); **h,** after an exposure of 10 minutes to this solution (epidermis opaque, intact, no movement); **i,** planula *h* after exposure to the solution for five hours (active, partially contracted); **j,** effect of exposure to solution of two parts sea water to one part fresh water (cessation of movement, partial contraction, normal activity resumed in 45 minutes); **k,** effect of exposure to solution of three parts sea water to one part fresh water (partial contraction, cessation of movement but resumed in three minutes); **l,** 12 hours after exposure to the solution (activity normal, slightly contracted, surface not affected).

TABLE 2.—BEHAVIOR OF CORAL PLANULAE ON SUDDEN EXPOSURE TO DILUTE SEA WATER FOR GIVEN PERIODS, THEN RETURN TO NORMAL SEA WATER

DILUTION	TIME EXPOSED (DILUTION)	POCILLOPORA DAMICORNIS (SEA WATER)	CYPHASTREA OCELLINA (SEA WATER)	DENDROPHYLLIA MANNI (SEA WATER)
1 part sea water, 4 parts fresh water	30 seconds	recovery in 17 minutes	recovery in 3 minutes	recovery in 24 hours
	1 minute	recovery in 16 minutes	recovery in 4 minutes	no recovery
	2 minutes	recovery in 15 minutes	recovery in 8 minutes	no recovery
	5 minutes	recovery in 24 hours	recovery in 15 minutes	no recovery
1 part sea water, 2 parts fresh water	5 minutes	recovery after 1 hour	recovery in 5 minutes	recovery in 5 minutes
	2 hours	no recovery	recovery in 20 minutes	recovery in 20 hours
1 part sea water, 1 part fresh water	1 minute	recovery at once	recovery at once	recovery at once

fresh water, planulae of *Pocillopora* are more seriously affected than others, at least during a period of five minutes. A brief contact of one minute, however, with a 50: 50 solution of sea water and fresh water has little or no effect upon any of the planulae tested. In such a solution planulae of *Cyphastrea* are capable of living for 25 days, but most of those of *Dendrophyllia* died within seven days.

The immediate effect of strong dilutions of sea water upon planulae is to cause a sharp contraction and paralysis of the organisms (figs. 3-5). Contacts with mixtures of one part sea water to three parts fresh water for periods of 10 to 30 minutes are fatal to all planulae tested, those of *Pocillopora* being more quickly injured. In lesser dilutions of sea water employed in the experiments, the contraction of planulae was brief or only partial and the surface was unaffected (figs. 3-5). In a mixture of three parts sea water to one part fresh water there was no cessation of movement in planulae of *Cyphastrea* and *Dendrophyllia* and only for two or three minutes in those of *Pocillopora* (figs. 3-5).

Comparative studies were also made by subjecting planulae to constant exposure with sea water of various dilutions (table 3). In lesser dilutions, planulae of the three species, if paralyzed, soon recovered and resumed normal activity. Planulae of *Cyphastrea* under non-lethal conditions seemed to be more adaptive than those of the other species.

