TRANSPLANTATION EXPERIMENTS WITH CARIBBEAN *MILLEPORA* SPECIES (HYDROZOA, COELENTERATA), INCLUDING SOME ECOLOGICAL OBSERVATIONS ON GROWTH FORMS

by

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ABSTRACT

The historical background of the taxonomic problems in the fire-coral, *Millepora*, is reviewed. The growth forms of the Caribbean species: *Millepora alcicornis* Linnaeus, *M. complanata* Lamarck and *M. squarrosa* Lamarck are investigated in relation with environmental factors: water movement, current, light and turbidity. Several sites on Curaçao and Bonaire were visited and all forms of *Millepora* collected. The localities have been divided in biotopes and the relative frequencies of the growth forms in these biotopes were studied. Some relations between growth forms and environment were found: delicately branched forms appear in deeper, quieter waters, sturdy forms in sites with strong water movement, incrusting forms in turbid and also in turbulent sites. At sites with strong current *Millepora* corals are most abundant. The effect of transplantations on the growth forms of the three species has been studied. The transplantations caused changes in the growth form, which was most conspicuous in *M. complanata*.

It is concluded that *M. alcicornis* and *M. complanata* most likely are distinct species. However, the materials from Curaçao and Bonaire commonly identified as *M. squarrosa* do not belong to that species, but probably represent variations of *M. complanata*.

RÉSUMÉ

On passe en revue les aspects historiques des problèmes taxonomiques du genre *Millepora*. Les différents écotypes des espèces communes de la Mer des Caraïbes (*M. alcicornis* Linnaeus, *M. complanata* Lamarck et *M. squarrosa* Lamarck) sont étudiés par rapport aux facteurs du milieu suivants: turbulence, courant, lumière et turbidité. Plusieurs stations de Curaçao et de Bonaire ont été explorées, et l'on y a collecté les différentes formes de *Millepora*. Ces stations ont été classées suivant des types de biotope, et les fréquences relatives de présence des différents écotypes dans ces biotopes ont été étudiées. On a mis en évidence certaines relations entre les écotypes et le milieu: les formes délicatement ramifiées sont rencontrées dans des endroits profonds à eau peu agitée, les formes trapues dans des endroits à mode battu, les formes encroûtantes dans des endroits à turbidité et à turbulence élevées. Les *Millepora* abondent surtout dans les endroits à courant élevé. On a étudié l'effet de la transplantation et de l'acclimatation des écotypes des différentes

espèces: ces transplantations ont entraîné les modifications les plus évidentes dans le cas des *M. complanata*.

On en arrive à la conclusion que *M. alcicornis* et *M. complanata* sont très probablement des espèces distinctes, alors que les exemplaires normalement appelés *M. squarrosa* à Curaçao et Bonaire, n'appartiennent pas à cette espèce, mais représentent vraisemblablement des variations de *M. complanata*.

INTRODUCTION

The genus *Millepora* Linnaeus 1758 (Milleporidae, Hydrozoa, Coelenterata) belongs to the hermatypic hydrocorals and is well represented in Recent coral reefs (e.g. Milliman, 1969; Roos, 1964, 1971; Mergner, 1971; Bak, 1975). The species delimitation within the genus is mainly based on the growth form of the corallum and geographical distribution. Five species are known from the Western Atlantic region, three of which are generally recognized in the Caribbean. The growth forms of these species are: "branching" in *M. alcicornis*, "bladed" in *M. complanata* and "boxwork" in *M. squarrosa* (terminology according to Stearn & Riding, 1973). Besides such more or less clearly distinguishable forms many intermediate forms exist, of which the specific status is doubtful, and also purely incrusting forms which cannot be identified at all. Because of the high proportion of growth forms differing from the original description of the species, the question arises whether the Caribbean species are real species or represent phenotypical variations of one or two highly variable species.

To investigate how far habitat-induced modifications of the growth forms were apparent in

the field, I visited several sites along the coast of Curaçao and Bonaire and studied the growth forms in their environment. A collection of all growth forms was made. According to differences in water movement, current and turbidity the sites have been grouped into types of biotopes. The effect of transplantations on the growth forms of the Caribbean *Millepora* species and of some incrusting forms is investigated. This was done to study the adaptability of the growth form, especially to different depths and to high turbidity. The fieldwork was done during a stay at the Caribbean Marine Biological Institute (Carmabi), Curaçao, from January 1976 till January 1977.

REMARKS ON THE TAXONOMY OF
MILLEPORA

Many authors have dealt with the classification in *Millepora*, which in the past led to an almost chaotic splitting and lumping (cf. Duchassaing & Michelotti, 1864; Hickson, 1898a; Boschma, 1948a). This taxonomic instability is not restricted to this Hydrozoan genus only. The Anthozoa, especially the Scleractinia, have also been and still are subject to taxonomic uncertainties. The main reason for this is the high variability of almost all characters used for the identification in this group of sessile marine animals, especially the growth form, which is influenced by their adaptability to various environmental circumstances (Crossland, 1928; Manten, 1960; Stoddart, 1969; Wijsman-Best, 1972, 1974).

Early students can be divided into three groups: those who called every specimen with a somewhat different appearance a new species (e.g. Duchassaing & Michelotti, 1864), those who wanted to diminish the number of species by emphasizing the environment-induced variability (e.g. Hickson, 1898a; Wood-Jones, 1907), and those who admitted the influence of the environment on the growth form but allowed for the existence of more species than supposed by the second group (e.g. Stephenson & Stephenson, 1933). A comprehensive survey of former studies on coral taxonomy is given by Vaughan & Wells (1943) and Wijsman-Best (1972). In recent studies most empha-

sis is given to the relation between different environmental conditions and the variation in identification characters (Roos, 1971; Wijsman-Best, 1972, 1974).

In the Milleporidae the taxonomic value of the following characters have been investigated: the texture of the surface of the corallum, the size and shape of the pores, the degree of isolation of the units formed by the dactylopores and gastropores, the distribution of the pores in the various parts of the corallum, the presence or absence of ampullae, the anatomy of the soft parts and the stinging properties (Moseley, 1877; Hickson, 1898 a & b; Boschma, 1948 a & b, 1949a, 1950). None of these characters proved to be of taxonomic value.

According to Boschma the growth form of the corallum, although very variable, is the only character which can be used for identification of the species. Boschma came to this conclusion after a visit to the Java Sea where he found colonies with different growth forms growing side by side (Boschma, 1948a). He also noticed that colonies in contact with each other did not unite to form one single colony, but the more slender colony was always overgrown by the more robust one. Boschma concluded from these two observations that the growth form is determined genotypically and not phenotypically, thus being species specific. In his search for other identification characters, more dependable than the growth form, Boschma found that the size and shape of the ampullae (in particular their coverings) might be of taxonomic value (Boschma, 1949a, 1950). Unfortunately his study was limited by the small number of corals with closed ampullae available. No definite statements about the taxonomic value of the ampullae could therefore be made.

