The Atrophy of Hermatypic Reef Corals Maintained In Darknessand their Subsequent Regeneration In Light

Ludwig Franzisket

Hawaii-Institute of Marine Biology
University of Hawaii

Landesmuseum für Naturkunde
44 Münster (Westf.)
Himmelreichalle 50

Converted to digital format by Aric Bickel (NOAA/RSMAS) in 2005. Copy available at the NOAA Miami Regional Library. Minor editorial changes may have been made.

LUDWIG FRANZISKET

Hawaii-Institute of Marine Biology, University of Hawaii

The Atrophy of Hermatypic Reef Corals Maintained in Darkness and their Subsequent Regeneration in Light')

Contents

1. Introduction

VAUGHAN (1912, 1919) and MAYER (1918) stated that reef corals live exclusively heterotrophically from zooplankton caught by tentacles. Both authors describe the survival of the coral *Siderastrea* in the dark when it was fed with zooplankton. The theory of VAUGHAN was criticized by GRAVIER (1913) who claimed that the zooxanthellae provide a supplementary nutrition for the polyps. Similar arguments are published by HICKSON (1924). BOSCHMA (1925) saw zooxanthellae in the mescnterial filaments in different stages of digestion and concluded that they were thusly making a nutritional contribution to the coral.

After a series of extensive experiments on the Great Barrier Reef of Australia, YONGE and NICHOLLS (1931) stated the zooxanthellae are only commensals without any nutritive value for the corals. They describe a crucial experiment in which reef corals kept in the dark for 228 clays and fed on zooplankton remained in good health. On the other hand after nine days, reef corals kept in the light but without zooplankton showed signs of starvation and died a few days later.

These experiments were repeated by GOHAR (1940) in the Red Sea with opposite results: His corals kept in the dark died after 2 weeks in spite of available

[1]) Mit Unterstutzung der Deutsche!' Forschungsgemeinschaft.
lam indebted to Mr. EMILE Keene: for his aid In photographic work and to 1)r. Philip Helfrich for working with me on the translation of this paper from German to English.
Contribution No. 335, Hawaii Institute of Marine Biology, University of Hawaii.

zooplankton, but the corals in light survived in sea water free of plankton. Goreaus observations (1960) were again in agreement with those of Yonge: Two species of corals remained in good health for three months in the dark loosing their zooxanthellae and obviously living heterotrophically. Kawaguti (1964) reported briefly that he kept. 4 species of corals for three months in light without external nutrition.

In spite of contrary evidence Yonges theory persisted (see BUCHNER-, 1955. p. 35). Yonge stated in 1968 (p. 335) : "Seleractinia are specialized carnivores." The research of Goreau and GOB EAU (1960) and Muscatine (1967) is pertinent to this matter. The Goreaus found a transfer of C14-tracer from the symbiont to the host. Muscatine found a transfer of glycerol from the algae to the corals. The dependence of corals on light for normal metabolism and growth was demonstrated recently using exact measurements of growth rates of 5 species of corals under controlled laboratory conditions (FRANZISKET. 1969).

The importance of the coral-zooxanthellae relationship to primary production of coral reefs was emphasized by McLaughlin and Zahl, (1966) who stated: "The problem of symbiotic algae-animal association is much like that of the reef itself". In view of the contradictory evidence regarding the roles of zooxanthellae and plankton in coral nutrition the problem must be reexamined.

2. Methods and and Material

Successful maintenance of corals in the laboratory has been possible since the advent of non-metallic materials for use in aquaria and sea water systems. The sea water system on Coconut Island. Hawaii. made it possible to support living corals in two large fiberglass tanks (112 x 43 x 2:5 cm) with a water flow of 600 1/h. This flow allowed a complete es. change of the water five times per hour. Between the inlet and the outlet at opposite ends of each tank the average velocity of the water flow was 10 cm/min. One tank was exposed to normal daylight until 13.00 hits when it was shaded by the overhang of an adjacent building which also served to protect the tank: from rainfall that might lower the salinity. The other tank was covered in a manner to exclude all light. This was confirmed by placing a S-50 photo-cell of a Standard Beleuchtungsmesser ll (Fa. Dr.. B. Lange. Berlin) in the tank. No reading was recorded even when the covered tank was exposed to bright sunlight.