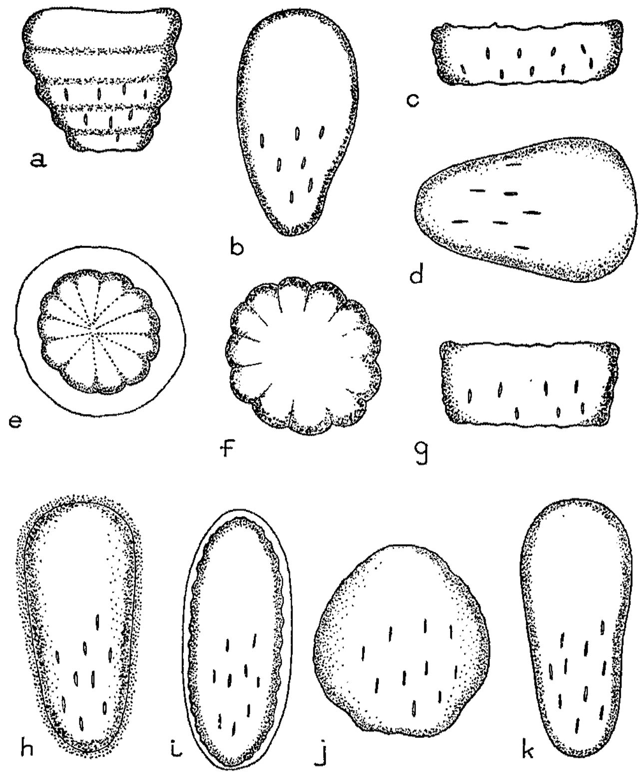

FIGURE 4.—Response of planulae of *Cyphastrea ocellina* to fresh water and dilute sea water: **a**, after 30 seconds in fresh water (sharp contraction, cessation of movement); **b**, two minutes after planula *a* is returned to normal sea water (normal activity resumed, surface not affected); **c**, after one minute in fresh water (sharp contraction, cessation of movement); **d**, recovery of planula *c* two minutes after being returned to sea water (activity resumed, surface not affected); **e**, after 12 minutes contact with fresh water (sharply contracted, epidermal zone swollen, opaque, no movement); **f**, planula *e* after removal to sea water (epidermal zone lost, body lobulated, disintegrates); **g**, effect of exposure to solution of one part sea water to three parts fresh water (sharp contraction, cessation of movement); **h**, planula *g* after 30 minutes in the solution (expanded, no movement, epidermis lost, disintegrates in 18 hours); **i**, six minutes after exposure to solution of one part sea water to one part fresh water (expands from contracted form and resumes activity); **j**, effect of exposure to solution of two parts sea water to one part fresh water (partial contraction, no cessation of movement, no effect on surface); **k**, effect of exposure to solution of three parts sea water to one part fresh water (resumes normal activity in one minute).

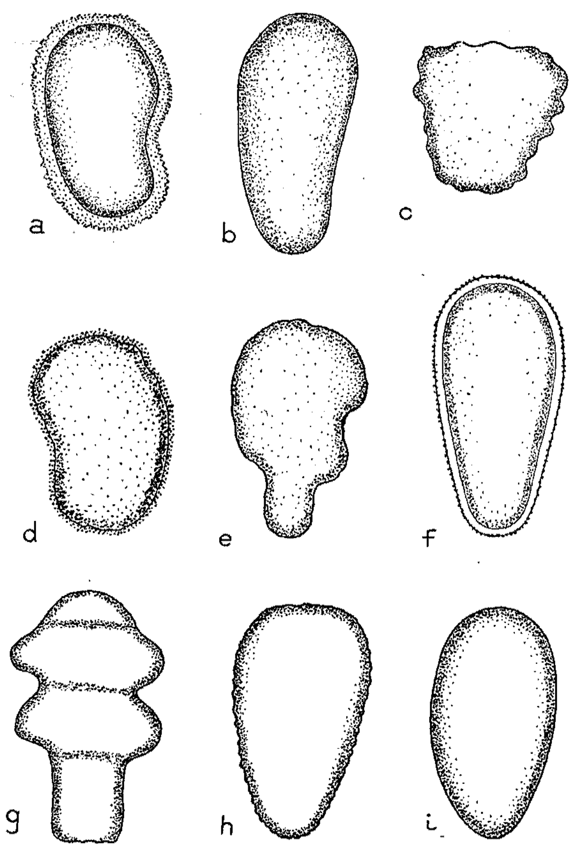

FIGURE 5.—Response of planulae of *Dendrophyllia manni* to fresh water and dilute sea water: **a,** after 30 seconds in fresh water (partial contraction, cessation of movement, surface granular); **b,** 24 hours after removal of planula *a* to normal sea water (normal activity resumed after loss of epidermis); **c,** after one minute in fresh water (recovery on return to sea water after 24 hours); **d,** effect of exposure to fresh water for three minutes (partial contraction, cessation of movement, surface granular); **e,** planula *d* 24 hours after removal to sea water (loss of epidermis, no recovery); **f,** 30 minutes after exposure to solution of one part sea water to three parts fresh water (cessation of movement, epidermis granular, no recovery on return to normal sea water); **g,** after 30 minutes contact with solution of one part sea water to one part fresh water (contraction, no recovery after return to sea water); **h,** after 30 minutes contact with solution of two parts sea water to one part fresh water (slight contraction, brief cessation of movement, little effect on activity); **i,** after 30 minutes contact with solution of three parts sea water to one part fresh water (no apparent effect on form or movement).