The extensive studies of Boschma eventually led to a division of the genus into 13 species: *M. alcicornis* Linnaeus, 1758; *M. braziliensis* Verrill, 1868; *M. complanata* Lamarck, 1816; *M. dichotoma* Forskål, 1775; *M. exaesa* Forskål, 1775; *M. intricata* Milne Edwards, 1857; *M. latifolia* Boschma, 1948; *M. murrayi* Quelch, 1884; *M. nitida* Verrill, 1868; *M. platyphylla* Hemprich & Ehrenberg, 1834; *M. squarrosa* Lamarck, 1816; *M. tenera* Boschma, 1949, and *M. tuberosa* Bosch-

ma, 1966. Crossland added *M. foveolata* Crossland, 1952 (Boschma, 1948a, 1949b, 1961, 1962, 1966; Crossland, 1952).

    M. alcicornis, M. complanata, M. braziliensis,

M. nitida and *M. squarrosa* occur in the Atlantic region (Boschma, 1948a, 1961, 1962). The other species are Indo-Pacific, although in the Red Sea only *M. dichotoma, M. exaesa, M. platyphylla* and
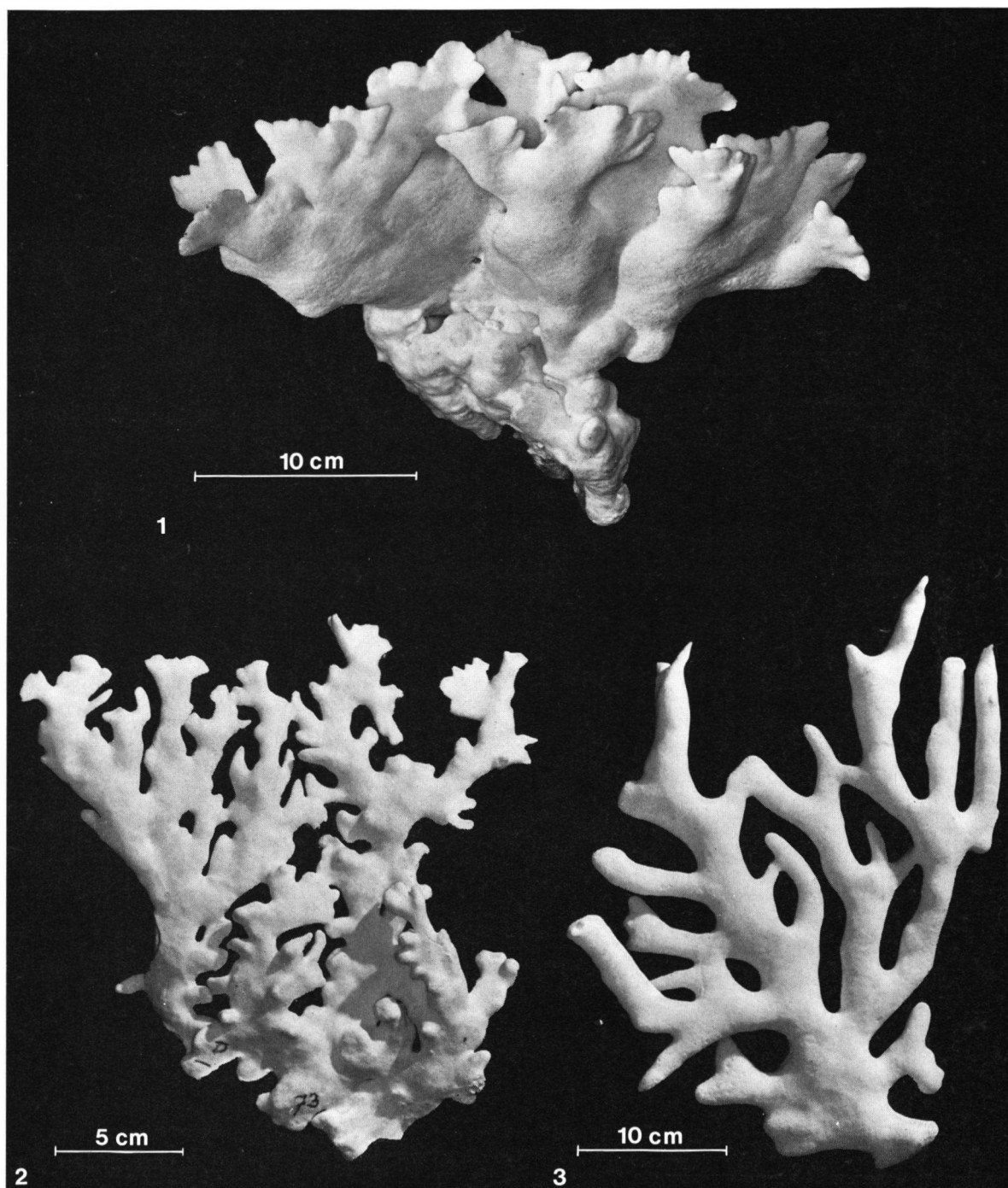

PLATE I

1, *Millepora alcicornis*, coarse branching; 2, *M. alcicornis*, fine branching; 3, *M. alcicornis*, fine branching.

M. tenera are found (Boschma, 1948a, 1949b, 1968).

The variation in growth form is a serious problem for a correct identification at the species level. Later studies on *Millepora* dealt with the depth distribution of the different growth forms (Stearn & Riding, 1973), the variation of the growth form (Mattraw, 1969), skeletal growth (Strömgren, 1975), orientated growth (Mattraw, 1969; Velimirov, 1974), direction of growth as a part of competitive interactions (Wahle, 1980) and skeletal structure (Von Fenninger & Flajs, 1974).

However, the effect of environmental conditions on growth forms has not yet been studied in detail in this genus and research on the taxonomic value of the above-mentioned characters has not been continued.