Four specimens of each of four principal reef building corals. collected in Kaneohe Bay (Oahu) Hawaii, were placed in each of the tanks. The species used were Pocillopora *elegans. Porites compressa, Montipora verrucosa* and *Fungia scularia.* In addition to the hermatypic corals studied, four specimens of a non-hermatypic coral *Dendraphctllia* spec. were placed in each tank to obtain comparative data. Each specimen was placed on the bottom of an overturned glass stacking dish (Fig. 1).

All 40 specimens studied were weighed every 10 days on a torsion balance; those from the dark tank were weighed at night in circler to minimize their exposure to light. Each specimen was quickly removed from the water, gently blotted with Kleenex tissue. weighed. and immediately returned to the water. The weighing error of this method was about ±0.1 g and was related to the amount of time the blotting paper is held in contact with the coral surface as well as the configuration of the coral. This entire procedure did not keep the corals out of water for more than 15 seconds. Such treat meat had no apparent adverse affects upon the corals. as those in the light tank exhibited continued growth. At each 10 day weighing period the Porites specimens were found to be firmly affixed to the substrate and after 2 months the interface of these specimens and the glass substrate was in general conformity. This was interpreted as a sign of favorable conditions for coral growth in the light tank.

Fig. 1. Colony of *Porites compressa* attached to a glass dish

3. Results

All specimens in the light tank showed linear growth in the four months period of observation. In specimens of this size their was no evidence of asymptotic growth. The specimens of the light tank were exposed to natural Kaneohe Bay plankton pumped through the water system for a period of two months, after which a filter was applied to the system to eliminate all plankton for additional 2 months period. No change in growth rate of the hermatypic corals was observed over 4 months period. The non hermatypic *Dendrophyllia* exhibited no growth during the second period when deprived of plankton (FRANZISKET, 1969).

In the dark tank the hermatypic species exhibited no growth during two months observation period, but the non hermatypic specimens grew normally in the unfiltered water of the dark tank. Specimens excluded from light bleached after 10 - 20 days and the coenosarc became progressively more hyaline (Fig. 2). The specimens of *Pocillopora elegans* became necrotic in appearance in the dark tank and none lived more than 30 days. Attempts to maintain this species in the dark were repeated twice with the same results.

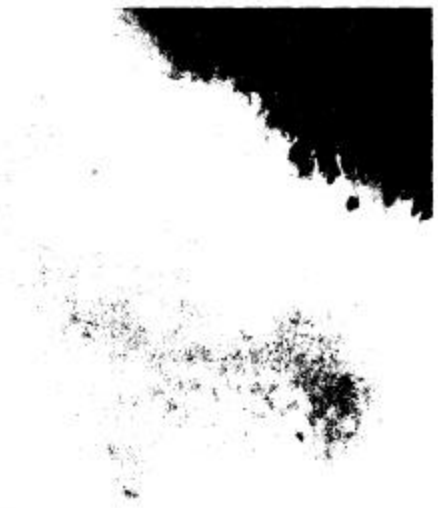

Fig. 2. *Montipora verrucosa* after 60 days in total darkness: The polyps and the coenosare are atrophied exposing the protruding sculptured skeletal structure

The 12 specimens of the other three species remained alive in the dark tank for 60 days with no weight increase. They were then transferred to the light tank with filtered water where a gradual regeneration of zooxanthellae followed by slow growth was observed l despite the absence of plankton.

Changes in the condition of species of corals in the dark tank differed but were constant, within each species. The smallest change was observed in *Fungia* where a. possible atrophy of the polyp tissue was masked by a massive uptake of water. -After transfer of the *Fungia* specimens to the light in plankton free water, following 60 days in the dark tank, regeneration of the zooxanthellae was first noticed on the 5th clay as a light brown luster. A measurable increase in growth was observed at the 6⁰ ten day weighing period. It is believed that two months were required for regeneration of the reduced polyps before any significant growth could take place.