TABLE 3.—BEHAVIOR OF CORAL PLANULAE ON SUDDEN AND CONSTANT EXPOSURE TO DILUTE SEA WATER

DILUTION	POCILLOPORA DAMICORNIS	CYPHASTREA OCELLINA	DENDROPHYLLIA MANNI
3 parts sea water, 1 part fresh water	activity resumed in 2-3 minutes	no cessation of movement	no cessation of movement
2 parts sea water, 1 part fresh water	activity resumed in 5-10 minutes	activity resumed in 2 minutes	activity in 5-8 minutes
1 part sea water, 1 part fresh water	activity resumed in 15-20 minutes	activity resumed in 5-6 minutes	activity in 30 minutes
1 part sea water, 3 parts fresh water	no recovery	no recovery	no recovery

RESISTANCE OF PLANULAE TO HIGH TEMPERATURES

It has been learned by observation and experimentation that many corals are capable of surviving quite high temperatures for short periods of time. On flat reefs some near-shore dwellers are occasionally subjected to temperatures which approach the lethal degree. I have recorded (5) a temperature of 31.6° C. for water barely covering a living colony of *Pocillopora damicornis* (*P. cespitosa*) on Waikiki reef, Oahu, during low tide on a hot afternoon. It has also been determined that about 70 percent of the corals on Waikiki reef are capable of surviving 34° C. for one hour.

Tests were made to determine the resistance of planulae to sudden exposure for short periods, to temperatures ranging up to and including 42° C. (table 4). The planulae of *Cyphastrea* seem to require a higher degree of temperature for paralysis, than do those of *Pocillopora* or *Dendrophyllia,* the latter being the most sensitive, failing to recover after five minutes at 39° C. Planulae of both *Pocillopora* and *Cyphastrea* survive for two minutes at 42° C., but those of *Pocillopora* are more seriously affected. Five minutes at 42° C. is fatal to all the planulae, those of *Dendrophyllia* disintegrating in the heated water.

The morphological effect of high temperature on planulae is comparable to that resulting from dilute sea water. The immediate effect at certain levels of temperature is a cessation of movement accompanied by a very pronounced or partial contraction of the body (fig. 6). Planulae of *Dendrophyllia* are temporarily paralyzed after five minutes at 35° C., those of *Pocillopora* after five minutes at 39° C., but those of *Cyphastrea* are unaffected as to movement after five minutes at 40° C. (table 4). Increasing temperatures did not cause a loss of epidermis in planulae of *Pocillopora* and *Cyphastrea* until the level of

42° C. was reached, but in planulae of *Dendrophyllia* the periphery is affected after five minutes at 38° C. which is also lethal to the organisms (table 4; fig. 6, *g*).

TABLE 4.—BEHAVIOR OF CORAL PLANULAE ON SUDDEN EXPOSURE TO HIGH TEMPERATURES FOR SHORT PERIODS, THEN RETURN TO NORMAL TEMPERATURE

TEMPERATURE DEGREES C.	TIME OF EXPOSURE	POCILLOPORA DAMICORNIS (NORMAL TEMP.)	CYPHASTREA OCELLINA (NORMAL TEMP.)	DENDROPHYLLIA MANNI (NORMAL TEMP.)
35	5 minutes	no cessation of movement	no cessation of movement	activity in 3 minutes
36	5 minutes	no cessation of movement	no cessation of movement	activity in 5 minutes
37	5 minutes	no cessation of movement	no cessation of movement	activity in 7 minutes
38	5 minutes	inactive; activity in 4 minutes	no cessation of movement	activity in 4-5 minutes
39	5 minutes	inactive; activity in 3-4 minutes	no cessation of movement	no activity after 2 hours; no recovery
40	5 minutes	inactive; activity in 3-5 minutes	no cessation of movement	slight activity in 1 hour; no recovery
40	10 minutes	inactive; dead in 15 hours	no recovery; dead in 24 hours	no recovery; dead in 5 minutes
42	1 minute	inactive; activity in 10 minutes	inactive; activity in 2 minutes	no recovery
42	2 minutes	inactive; slight activity in 15 minutes	inactive; activity in 2 minutes	no recovery
42	5 minutes	no recovery	no recovery	disintegrates at once