DIAGNOSIS OF THE CARIBBEAN *MILLEPORA* SPECIES

Three Caribbean *Millepora* species are distinguished, viz. *M. alcicornis*, *M. complanata* and
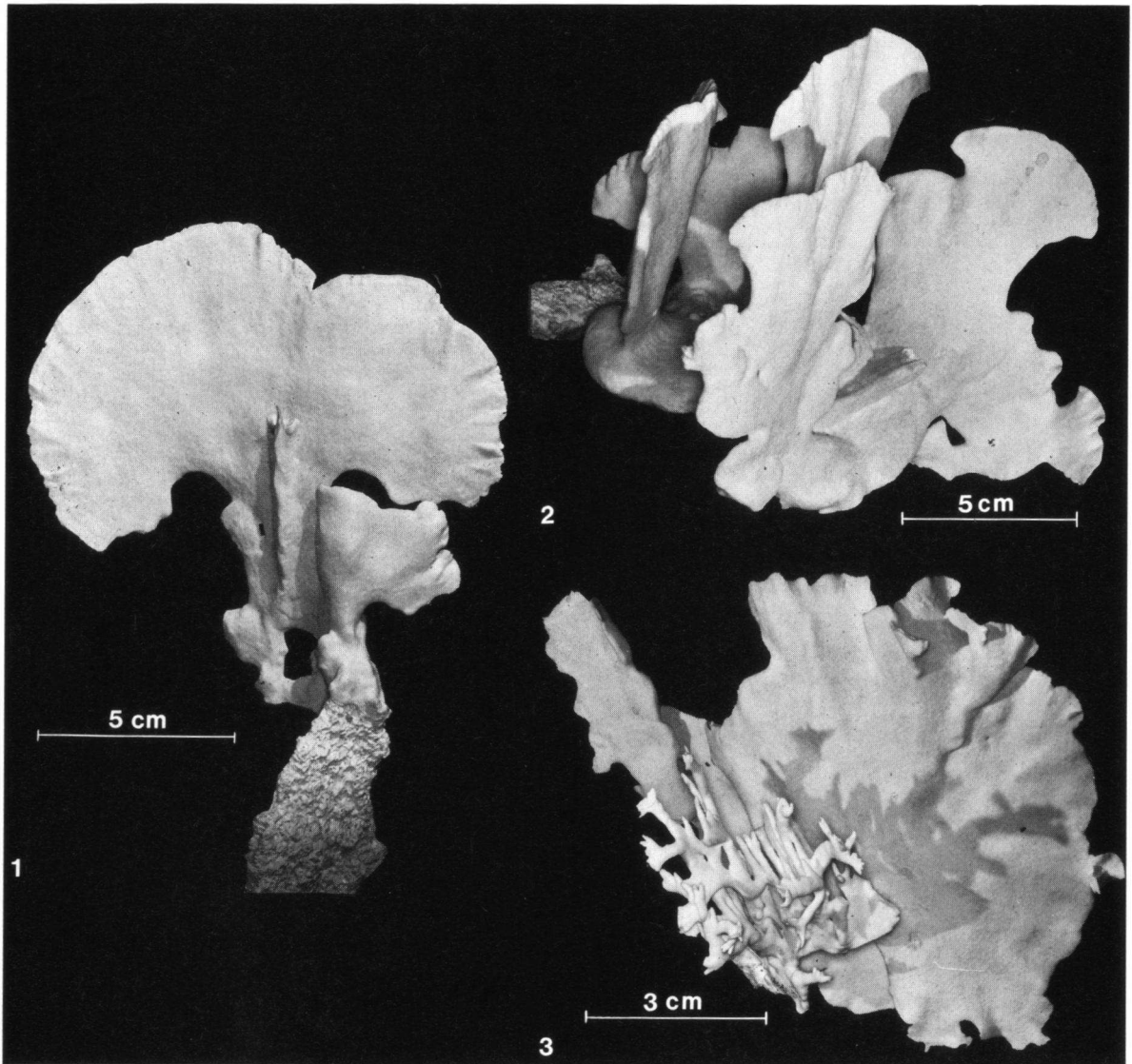

PLATE II

1, *Millepora complanata*; 2, *M. complanata*, blades growing from a common base; 3, two colonies, the one bladed (*M. complanata*), the other branching (*M. alcicornis*), growing side by side.

M. squarrosa. The remaining Atlantic species (*M. braziliensis* and *M. nitida*) are known only from Brazil. Diagnoses of the species are given below, quoted from Boschma (1948a). In the present paper, however, the species names have been avoided as much as possible. This is done to prevent misidentifications, since especially in the bladed and boxwork forms the number of colonies with an intermediate form was extremely high.

Millepora alcicornis Linnaeus, 1758. (Plate I figs. 1-3.)
"Corallum of extremely variable shape, at the growing edge divided into branches which as a rule are laterally compressed, but may be more or less finger-like. In the older parts the branches generally are united into plate-like growths or thicker compounds. Some colonies are decidedly delicately branched, others are of a very compact growth form. The surface of the corallum is even or shows shallow depressions in the centres of which the gastopores are found." (Boschma, 1948a: 18.)

Millepora complanata Lamarck, 1816. (Plate II figs. 1-3.)
"Corallum consisting of thin upstanding plates growing out from a common part. The plates are of various breadth and height, as a rule they have a truncated free edge. Surface of the corallum very smooth and even. The minute structure of the surface may be flat or may present insignificant depressions in the centre of which there are the gastropores." (Boschma, 1948a: 20.)

