Zoology. — *"On the food of Reef-corals."* By H. BOSCHMA. (Communicated by Prof. C. PH. SLUITER.)

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Fifty years ago it was generally believed that the food of reef-corals consisted of the plankton organisms floating in the surface water of the sea. The first note on investigations of the food of reef-corals, as far as I am aware, is found in a paper by Sir JOHN MURRAY (1889), based on observations during the Challenger Expedition. He mentions shortly that during this Expedition actual observations on the feeding of corals were made and also investigations on the contents of the gastric cavity. These researches convinced him that the food of the reef-corals consisted of the organisms floating in the sea water.

In the later part of the 19th century KRÄMER (1897) studied the plankton of Samoa and the other regions, as well in tropical as in colder seas. According to him in the Baltic Sea the quantity of plankton is about four times as large as that in the tropics, but he still is convinced that this quantity is sufficient for the feeding of reef-corals.

Now it is well known that reef-corals contain in their entoderm numerous unicellular algae, zooxanthellae. It is generally understood that the association of the two organisms, polyp and algae, is a kind of *symbiosis,* which may be defined as *"a condition of conjoint life existing between different organisms that in varying degree are benefited by the partnership"* (NUTTALL, 1924, p. 213). The nature of this symbiosis has been studied in a number of actinians. BRANDT (1883) made various experiments with *Anthea cereus and Aiptasia diaphana,* actinians which harbour zooxanthellae in their entoderm. Some of these were kept without food in daylight, others without food in darkness. After some months the actinians in daylight were as healthy as at the beginning of the experiment and had but slightly diminished in size. Those which were kept in darkness had after two months lost their zooxanthellae and had died from starvation or were in a decidedly weakened condition. BRANDT concludes from those experiments that the algae in light contributed food in a dissolved form to the actinians. He did not find any zooxanthellae which were being digested (at this time it had recently been discovered where the food of actinians is digested and BRANDT probably did not know this.)

TRENDELENBURG (1909) made accurate gas analyses of the water in which actinians with zooxanthellae in their tissues *(Anemonia sulcata)* lived, as well in darkness as in light. He found that the algae by day furnish oxygen to the polyp and at night utilize oxygen, whilst they derive

their carbon dioxide partly from the animal and partly from the surrounding water. PÜTTER (1911) found that in *Aiptasia* the algae use the nitrogenous waste products of the polyps (ammonia) for the synthesis of their proteins. These researches together with the results obtained by BRANDT show that the association of the actinians with the zooxanthellae has to be regarded as a true symbiosis.

After the study of the contents of the gastric cavity of coral polyps GARDINER (1903) came to the conclusion that the food of reef-corals consists chiefly of their zooxanthellae. In preserved polyps of *Pocillopora* and *"Astraea"* only in 1 or 2 per cent remains of foreign organisms were found. GRAVIER (1908) also was convinced that the food of reef-corals consists for the greater part of the symbiotic algae ; his opinion was based on GARDINER's and his own investigations on the contents of the gastric cavity of the polyps and KRÄMER's statement on the scarcity of the plankton in warmer seas. I came to a similar conclusion (BOSCHMA, 1924) after the study of the contents of the gastric cavity of a great number of East Indian coral polyps. The polyps of smaller size *(Porites, Acropora)* very seldom contained other matter than mucus with zooxanthellae, those of larger size *(Fungia, Favia)* had a mass of mucous matter in their gastric cavity which besides many zooxanthellae consisted of remains of different plankton organisms. I concluded that the food of reef-corals for a considerable part is derived from the zooxanthellae which are digested by the polyps.

These investigations, however, do not prove that the coral polyps derive a part of their nourishment from their zooxanthellae. Coelenterates have no separate system for ingestion and for excretion. These contents of the gastric cavity were for a part certainly food-remnants (the animal remains) but the zooxanthellae might as well have been the products of excretion : the surplus of the quantity needed by the polyps in the tissues. The zooxanthellae are constantly multiplying in the entoderm ; when the cells contain too many algae these are extruded into the gastric cavity. The fact that these algae are found in the gastric cavity does not prove that they are being digested here.

Besides the study of the contents of the gastric cavity feeding experiments have been made on reef-corals. The first who made more or less elaborate investigations of this kind was DUERDEN (1906). He saw that small particles, also plankton organisms, became entangled in the mucus which is secreted on the surface of the polyps of *Fungia* and *Favia*. This mucous layer is afterwards ingested and the food-particles it contains are digested. Much more extensive feeding experiments were made by VAUGHAN (1912) with Floridian and Bahamian reef-coral polyps. Meat of crabs, molluscs or fish, or meat juice was given to the polyps and these substances always brought about the feeding reactions. Also animal plankton (copepods) was eagerly ingested by the polyps. In fact the coral-polyps would feed very readily upon all kinds of animal matter. VAUGHAN also tried vegetable matter : pieces of seaweed and mats of diatoms. This

was invariably refused. Only when the vegetable objects were coated by animal matter it was taken, but soon afterwards the seaweed or the diatoms were removed in an undigested state from the gastric cavity. On the reef also observations were made on corals which had captured animals from the sea-water. VAUGHAN concluded from his experiments: *"The food of reef-corals consists solely of animal matter"* (VAUGHAN, 1912, p. 161). This conclusion in my opinion should be put in a slightly modified form: *"The food of reef-corals as far as it is taken from the outside, in all probability consists solely of animal matter."*