To reach conclusions regarding the prolonged endurance of planulae in water of supernormal temperatures some tests were made in which the organisms were subjected to gradually increasing heat and maintained at a given level, with some vacillation, by thermostat control. The results are set forth in table 5. Although the time element and temperature levels vary in the several observations, there are indications that planulae of each species may survive temperatures ranging from 32° to 33° C. for one or two days, and perhaps longer.

My previous observations (6) on the behavior of planulae of *Cyphastrea* and *Dendrophyllia* were that those of the former species survived 36.5° C. for 24 hours and those of the latter survived 35° C. for 24 hours. Adults of both species succumbed during the tests.

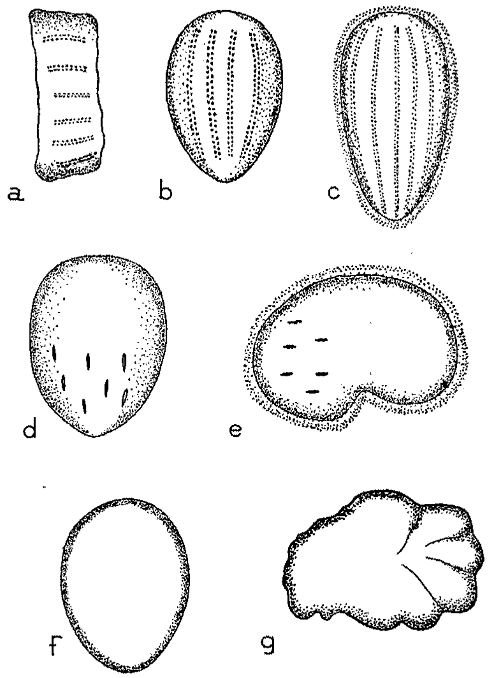

FIGURE 6.—Response of coral planulae to increased temperatures. **a-c,** *Pocillopora damicornis: a,* effect of sudden exposure to 37° C. for five minutes (sharp contraction, momentary cessation of movement or none, recovery at once on return to normal temperature); *b,* effect of sudden exposure to 40° C. for five minutes (cessation of movement, partial contraction, activity resumed in three minutes); *c,* effect of sudden exposure to 42° C. for five minutes (cessation of movement, slight contraction, loss of epidermis, dead after 15 hours). **d-e,** *Cyphastrea ocellina: d,* effect of sudden exposure to 40° C. for five minutes (no cessation of movement, partially contracted, movements cease after return to normal temperature, dead after 24 hours); *e,* effect of sudden exposure to 42° C. for five minutes (distorted and partially contracted, loss of epidermis, dead in four hours after return to normal temperature). **f-g,** *Dendrophyllia manni: f,* effect of gradual rise of temperature from 25° C. to 32° C. in 55 hours (partially contracted, active); *g,* effect of sudden exposure to 39° C. for five minutes (cessation of movement, loss of epidermis on return to normal temperature, no recovery).

TABLE 5.—BEHAVIOR OF CORAL PLANULAE UNDER CONSTANT SUBJECTION TO SUPERNORMAL, CONTROLLED TEMPERATURES (DATA WITHIN EACH BRACKET REPRESENT A CONTINUOUS OBSERVATION)