Millepora squarrosa Lamarck, 1816.
"Corallum forming upstanding thin plates with numerous lateral expansions which among each other are united to form a more or less honeycombed complex. The surface of the corallum besides the larger lateral outgrowths presents numerous crests and tubercles, giving the corallum a frilled appearance. Between the ridges and tubercles the surface of the corallum is even or showing shallow depressions each with a central gastropore." (Boschma, 1948a: 19.)
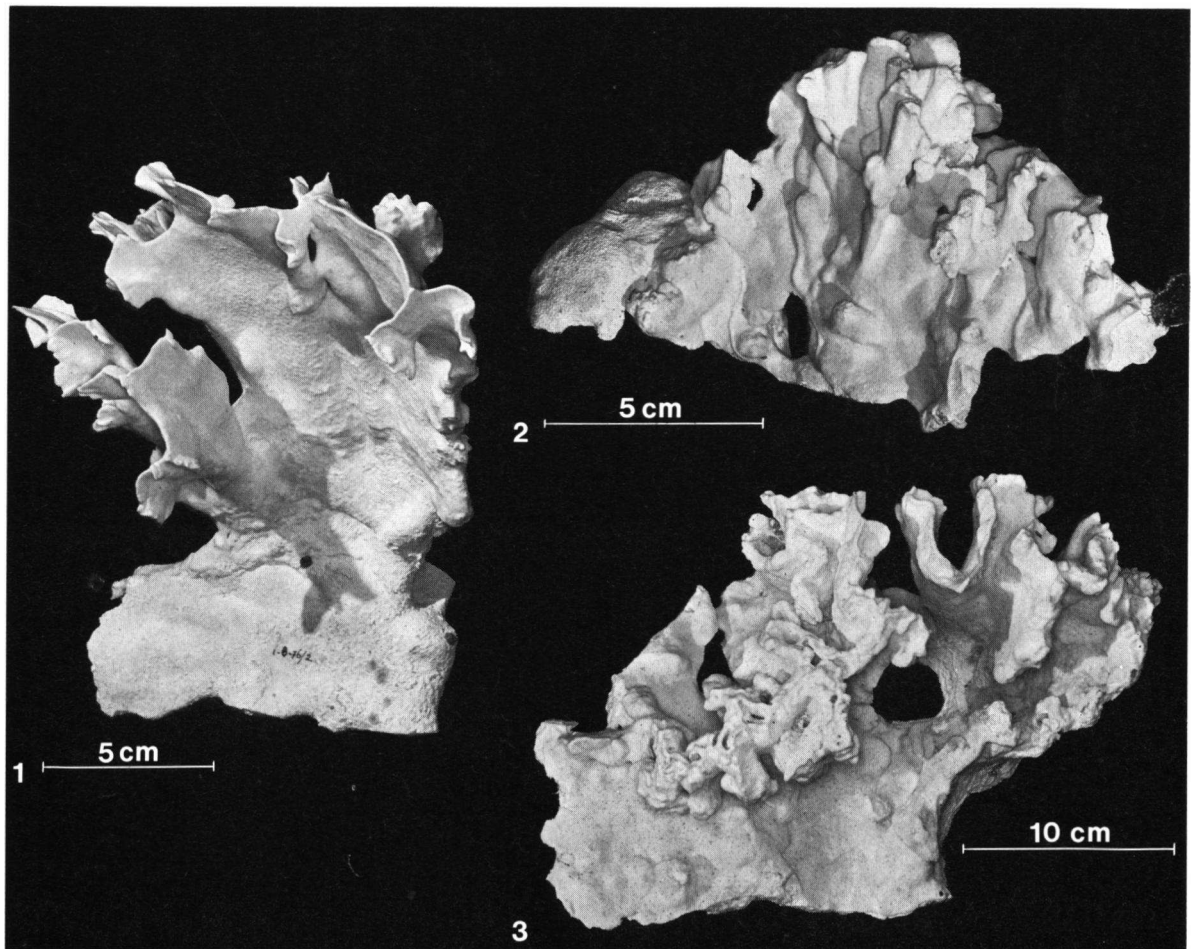

PLATE III

1, Colony of *Millepora* with a growth form intermediate between *Millepora complanata* and *M. "squarrosa"* (thin bladed boxwork); 2, *M. "squarrosa"*, thick bladed boxwork; 3, *M. "squarrosa"*, dwarf form.

In plate III figs. 2 & 3, two colonies generally considered to be *M. squarrosa* are shown. However, they may represent growth forms of *M. complanata*, instead of being the real *M. squarrosa* (see Conclusions and Discussion section in the present paper).

In plate IV figs. 1 & 2, two incrusting forms, one incrusting a head of dead coral, the other incrusting a gorgonian, are shown.
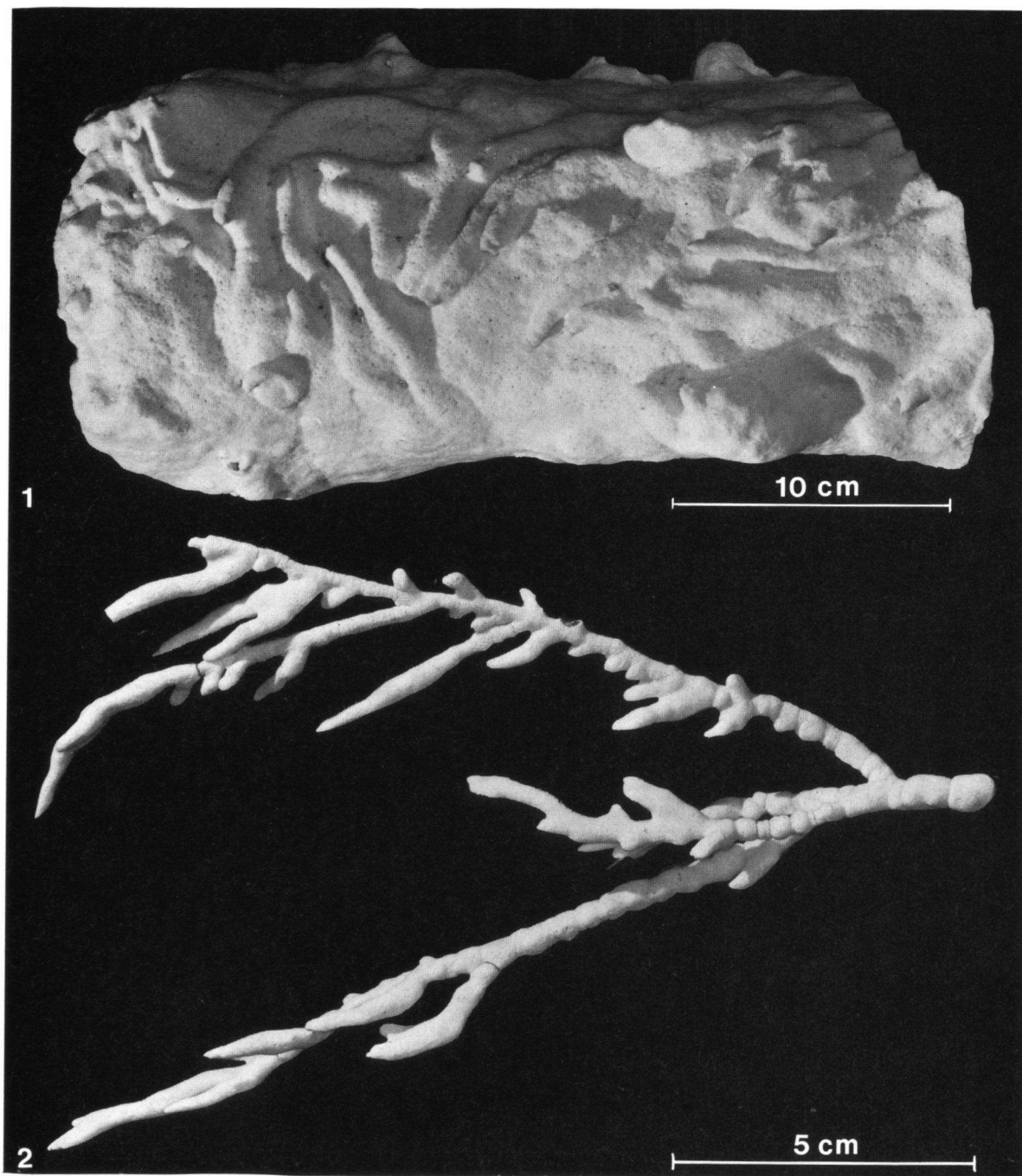

PLATE IV

1, Colony of *Millepora*, incrusting dead coral; 2, colony of *Millepora*, incrusting a gorgonian.