The investigations of METSCHNIKOFF (1880), KRUKENBERG (1880) and WILLEM (1892) showed that the food of actinians is digested in the mesenterial filaments, the free edges of the mesenteries. Next to the border with its numerous nematocysts there is a region the entoderm cells of which ingest small particles in an amoeboid way and digest these particles there. Further particulars on the digestion of actinians are found in papers by MESNIL (1901) and JORDAN (1907). Besides intracellular digestion in the mesenterial filaments there is much evidence for the secretion of a digestive fluid on the larger objects which come into contact with the mesenterial filaments. This fluid causes the disintegration of these objects into small particles, fit to be ingested by the entoderm cells (cf. also BIEDERMANN, 1911).

In 1924 I made some experiments on the feeding reactions and the digestion in the coral *Astrangia danae* in the Marine Biological Laboratory at Woods Hole, Mass. (BOSCHMA, 1925*a*). As in actinians the food is digested in the mesenterial filaments in the region next to the border with its nematocysts. This can be proved by mixing the food with some colouring matter (e.g. India ink, litmus or ammonium carminate). After ingestion of the food the food-vacuoles then contain coloured particles. Most of the colonies of *Astrangia danae* have polyps without any zooxanthellae; the food of these polyps consists exclusively of plankton. On the other hand there are other colonies the polyps of which harbour a great many zooxanthellae in their tissues. In the contents of the gastric cavity of these polyps when freshly collected, besides remains of plankton organisms zooxanthellae are always present. Moreover in the mesenterial filaments of such polyps with zooxanthellae a number of these algae are found in the exact place where after feeding experiments the food is ingested. These zooxanthellae in the mesenterial filaments have lost their natural appearance. Whilst the algae from the entoderm cells of the tentacles and oral disk have a more or less uniform yellow colour, those in the mesenterial filaments contain some brown patches and parts of the cells are completely discoloured. They have undergone here similar changes as occur when zooxanthellae die. It seems to me safe to conclude from this that the disintegration of the zooxanthellae in the mesenterial filaments is due to their being digested here by the polyps.

When polyps containing zooxanthellae are abundantly fed with animal

matter no more zooxanthellae are ingested in the mesenterial filaments. Those already present gradually diminish in size and disappear, evidently by being completely digested, and in the course of a few days during abundant feeding the mesenterial filaments of these polyps become completely devoid of zooxanthellae.

Experiments conducted in the Bermuda Biological Station, (cf. BOSCHMA, 1925*b*) and in the Laboratory of the Carnegie Institution of Washington at Tortugas with various Coelenterates which contain zooxanthellae in their entoderm, viz. reef-corals, actinians, Zoanthids, and Gorgoniids, proved that the mesenterial filaments of these organisms in the natural state always contain a number of zooxanthellae in various stages of disintegration. The symbiotic algae therefore constitute a part of the food of the polyps. As for reef-corals it was possible to make the mesenterial filaments devoid of zooxanthellae by feeding the polyps abundantly with animal food.

To study the role of the zooxanthellae in the feeding of actinians I made some experiments with *Cribrina xanthogrammica* at the Scripps Institution for Oceanography in La Jolla, Calif. The feeding reactions of this species have been studied by GEE (1913). The study of the mesenterial filaments in my experiments gave the following results: Hungry actinians kept in full light ingested many zooxanthellae in the mesenterial filaments and extruded a great number of zooxanthellae in masses of mucus through the mouth. For a month they did not diminish noticeable in size. Though a great number of zooxanthellae were extruded through the mouth the actinians kept the same colour. In diffuse daylight the results were quite similar to those in full sunlight. In general the quantity of zooxanthellae ingested in the mesenterial filaments of hungry polyps in diffuse daylight exceeded that of those in full sunlight. In darkness hungry polyps lost the greater part of their zooxanthellae, thereby assuming a much lighter colour; on the whole these actinians were in an ill state of health, probably owing to the lack of oxygen: as the zooxanthellae could not assimilate in the darkness they could not act as source of oxygen to the tissues of the polyp. The size of these actinians after a month in darkness was about one half of what it originally was. Well fed actinians in all different intensities of light increased in size, though those in darkness were more or less ill, as often bladdery lobes of the stomodaeum were extruded through the mouth, probably due to the lack of oxygen. A result of abundant feeding of the polyp was that as well in light as in darkness no zooxanthellae were ingested in the mesenterial filaments. Great quantities of these algae were removed from the gastric cavity through the mouth. After a month the well fed actinians were often more than twice as large as at the beginning of the experiment.

From these experiments we may conclude the following statement: *The food of reef-corals and of actinians which live in association with zooxanthellae consists for a part of these zooxanthellae and for another part of animal matter. The polyps try to get as much animal matter as*

possible, but in case of starvation they depend chiefly upon the zooxanthellae. The surplus of the rapidly multiplying zooxanthellae in the tissues is removed from the entoderm cells to the gastric cavity, and, as far as needs may be, these algae are digested or removed through the mouth.

The experiments prove that the zooxanthellae are not ingested in the mesenterial filaments because they happen to be in the gastric cavity. The algae are ingested as a source of food, but when sufficient other food is available, they are simply removed through the mouth.

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