After 60 clays in the dark the polyps of Mon*tipora* specimens were greatly reduced and the tentacles no longer visible. The cœnosarc was atrophied until it gave a net-like appearence (Fig. 2). and in deep calices the 12 skeletal septa were visible. but normal polyp structure was not evident. Microscopic examination did not reveal zooxanthellae but unidentified non-pigmented particles of the size of zooxanthellae which became brown in color after a few days of exposure in the filtered water of the light tank (Fig 3). The polyps were completely restored to a normal condition after three weeks of exposure to light (Fig. 4.). This species also began to grow after two months exposure to light following the dark period.

The most impressive atrophication was observed in Porites because of arrangement of the calices near the surface. Follo$_{\text{wing two}}$ months of dark exposure all four specimens appeared as they had lost their polyps completely. Macroscopically¬ they appeared as dead skeletons with the remaining tissue being completely hyaline with no inclusions (Fig. 5). Obviously earlier authors might have concluded in such cases that the coral was dead. I could find the tissue only by

Fig. 3. The same *Montipora* after 5 days of daylight exposure: Beginning regeneration of zooxanthellae, seen as the dark points on the coral surface

Fig. 4. The same *Montipora* after 3 weeks of daylight exposure: The polyps are regenerated, the coenosarc again fills the sculptured skeletal structure

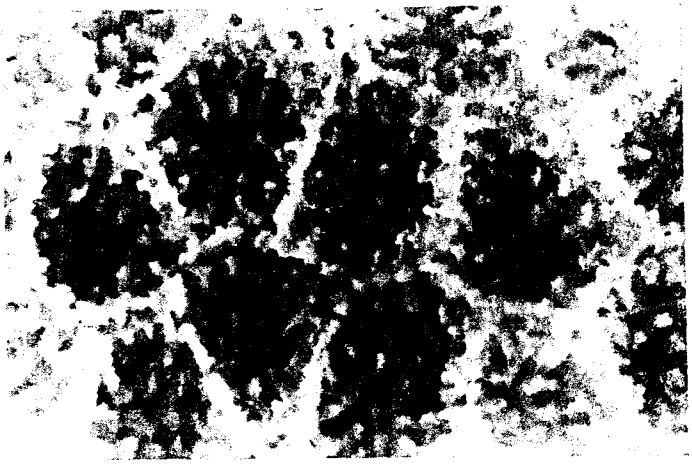

Fig. 5. *Porites* after 60 days in total darkness: The tissue covers the calices as a thin, nearly invisible hyaline skin

careful probing with a needle under a microscope. This atrophied tissue encloses the calices as a thin, unpigmentated. undifferentiated skin which penetrate the skeleton between polyps in strands. No septa are visible. Five days after transfer to the light tank I observed some zooxanthellae and other particle, and the first indications of septa (Fig-6). After 7 days of exposure to light primordial tentacles were observed in the form of small noduls (Fig. 7). On the 8th day the polyps appeared as relatively undifferentiated cylinders which retracted on contact (Fig. S). After three weeks exposure to light the polyps seemed to

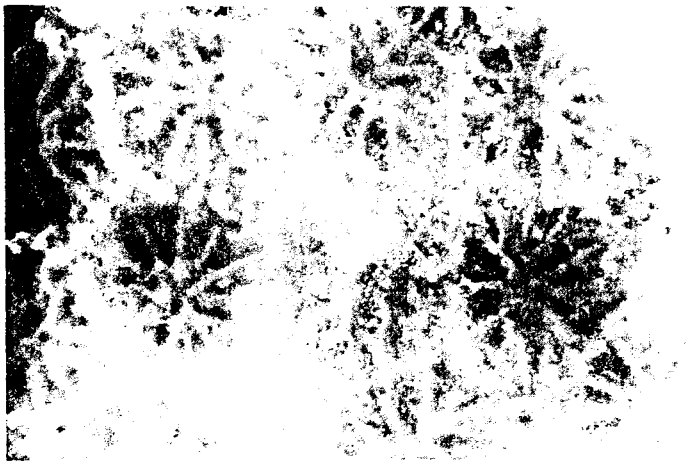

Fig. 6. The same *Porites* after 5 days of daylight exposure: The tissue has become opaque, the structure of the 12 septa begins to take on form