MATERIALS AND METHODS

Classification of the growth forms

To study the growth forms of *Millepora* in the different types of biotopes, a rough classification of the growth forms was made. The branching form has been subdivided into coarse branching and fine branching. The boxwork form has been subdivided into thick bladed and thin bladed boxwork. Furthermore, a dwarf form of boxwork could be recognized with a remarkable compactness and sturdiness, often growing from a large incrusting base. All growth forms encountered could finally be grouped according to the following seven growth patterns: incrusting (plate IV figs. 1 & 2), coarse branching (plate I fig. 1), fine branching (plate I figs. 2 & 3), bladed (plate II figs. 1-3), thin bladed boxwork (plate III fig. 1), thick bladed boxwork (plate III fig. 2) and boxwork dwarf form (plate III fig. 3). A collection was made of all growth forms (ca. 250 specimens).

Classification of the biotopes and abundances

Twenty-two localities on Curaçao and Bonaire were visited and the distribution of the growth forms along several depth intervals recorded. For the frequency of growth forms an arbitrary scale was used, viz. high abundance, mean abundance, low abundance, absent. Some localities could only be visited occasionally. To get a general impression of the relative abundances of growth forms in the time available this method was preferred. The localities were grouped into nine biotopes according to three ecological parameters, viz. water movement (turbulence), current and turbidity. The biotopes were subdivided into four depth intervals, viz. 0-2 m (surf zone), 2-10 m (shelf), 10-15 m (drop-off), and 15-45 m (slope).

Transplantation experiments

The transplantation experiments were carried out at two different sites (stations *a* and *b*) near the Caribbean Marine Biological Institute (fig. 1).
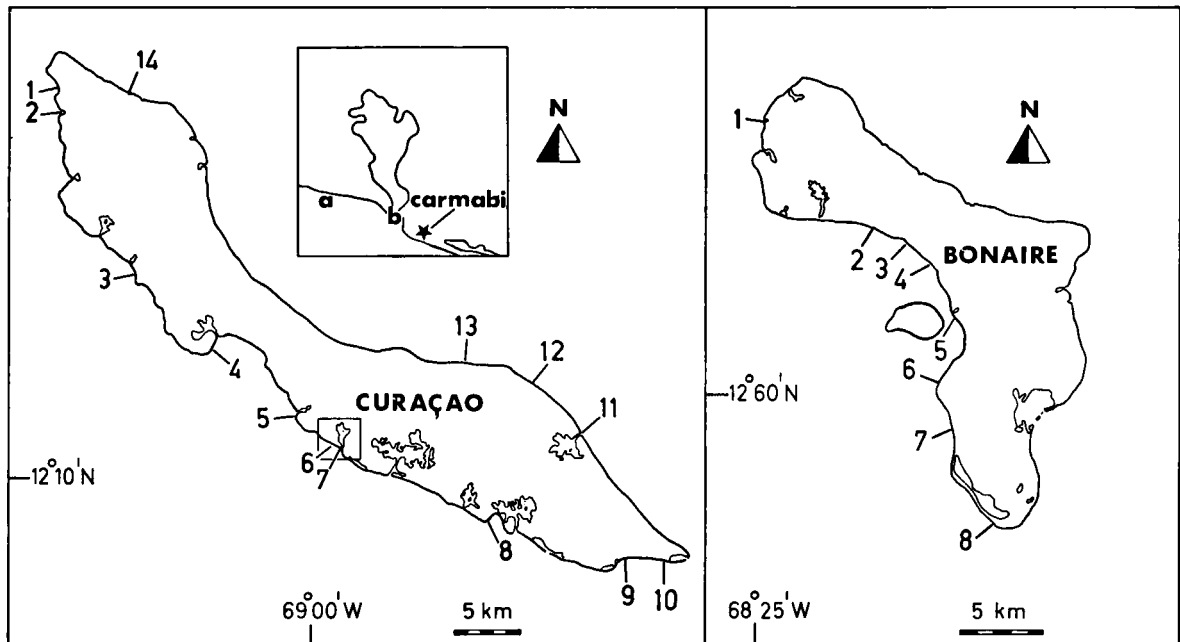

Fig. 1. Localities visited on Curaçao (C) and Bonaire (B), including the experimental stations *a* and *b* (inset). C1 = Playa Kalki, C2 = Playa Abao, C3 = Playa Mansaliña, C4 = Cape St. Marie, C5 = St. Michiels Bay, C6 = 500 m NW of Piscadera Bay, C7 = Piscadera Bay, entrance, C8 = Lijhoek, C9 = 5 km W of Oostpunt, C10 = 3 km W of Oostpunt, C11 = Boca St. Joris, C12 = Ronde Klip, C13 = Boca Santu Pretu, C14 = Boca Tabla. B1 = Playa Funchi, B2 = Karpata, B3 = Barcadera, B4 = Santa Barbara, B5 = 2 km N of Kralendijk, B6 = Bachelor's Beach, B7 = Blauwe Pan, B8 = Rode Pan.
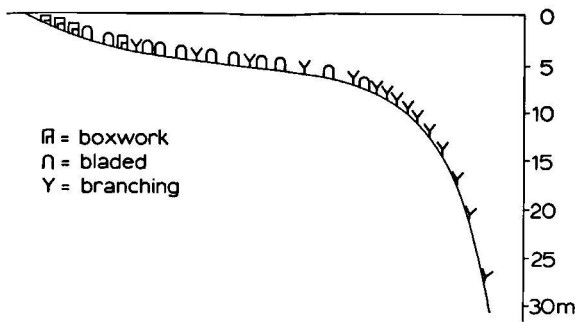
Fig. 2. Profile of station *a* with bathymetric zonation of the growth forms representing the three Caribbean *Millepora* species. Branching = *M. alcicornis*, bladed = *M. complanata*, boxwork = *M. "squarrosa"*.

Colonies were used with a growth form classically considered characteristic of the species and incrusting colonies, on both gorgonians and dead coral, were used as well. According to the literature the growth forms which should represent the three Caribbean *Millepora* species show a bathymetric zonation (Stearn & Riding, 1973).

This was apparent at station *a* (fig. 2). The boxwork form occurred in the surf zone down to about 3 m. The bladed form occurred from about 2 m down to about 12 m. Its greatest abundance was on the shelf at about 5 m. The branching form appeared to have the greatest depth range. It occurred from about 3 m down to about 45 m. Its greatest abundance was near the drop-off at 12 to 15 m. The depth with greatest abundance of one of these forms will be called "optimum depth" in the sequel. In the incrusting forms a bathymetric zonation was not apparent. However, purely incrusting forms were difficult to find, for mostly they have some little outgrowths. In the upper surf zone purely incrusting forms were not found at station *a*.