DURATION OF EXPERIMENT		TEMPERATURE OF WATER IN DEGREES C.	BEHAVIOR OF PLANULAE
Pocillopora damicornis			
Dec. 2	2:30 p.m.	25.5	
Dec. 3	11 a.m.	32	all active, some contracted
Dec. 4	7:45 a.m.	32	all active, some contracted
	3 p.m.	31	contracted, alive
Dec. 5	12 m.	32	contracted, alive; 2 affixed
Dec. 6	8 a.m.	31.5	contracted, alive
Dec. 9	8:30 a.m.	24	
	3:30 p.m.	33	all active, contracted
	9:10 p.m.	33	all active, contracted
Dec. 10	7:30 a.m.	33.5	some alive, some dead
	9 p.m.	32.5	all dead
Dec. 10	9 p.m.	24.5	
Dec. 11	7:30 a.m.	34	all dead but one
	7:10 p.m.	32	one alive, deformed
Cyphastrea ocellina			
Feb. 20	10:30 a.m.	25	
	12 m.	33	no cessation of movement
	5:45 p.m.	33	all alive, active, contracted
Feb. 21	9:15 a.m.	34	all dead, disintegrating
Dendrophyllia manni			
Dec. 9	8 a.m.	24	
	3:30 p.m.	33	contracted, active
	9:10 p.m.	33	contracted, active
Dec. 10	7:30 a.m.	33.5	contracted, active
	9 p.m.	32.5	contracted, alive
Dec. 11	7:30 a.m.	34	all alive, contracted
	7 p.m.	34	all dead but one

RESISTANCE OF PLANULAE TO SUBNORMAL TEMPERATURES

It is well established that living organisms are capable of withstanding greater reduction than advancement of temperature, measured from the norm. As explained by Pfeffer (11), low temperature depresses metabolism, whereas a rising temperature gradually accelerates respiration and brings about fatal effects more quickly. I have previously showed this to be true for living Hawaiian corals, and the current investigations support that view with respect to coral planulae.

On suddenly subjecting planulae to low temperatures, for short periods, it is seen (table 6) that those of *Pocillopora* regain activity more quickly than do those of *Cyphastrea,* at levels below 3° C. At temperatures of 3° C. and lower, planulae of *Dendrophyllia* seem to be more seriously affected than those of other species. All planulae are capable of resisting temperatures down to 12° C. for a considerable period of time. After 45 minutes at 12° C. they are paralyzed, but none seriously injured; and those of *Cyphastrea,* apparently least of all.

TABLE 6.—TIME REQUIRED FOR RESUMPTION OF ACTIVITY OF CORAL PLANULAE IN SEA WATER OF NORMAL TEMPERATURE AFTER HAVING BEEN RENDERED INACTIVE BY SUDDEN EXPOSURE TO SUBNORMAL TEMPERATURES FOR GIVEN PERIODS

TEMPERATURE DEGREES C.	TIME OF EXPOSURE (MINUTES)	POCILLOPORA DAMICORNIS	CYPHASTREA OCELLINA	DENDROPHYLLIA MANNI
0.5	5	activity in 4 minutes	activity in 10 minutes	no recovery
1	1	activity in 2 minutes	activity in 1-4 minutes	activity in 1-2 minutes
2	5	active in 1-2 minutes	active in 16-30 minutes	active in 11 hours
3	5	active in 1-4 minutes	active in 1-4 minutes	no activity in 1 hour, dead in 24 hours
8	1	active in 1 minute	active in 30 seconds	active in 30 seconds
12	10	active at once	active at once	active in 2 minutes
12	45	active in 1-2 minutes	active at once	active in 2-3 minutes

The physical changes brought about in planulae by reduced temperatures depends upon the thermal degree and the duration of contact. A gradual reduction to a level of 10° C. results in no cessation of movement in planulae of *Pocillopora* and only slight contraction of the body (fig. 7, *a*). Such a decline to 7° C., however, paralyzes the organism but has no permanent effect (fig. 7, *b*). A gradual reduction to 1° C. is fatal after a loss of the epidermis (fig. 7, *c*). In planulae of *Cyphastrea,* a sudden exposure to 5° C. for one hour results in lobulation and disintegration (fig. 7, *d*). A contact for five minutes at 3° C. is followed by no permanent injury (fig. 7, *e*), but the result of an exposure for 10 minutes at —2° C. is fragmentation of the pla-