Fig. 7. The same *Porites* after 7 days of daylight exposure: The regenerating tentacles are visible

Fig. 8. The same *Porites* after 8 days of daylight exposure: The polyps appear as small cylinders

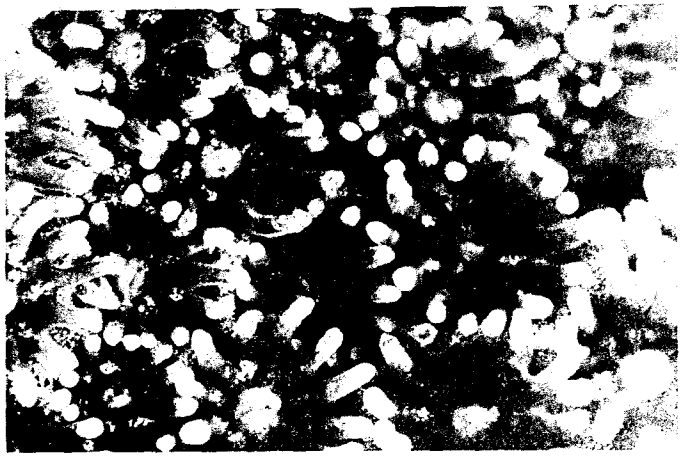

Fig. 9. Fully regenerated *Porites*, polyps expanded

be completely regenerated morphologically (Fig. 9). and even in the retracted state the tentacles were clearly visible (Fig. 10). I think there is a clear differentiation between the partially and fully regenerated forms. Also an increase in weight was not detectable until specimens had been exposed to light for two months.

When corals were moved from dark condition to the light, all showed normal regeneration for the first ten days as described above. On the morning of the 11-1' day one piece of *Poriles* was observed to extrude all of' its zooxanthellae in long microscopic strings of mucus from the area of the mouth which at this