At station *a* the effect of transplantations to a different depth on the growth form was studied. Colonies of each growth form were taken from their optimum depth and transplanted to the optimum depth of the two other growth forms. The transplantation experiments thus have been carried
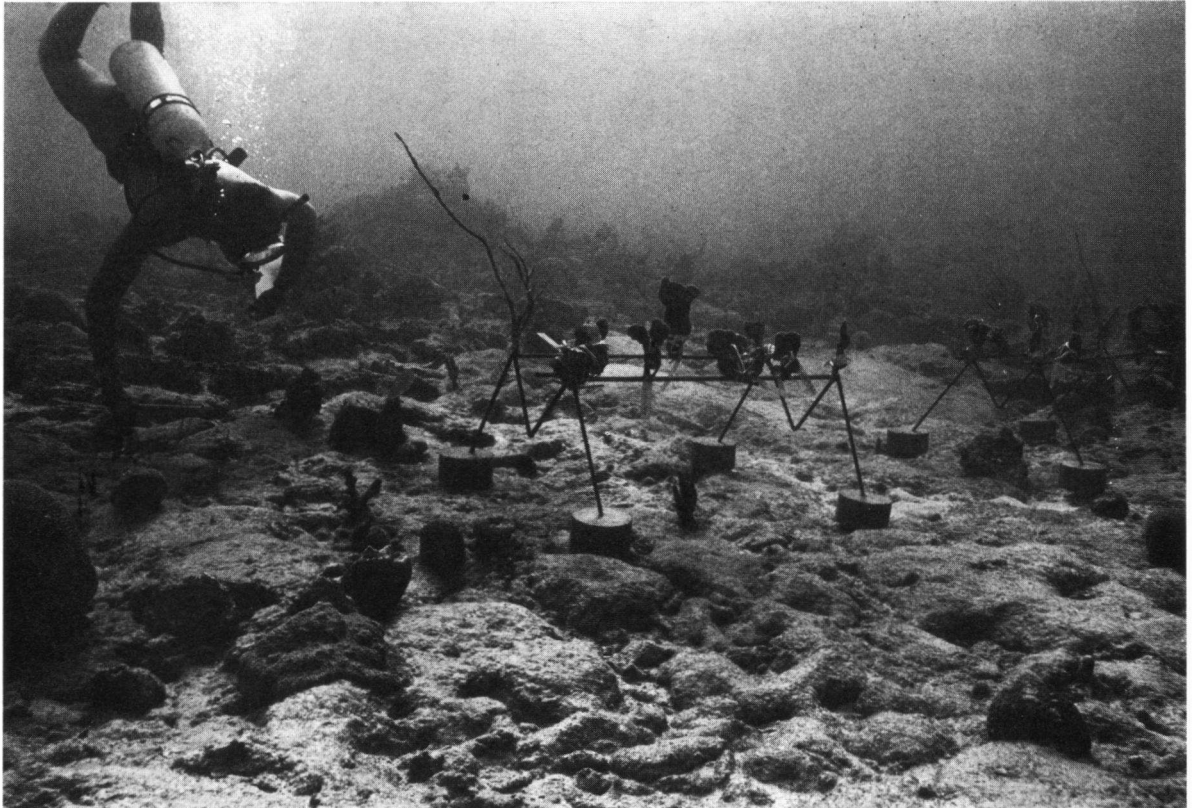

Fig. 3. Iron frames with pins to which transplanted colonies of *Millepora* are fixed with plastic rope.

Fig. 4. Concrete blocks each with one colony. They were used in the surf zone.

out at three different depths: 1, 5 and 15 m. Al-
though the incrusting forms had no optimum
depth, for convenience the same depths were used
(except for 1 m). Control colonies remained at
their original depth but were handled in the same
way as the transplanted colonies.

At station *b* the effect of high turbidity was
studied. Except for some incrusting *Millepora*
colonies no corals were growing at this site. Corals
transplanted to station *b* (depth 5 m) originated
from the nearby reef (ca. 20 m NW of the
entrance of Piscadera Bay). Colonies of more or
less the same size were used (height 10-15 cm).
After collecting they were individually transported
under water to their new growing place. The
colonies were in their original position and orien-
tation fixed with plastic rope to metal pins, at-
tached to iron frames. Each frame carried ten of
these pins (fig. 3). A more heavy construction
was needed in the surf zone. Here concrete blocks
were used, carrying one colony each (fig. 4).
Immediately after the transplantation the colonies

were photographed in situ together with a mea-
suring scale. An underwater Nikonos II camera
with a 28 mm lens provided with a close-up lens
was used. During the experiments the colonies
were photographed from the same position each
third month. At the end of the experiments they
were removed from the pins and taken out of the
water. They were immersed during 24 hours in
undiluted household bleach (Chlorox) and after
this rinsed with fresh water for about two hours.
The colonies were dried in the open air for about
two days. This treatment, which completely re-
moved the living tissue, was necessary for the
investigation of the skeleton structure. The dura-
tion of the experiments was nine months. All
underwater work was done using SCUBA.

Localities studied

Short descriptions of the nine biotopes recognized
are given below. The localities in Bonaire (B)
and Curaçao (C), including the experimental sta-
tions, are shown in fig. 1.

B i o t o p e I (localities: C11a (reef outside the entrance), C12, C13, C14).
Water movement: extremely strong wave action.
Current: absent in the time the localities were visited.
Turbidity: low.
Additional information: all these localities are situated at the windward side of Curaçao, where the water movement is extremely strong. Except for a few days a year, when the permanent northeastern trade wind decreases in velocity, the area is unaccessible for divers. Remarkable is the great abundance of the alga *Sargassum platycarpum* and the relatively low abundance of corals at the shelf.

B i o t o p e II (locality: C11b (entrance of a lagoon)).
Water movement: extremely strong.
Current: absent in the time the locality was visited.
Turbidity: high.
Additional information: at this site a "bottle-neck" situation exists, causing a strong water movement to and from the narrow entrance of the inner bay. *Sargassum platycarpum* is very abundant and coral growth scarce. Turbidity is much higher than at the reef outside the entrance, due to sediments from the inner bay.

B i o t o p e III (localities: C4, C8, C9, C10).
Water movement: strong.
Current: not permanent, sometimes rather strong.
Turbidity: very low.
Additional information: this biotope represents the "open cliff" situation which could only be studied in Curaçao. The sites are, because of their exposition, the most turbulent spots of the south (leeward) coast of the island. The coverage of living corals and gorgonians amounts to nearly 100%.