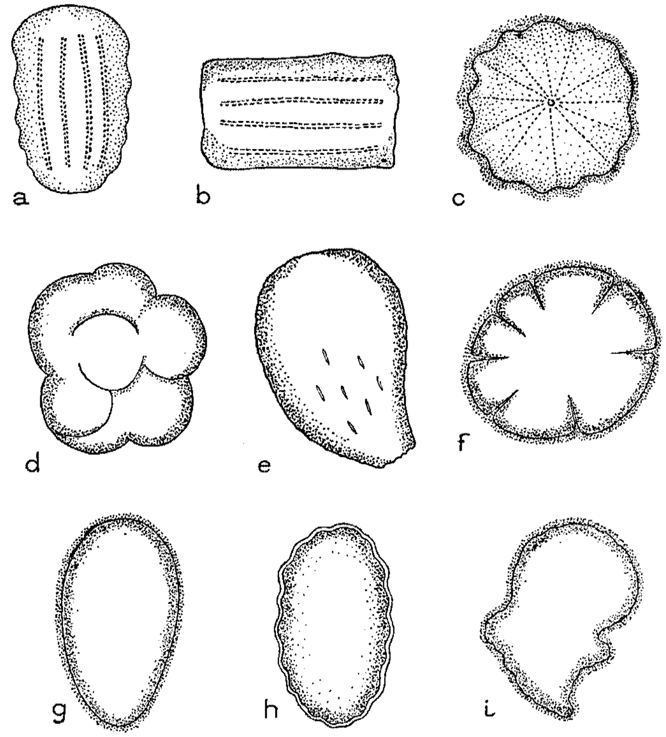

FIGURE 7.—Response of coral planulae to subnormal temperatures. **a-c,** *Pocillopora damicornis: a,* effect of gradual reduction from 25.5° C. to 10° C. in one hour and 27 minutes (partial contraction, no cessation of movement); *b,* effect of gradual reduction to 7° C. in one hour and 45 minutes (cessation of movement, activity resumed on rapid reversal of temperature to 17° C.); *c,* effect of gradual reduction to 1° C. in one hour and 22 minutes (no movement, epidermis lost, no recovery). **d-f,** *Cyphastrea ocellina: d,* effect of one hour at 5° C., after sudden exposure (lobulation of surface, no recovery); *e,* effect of sudden exposure for five minutes at 3° C. (sharp contraction, recovery in one to four minutes, surface not affected); *f,* effect of sudden exposure for 10 minutes at —2° C. (loss of epidermis, fragmentation, no recovery). **g-i,** *Dendrophyllia manni: g,* effect of sudden exposure for five minutes at 2° C. (cessation of movement, loss of epidermis, recovery after 11 hours); *h,* effect of sudden exposure for one minute at 1° C. (recovery of activity in one to two minutes); *i,* effect of sudden exposure for 10 minutes at 1° C. (distorted, loss of epidermis, no recovery).

nula, after a loss of the epidermis (fig. 7, *f*). In planulae of *Dendrophyllia,* an exposure for five minutes at 2° C. causes loss of epidermis, but recovery of movement is noted after 11 hours (fig. 7, *g*). A sudden exposure for one minute at 1° C. results in only slight contraction and temporary paralysis. Recovery occurs within two minutes (fig. 7, *h*). Contact for 10 minutes at 1° C., however, is fatal to the planula (fig. 7, *i*).

My previous work on the behavior of planulae of *Cyphastrea* and *Dendrophyllia* indicates that those of both species may survive a temperature of 5° C. for 24 hours, after a rapid reduction from normal. Both, however, were seriously injured, those of *Cyphastrea* being shriveled and lobulated, all dying within six days after return to normal temperature. The planulae of *Dendrophyllia* required 24 hours to resume movement and apparent normality after return to normal temperature. Planulae of both species recovered after 48 hours at temperatures between 16° C. and 14° C.

AFFIXATION OF PLANULAE

The physical or chemical factors responsible for the settling and affixation of coral planulae are as yet unknown. Numerous observations on the phenomenon have been made but the possible conclusions are few. During the current and previous observations I have noted the following facts with respect to the attachment of planulae of the three Hawaiian species under consideration.

Free Swimming Period of Planulae

Based upon a large number of observations, under laboratory conditions, the free period of *Pocillopora* ranged from one to 18 days, of *Cyphastrea* two to 10 days, and of *Dendrophyllia* one to 21 days. Many planulae failed to become attached through much longer periods.