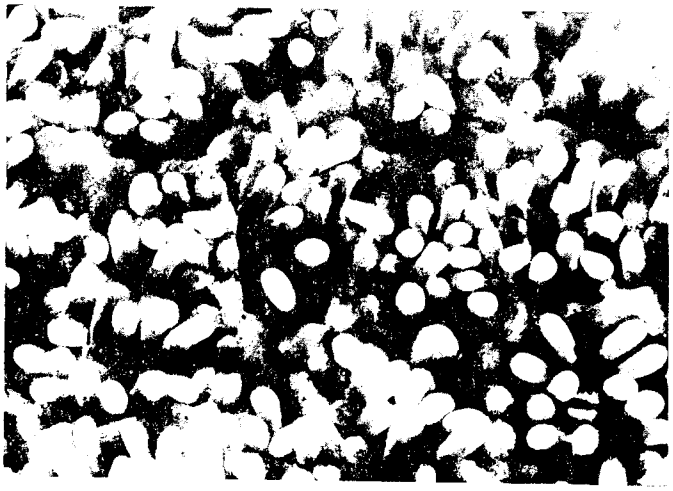

Fig. 10. Fully regenerated *Porites*, polyps retracted

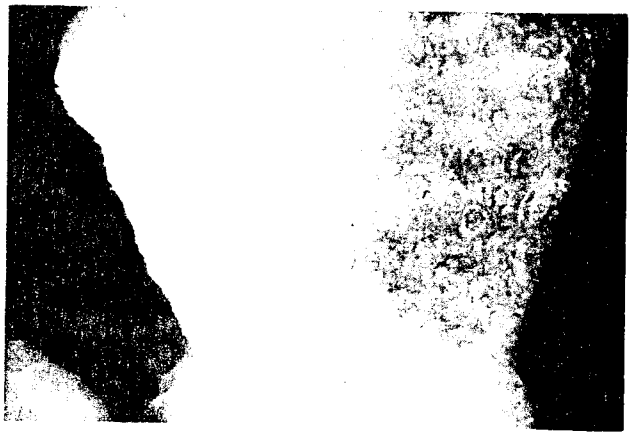

Fig. 11. *Porites* after reinfection with zooxanthellae: Right side of the branch again possesses zooxanthellae, while the left side is free of them. The light-dark difference on the surface is only the result of the pigmentation and not due to a difference in light intensity between sides

point had not regenerated its tentacles. In one hour after this specimen had begun to extrude its rooxanthellae in mucus streams it changed from a light greenish-grey-brown color to pure white. The only treatment of this specimen that differed from the others was that it had been in a position in the tank that received longer exposure to the sun. Following this event, this coral showed no further signs of regeneration, despite normal regeneration in the other three specimens of *Porites*. *Th*ree weeks after transfer from the dark tank I attempted to stimulate regeneration in this specimen of *Porites* by bringing it in direct contact with a normal specimen of *Porites* in such a way as to perforate the

surface and cause protoplasmatic contact. Apparently reinfection of the abnormal specimen was accomplished, and in the following days a gradual spreading of regeneration from the point of contact was observed as shown in fig. 11. Thus different stages of regeneration were seen on the same specimen: more fully regenerated polyps at the point of contact and less developed polyps peripherally, as though a regeneration stimulant had spread out concentrically from the point of contact. Eventually the entire piece regenerated fully.

4. Discussion

Despite atrophication of all specimens maintained in the dark there was no detectable decrease in weight. When in an atrophic state, sea water fills the intercies in the skeleton normally occupied by tissue and sea water substitutes for lost tissue in the total weight.

In atrophied *Montipora* skeletal projections can be seen protruding more prominently than in the non-atrophied specimens (see fig. 2 and 4). But there was no measurable difference in the total mass of specimens in these two conditions, each with different relative proportion of protoplasm, skeleton and sea water.

There is an obvious explanation for the short survival time of *Pocillopora*. Species of this genus have a relatively high metabolic rate : about 540 ml 0_2/kg/h compared with *Porites* with 310 ml O_2/kg/h and *Fungia* with 290 ml 0_2/kg/h (FRANZISKET,1964). Of the four genera investigated, *Pocillopora* has the most rapid growth (FRANZISKET, 1969). They also have the smallest polyps(0.6—0.8 mm in diameter compared to 1.5 mm for *Porites)* and they have the greatest density of polyps (70—80/em^2 compared with 38—42/cm^2 in *Porites).* With this high density of polyps and high metabolic rate, *Pocillopora* seems to have stringent ecological requirements and is least adepted to withstand environmental changes. *Siderastrea* with which VAUGHAN and MAYER attempted to demonstrate the ability of corals to survive in the dark is the coral with the lowest metabolic rate measured (25.6 ml 02/kg/h). *Siderastrea* as well as *Astrangia* have relatively large polyps and appear to be able to survive in relatively broad range of environmental conditions.

The contradictory results of YONGE, GOHAR, GOREAU and KAWAGUTI might he explained as follows: Those species with a lower metabolic rate and large polyps, which presumably are more efficient in capturing zooplankton, are better able to survive than those species with a higher metabolic rate and smaller polyps with less efficient plankton capturing capabilities. A rather different situation is observed in *Fungia,* which has a single large polyp and high metabolic rate as a result of extensive convolutions of the surface. It is suggested that hermatypic corals with large polyps can live heterotrophically successfully but that those with small polyps cannot survive without light.

It is suspected that some of the contradictory evidence cited in the literature may have resulted from two sources of error in experimental procedures affecting coral survival: 1. a lack of total exclusion of light in experiments maintaining corals in the dark, and 2. contamination of the sea water supply with metallic ions.