B i o t o p e IV (localities: C1, B1).
Water movement: moderate, a surf zone exists.
Current: a permanent NW current, which sometimes is very strong.
Turbidity: moderate.
Additional information: Noteworthy in both sites is the high abundance of reef building *Millepora* corals, which seem to have their optimum habitat here.

B i o t o p e V (localities: B2, B3, B4, B5, B6, B7).
Water movement: moderate, a surf zone exists.
Current: absent.
Turbidity: very low.
Additional information: diversity and abundance of corals is remarkably high.

B i o t o p e VI (locality: B8).
Water movement: moderate, surf sometimes strong.
Current: absent.
Turbidity: high.
Additional information: the reef consists of channels and ridges with much sediment and coral debris; living corals are rare.

B i o t o p e VII (localities: C2a (cliffs at both sides of the bay), C5, C6 = station *a*).
Water movement: moderate, a surf zone exists.
Current: moderate.
Turbidity: moderate.

B i o t o p e VIII (localities: C2b (bay), C3)
Water movement: low.
Current: absent.
Turbidity: high.
Additional information: sandy bays without surf and with rather high turbidity; at the shelf coral growth is rare but becomes more abundant near the drop-off and along the slope.

B i o t o p e IX (locality: C7 = station *b*).
Water movement: absent.
Current: absent.
Turbidity: extremely high.
Additional information: no corals are growing at this site, except for some incrusting *Millepora*; the high turbidity is due to sediments from the inner bay, where a mangrove zone exists.

RESULTS

Growth forms of Millepora *and environmental factors*

In fig. 5 the relative abundance of the growth forms in the various biotopes is shown. The biotopes are arranged according to increasing turbulence, the growth forms according to increasing abundance at greater depths.

The quantity of *Millepora* and the variety of growth forms was lowest in biotope I. The scarce growth of corals is partly due to the strong water movement, and partly to the absence of herbivores, (Bak, 1975). The absence of herbivores, which allows the high abundance of *Sargassum platycarpum* seems to be the main reason for the low density of *Millepora*, for in other biotopes with strong water movement (especially biotope III), they were more abundant. In another extreme environment, the bottle-neck situation in a narrow channel (biotope II) and in the upper surf zone of the most turbulent localities the dwarf form of boxwork was found. This form, often growing from a large incrusting base, is quite capable of resisting strong water movement.

The diversity of growth forms was highest in biotopes III and V. The localities of both biotopes were characterized by a remarkable rich coral growth. This may be explained as follows. The two biotopes have two characters in common: (1) extremely transparent water; (2) no destruction caused by people. In Bonaire gathering of corals and spearfishing have been forbidden earlier than
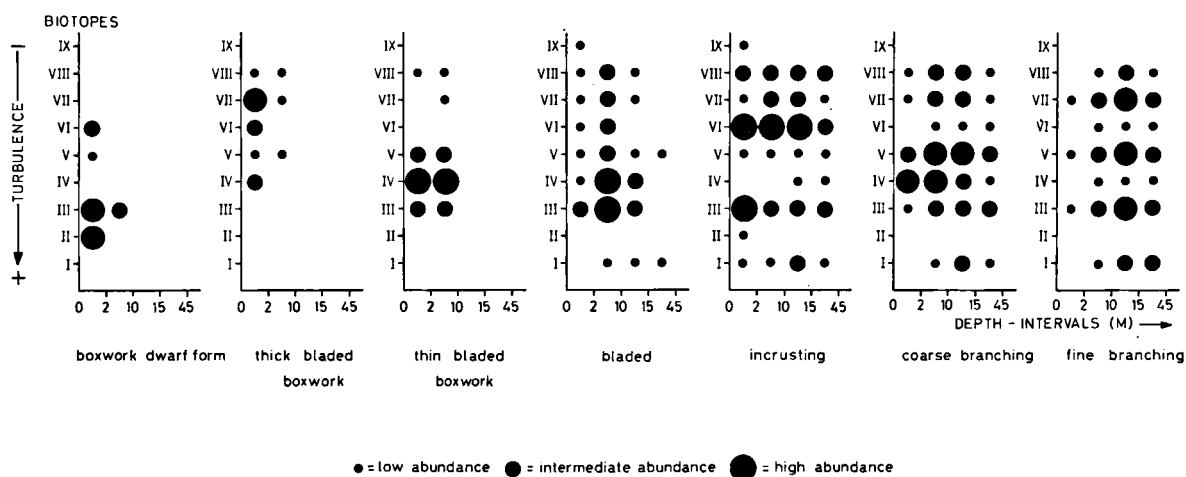
Fig. 5. Relative abundance of the growth forms of *Millepora* in the nine biotopes distinguished (see text). Biotopes are arranged according to decreasing turbulence, growth forms according to increasing abundance at greater depths.

in Curaçao (Curaçao: 1976). As a whole the Bonaire localities are much richer in coral growth and variety of fish than those in Curaçao. The localities of biotope III in Curaçao, however, are among the less accessible spots at the island's south coast. At these sites coral growth was also relatively abundant, characterized for instance by the presence of species of *Antipathes* ("black coral"), which are almost completely lacking in the other localities. Playa Kalki (C1) and Playa Funchi (B1) are characterized by a co-dominance at the shelf of the bladed, thin bladed boxwork and coarse branching growth forms, all occurring in very great quantities. As a whole the amount of different growth forms of *Millepora* colonies and their abundances are remarkably high in these localities. Only in one instance this co-existence can be explained by differences in micro-habitat. The bladed forms grow perpendicular to the current (cf. the observation by Velimirov, 1974, for the Indo-Pacific species, *M. dichotoma*). The space behind the blades will thus form a sort of "stream shade" allowing growth of more delicate forms. Abundant growth of branching forms "behind" the sturdy, bladed forms was frequently observed. In plate II fig. 3, two colonies with different growth forms, the one bladed, the other fine branched are shown growing side by side.

Current seems to be a favourable abiotic factor for *Millepora* corals, in agreement with Mergner

(1977) who called *M. complanata* extremely rheophilic. When turbulence is low little damage will be suffered by the mechanical forces of the water. There is no need to develop a very sturdy growth form, so all calcium deposited will contribute to a growth in height and breadth instead of growth in thickness. The current also ensures a permanent food supply which enables a luxurous growth. In the biotopes VI-IX a decreasing variety in growth forms and in abundance was observed. In biotope VI the zonation of the growth forms as mentioned earlier was obvious. In these localities (biotopes VI-IX, with higher turbidity) more incrusting forms were found than in biotopes with clearer water, especially in the localities of biotopes VIII and IX where turbidity was very high. From this one might conclude that *Millepora* is quite capable of surviving non-optimal conditions by remaining incrusting. This was already mentioned by Crossland (1928).