Affixation in Aggregations

Planulae of *Dendrophyllia* have on several occasions settled in aggregations, closely adhering together. The planulae of this species have a tendency to adhere, even in a free swimming stage. The fixation in masses has also been observed among planulae of *Cyphastrea,* but not among those of *Pocillopora.* Records of similar behavior of planulae of other corals have been made by Mavor (10), Duerden (4), Boschma (2), and Abe (1). The phenomenon may follow a crowded condition of the organisms.

Affixation Influenced by Light

The planulae of the Hawaiian species under consideration exhibit positive phototaxis when first extruded. This is true for *Dendrophyllia,* which lacks zooxanthellae. In *Cyphastrea* and *Dendrophyllia,* however, the response of the planulae may soon be altered and they move near or to the bottom of the container, where light is subdued. Planulae of both *Cyphastrea* and *Dendrophyllia* become affixed in total darkness. Those of the former species settled and became attached less readily than did those of the latter, the ratio being 1:2. The resulting polyps of *Cyphastrea* were weak and did not live long, whereas those of *Dendrophyllia* grew slowly in darkness for seven months.

As Kawaguti (9) suggests, thigmotaxis, rheotaxis, geotaxis, and phototaxis all probably play a part in the settling and attachment of planulae. He concludes that positive phototaxis and negative geotaxis were mainly concerned with the distribution of the species with which he worked.

Affixation Under Altered Temperature

Only planulae of *Pocillopora,* and few of those, became attached at temperatures ranging from 31.5° C. to 32° C. after having been maintained at that level for three days. Planulae of *Cyphastrea,* extruded at 35° C., readily settled and became affixed within a few days after being transferred to normal temperature, indicating that the excessive heat in their initial phase was not injurious. Likewise, planulae of this species became attached within eight days after the return to normal temperature from a period of 18 hours at a level of 16° C. to 14° C.

Affixation Under Altered pH

Planulae of all three species may become affixed in sea water reduced from normal hydrogen ion concentration to pH 7. Polyps of *Cyphastrea* and *Dendrophyllia* continued to live under this neutral condition for four and five months, respectively, without artificial feeding. Little skeletal material was deposited. Planulae of *Pocillopora* and *Dendrophyllia* have become affixed in sea water at pH 6. In neither instance did the polyps live long and only traces of skeletal deposits were seen.

SUMMARY

In Hawaii planulae of *Pocillopora damicornis, Cyphastrea ocellina,* and *Dendrophyllia manni* may be obtained in great quantity. The responses of these planulae to altered conditions, especially of salinity and temperature, are recorded.

Of the planulae considered, those of *Cyphastrea* show greater resistance than others to certain dilutions of sea water and are less affected by brief contacts with fresh water. Planulae of none of the species seem to be much affected by mixtures of sea water and fresh water in the proportion of one to one.

Planulae of *Cyphastrea* are less affected than others by brief periods at high temperatures. Those of *Dendrophyllia* apparently are the most sensitive to rising temperature. Planulae of *Cyphastrea* and *Pocillopora* survive for at least five minutes at 40° C., those of the former showing no cessation of movement during the period. There are indications that all planulae may endure temperatures ranging from 32° C. to 33° C. for several days.

Planulae of *Dendrophyllia* are the most sensitive to falling temperatures. Planulae of *Cyphastrea* and *Pocillopora* are not seriously affected by a contact for five minutes at 0.5° C. All planulae are likely to survive indefinitely at temperatures ranging from 16° C. to 14° C.

Affixation of planulae may take place under conditions varying considerably from the normal. Planulae of *Cyphastrea* and *Dendrophyllia* both become affixed in total darkness. Under this condition the young polyps of *Dendrophyllia* (without zooxanthellae) live for several months; those of *Cyphastrea* (with zooxanthellae) are very short lived. Planulae of *Pocillopora* have become affixed at temperatures ranging from 31.5° C. to 32° C. Planulae of all three species have become affixed in sea water at pH 7, and those of *Pocillopora* and *Dendrophyllia* at pH 6.

There is a tendency for planulae of *Dendrophyllia* and *Cyphastrea* to settle and become affixed in aggregations. This frequently occurs under crowded conditions. I have not observed this phenomenon among planulae of *Pocillopora.*

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