Atrophication of tissue in starved animals is well known in coelenterates (Brandt. 1883). but the reduction to undifferentiated tissue as in *Porites* is surprising.

The results of this investigation may make a significant contribution to the problem of autot rophy versus heterotrophy in reef building corals. Hermatypic corals with small polyps appear to depend largely upon energy from the photo-synthesis of their zooxanthellae for survival. The absence of light leads to starvation atrophy in which even the systems for capture and digestion of food disappear. Even in species where, heterotrophic nutrition appears to he unnecessary, atrophic coral tissue regenerates the complete polyp structure in light in the absence of plankton. As shown by the figures, in the process of regeneration there is a complete morphological renewal from apparently undifferentiated tissue.

5. Summary

1) Four pieces each of four species of hermatypic corals from Hawaii were kept for several months in a light tank and in a dark tank. For comparison four small colonies of the non-hermatypic coral *Dendrophyttia* were also placed in each tank. The tanks were supplied with running sea water forced through plastic pipes and pump heads. The water in the tanks was renewed five times per hour.

2) The growth rates of all pieces were determined by weighing them every 10 days. In the light, tank the growth of the hermatypic species was independent of the plankton supply. When the sea water was passed through an "Aqua-Pure Filter" the weight increase of these species was as great as in unfiltered water. .*Dendrophyttia* immediatety stopped growing when supplied with filtered water. In the dark tank growth of the hermatypic species ceased. beginning with the first dark day; this pattern was independent of the plankton supply.

3) All specimens of *Pocillopora* died within 30 clays when kept in the dark. The four specimens each of *Fungia, Montipora.* and *Porites* survived the 60 dark days of the experiment. The tissues and organs of all these specimens atrophied in a manner which was different but characteristic for each species.

4) After 60 days the specimens which had been held in continuous darkness were put into a light tank supplied with filtered water. In spite of the lack of plankton these coral-regenerated their zooxanthellae and rebuilt the atrophic tissues and organs within three weeks. Further skeletal growth had not begun after two months.

5) It is noteworthy that in *['wiles* all digestive organs (tentacles, mouth, gastroeoel) Were so reduced during the dark period that, only an undifferentiated tissue remained. but after the specimen was returned to the light all these organs reformed without heterotrophic nutrition.

6) In one ease a colony of *Porites* formerly held in the dark expelled its renewed zooxanthellae after 10 clays in the light. No further development of the polyps occurred as long as the colony was free of its algae. After another 10 days the colony was artificially reinfected with algae by perforation with an intact *Porites,* and regeneration continued.

7) These results prove that some hermatypic corals are able to live from the photosynthetic products of their symbiotic algae.

Zusammenfassung

1. Je vier Fragmente von vier herntatypischen diffbildnern von Hawaii warden fiber meltrere Monato sowohl in einem Helltank als auch einem Dunkeltank gehaltcn. Die Seewasscrversorgung durclt Ktmststoffptunpen and -riihren erneuerte den Beckeninhailt fiurfmal in der Stunde. Zorn Vergleiclt waren in jedem Tank vier Kolonien der ohnc svntbinntische Algen lebenden *Dentdrophyttia.*

2. Der Ztnvaclts wurde Ale 10 Tage durch Wagung ermitlelt. Wahrend die Versuchsstucke im Helltank gleichmabig in artspezifischer Progression wuchsen. stellten alto hernia-

typischen Korallen im Dunkeltank ihr Wachstum vom ersten Tage an ein, die Dendrophyllien dagegen wuchsen im Dunkeln gleiehmiBig weiter.

3. Die Fragmente der Art *Pocillopora elegans* starben alle bei Dunkelhaltung innerhalb von 30 Tagen. Die Fungien, *Montipora*- and Porites-Arten dagegen iiberlebten die Versuchsdauer von 60 Tagen, wobei sic in verschiedener, aber arttypischer Weise atrophierten.

4. Die nach 60thgiger Dunkelhaltung in den Lichttank umgesetzten Stiieke regenerierten dire oxaatli dlen, bildeten das atrophierte Gewebe und die Polypen innerhalb von drei Wochcn wieder voll aus, nahmen aber ein wagbares Skelettwachstum erst nach zwei Monaten u iecler auf.

5. Es war bemerkenswert, daB bei den Dunkelstucken der Gattung *Porites* der Verdauungsapparat (Tentakel, Mund and Gastralraum) vollig eingeschmolzen war. Mach Wiedercinbringen in das Licht regenerierten diese Organe ohne Aufnahme heterotropher Nahrung.

6. Eine Porites-Kolonie spuckte nach begonnener Regeneration (nach 10 Tagen) alle Zooxantluellen aus. Im zooxanthellenfreien Zustand unterblleb die weitere Regeneration, be, 111 Tage spiiter eine kiinstlicheReinfcktiondie Besiedlung mit Symbionten erneuerte and die Regeneration weiterging.

7. Die Ergebnisse beweisen die Fahigkeit hermatypischer Korallen, von den Assimiaten ihrcr Symbionten zn leben.

6. Literature

BOSCHMA, H.. 1925: The nature of association of anthozoa and zooxanthellae. — Proc. Amer. Acad. Arts and Sc. 60: 65-67.

BUCH\ER. P., 1953: Endosymbiose der Tiere mit pflanzlichen Mikroorganismen. —Basel-St uttgart

BRANDT, K., 1883: -Ober die morphologische and physiologische Bedeutung des Chlorophylls bei Tieren. — Mitt. Zoo]. Station Neapel 4: 191-292.

FRANZISKET, L., 1964: Die Stoffwechselintensitiit der Riffkorallen and ihre okologische, phylogenetisehe and soziologische Bedeutung. — Z. Vergl. Physiol. 49: 91—113. — 1969: Riffkorallen kW-men autotroph leben. — Die Naturwissenschaften 56: 144. (loaAR, H. A. F., 1940: Studies on the Xeniidae of the Red Sea. — Pub]. Mar. Biol. St. Ghadarqa 6: 25—118 .

GOREAU, T. F., and N. J. GOREAU, 1960: Distribution of labelled carbon in reef building corals with and without zooxanthellae. — Science 131: 668—669.

GOREAU, T. F., 1961: Wachstum and Kalkanlagerung bei Riffkorallen. — Endeavour 20: 32—38.

GaAVIER, C.. 1913: Le Laboratoire de Biologic Tropicale Tortugas (Floride). — Revue gen. des Sciences, 24.

HlCKSOF, S. J.. 1924: An introduction to the study of recent corals. — Manchester.

KA\~guTr. S.. 1964: An electron microscopic proof for a path of nutritive substances from zooxanthellae to the reef coral tissue. — Proc. Japan. Acad. 40: 832—835.

MAYER, A. G., 1918: Toxic effects due to high temperature. — Carnegie Inst. Wash. Papers Dept. Mar. Biol. 12: 175-178.

McLaughlin, J. J. A., and P. A. ZA E, 1966: Endozoic algae, in "Symbiosis" — S. M. Henry Ed.. Acad. Press, New York and London.

Muscatine, L., 1967: Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. — Science 156: 516—519.

Vaughan, T. W., 1912: Madreporaria and marine bottom deposits in Florida. — Yearb. Carnegie Inst. Wash. 10: 147-156.

— 1919: Corals and the formation of coral reefs. — Rep. Smithsonian Inst. 1917: 189 bis 276.

Yonge, C. M.. and A. C. Nicholls, 1931: Studies on the physiology of corals. IV. Thu structure, distribution and physiology of the zooxanthellae. — Sri. Rep. Cr. Barrier Reef Exped. 1928—29, Brit. Mus. (Nat.Hist.) 1: 135—176.
Yonge, C. M., 1968: Living corals. — Proc. Boy. Soc. 109: 329—344.

Prof. 1)r. Ludwig Franzisket
Landesmuseum fur Naturkunde
44 Munster (Westf.)
Himmelreichallee 50