Transplantation experiments

In table I the number of colonies involved in the transplantation experiments and the mortality of the colonies are given. Mortality was caused by breaking off, especially by destruction in the surf zone, and by algae overgrowth. To obtain a general view all forms were involved in these experiments but in some cases sample sizes are

Number of colonies transplanted to different depths at station *a* and to station *b*. The growth forms branching, bladed and boxwork represent the species *Millepora alcicornis*, *M. complanata* and *M. "squarrosa"*, respectively (see text).

growth form	depth of growth	depth of transplantation				total number of colonies transplanted	mortality	
		station *a*			station *b*			
		1 m	5 m	15 m	5 m			
		number of colonies transplanted (died colonies)					number	%
branching	15	5 (1)	2 (0)	2 (0)	2 (0)	11	1	9.9
bladed	5	30 (7)	2 (0)	8 (1)	2 (0)	42	8	19
boxwork	1	2 (0)	15 (3)	2 (0)	2 (0)	21	3	14.3
IC	5	2 (2)	2 (0)	2 (0)	2 (0)	8	2	25
IC	15	2 (2)	2 (0)	2 (0)	2 (1)	8	3	37.5
IG	5	2 (1)	2 (1)	2 (1)	2 (0)	8	3	37.5
IG	15	2 (2)	2 (1)	2 (1)	—	6	3	50
IC (stat. *b*) *)	5	—	—	—	2 (1)	2	1	50
		45 (15)	27 (5)	20 (3)	14 (2)	106	24	22.6

IC = incrusting dead coral; IG = incrusting gorgonians.

*) Incrusting dead coral in the entrance of the Piscadera Bay (station *b*); used as control colonies of this site.

rather small. Only the growth forms bladed and boxwork received special emphasis and were transplanted to each other's optimum depths in larger numbers.

Station *a*

Branching forms. — The four surviving colonies of this growth form, transplanted from 15 m to the surf zone (1 m) adapted themselves very well to the new depth. At the end of the experiment their growth form was much more sturdy than at the beginning and also in comparison with the control colonies. In plate V figs. 1 and 2 the growth of one colony, transplanted to the surf zone is shown. Two colonies, transplanted to 5 m also became more sturdy, but in a lesser degree than those transplanted to the surf zone.

Bladed forms. — The 30 colonies transplanted from 5 m to the surf zone showed a very fast growth in comparison with the colonies transplanted to 15 m and the control colonies. Because of their growth form it was possible to make some

rough measurements of the two-dimensional growth of some colonies. This was done by using the photographs and transparent paper on which the outlines of the colonies were drawn. In fig. 6 the outline of one colony, transplanted to 15 m is shown. The black zone represents the growth after 260 days. The results of the measurements are shown in table II. Growth is expressed in square mm · cm^{-1} growing edge per month.
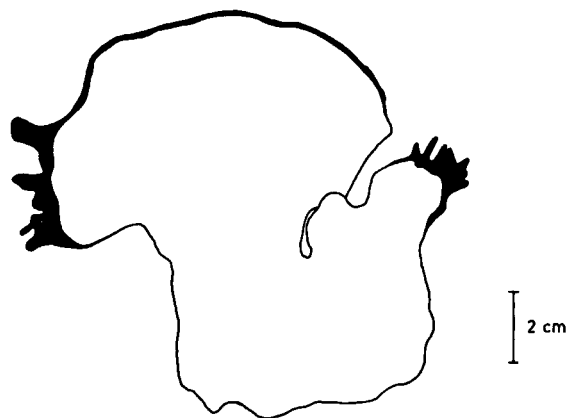

Fig. 6. Growth (black edges) of a bladed colony, transplanted from 5 m to 15 m (after 260 days).

TABLE II

Growth of individual bladed colonies, transplanted to different depths at station *a*.

depth of growth (m)	depth of transplantation (m)	total length growing edges (cm)	mean growth of the different growing edges ($mm^2 . cm^{-1}$ growing edge/month)
5	1	1.8	12
5	1	6	18
5	1	13.7	11
5	1	4.6	18
5	1	3.8	12
5	5	2	6
5	5	17.3	6
5	15	17	3
5	15	19	3

The growth rates of the colonies transplanted to different depths show marked differences. It is known that the growth rate of hermatypic corals is highly dependent on the light available because of their symbiosis with zooxanthellae (Goreau, 1959, 1963; Goreau & Goreau, 1959). The amount of light decreases with increasing depth and an inverse relation between the growth rate of some coral species and depth was reported by these authors. The Milleporidae also have zooxanthellae in their living tissues (Boschma, 1925; De Kruijf, 1975) and the amount of light available is known to influence their growth rate (Goreau, 1963; Strömgren, 1975). The results of the measurements of this study, which indicate that growth rate was highest in the colonies transplanted to 1 m and lowest in the colonies transplanted to 15 m, are in agreement with this. In two colonies, transplanted to the surf zone lateral outgrowths began to develop. The growth of one of these colonies is shown in plate VI figs. 1-4.

Most interesting are the colonies transplanted to 15 m. Five of the eight colonies developed delicate, branchelike outgrowths. In plate V figs. 3 and 4 the growth of one colony is shown.

Boxwork forms. — The colonies with this growth form were less able to adapt to the new depths. The colonies transplanted from 1 m to both 5 and 15 m did hardly show any growth. See plate VII figs. 1 and 2 for the growth of one colony, transplanted to 5 m. However, some growth can be observed in this colony. The lateral outgrowths seem to disappear and the colony becomes more bladed.

Incrusting forms. — Only 5 of the 24 colonies, transplanted to various depths, showed any growth. Eleven colonies died, 13 colonies were still alive at the end of the experiments but 8 of them showed no growth. Death rate was highest in the surf zone and among the growth forms incrusting gorgonians. In plate VII figs. 3 and 4 the growth of an incrusting colony on a coral head, used as control colony at 5 m is shown. It is clear that this incrusting form was the incrusting initial phase of four bladed outgrowths. The same happened with a colony growing at 5 m, transplanted to 15 m. Delicate outgrowths developed in both control colonies of 15 m as well. One colony however was not really incrusting at the start; some branched outgrowths already existed. Some delicate outgrowths developed in a gorgonian incrusting colony from 15 m, transplanted to 5 m and also in one control colony from 5 m.

Station *b*

Most colonies transplanted to station *b* suffered from sedimentation and algal growth, but they were still alive (the polyps being active) at the end of the experiments. Growth could be observed in the two colonies of the bladed form and in three incrusting forms. The boxwork colonies only partly recovered from algal overgrowth. One colony formed ampullae, which might be a survival mechanism (see plate VIII figs. 1 and 2).
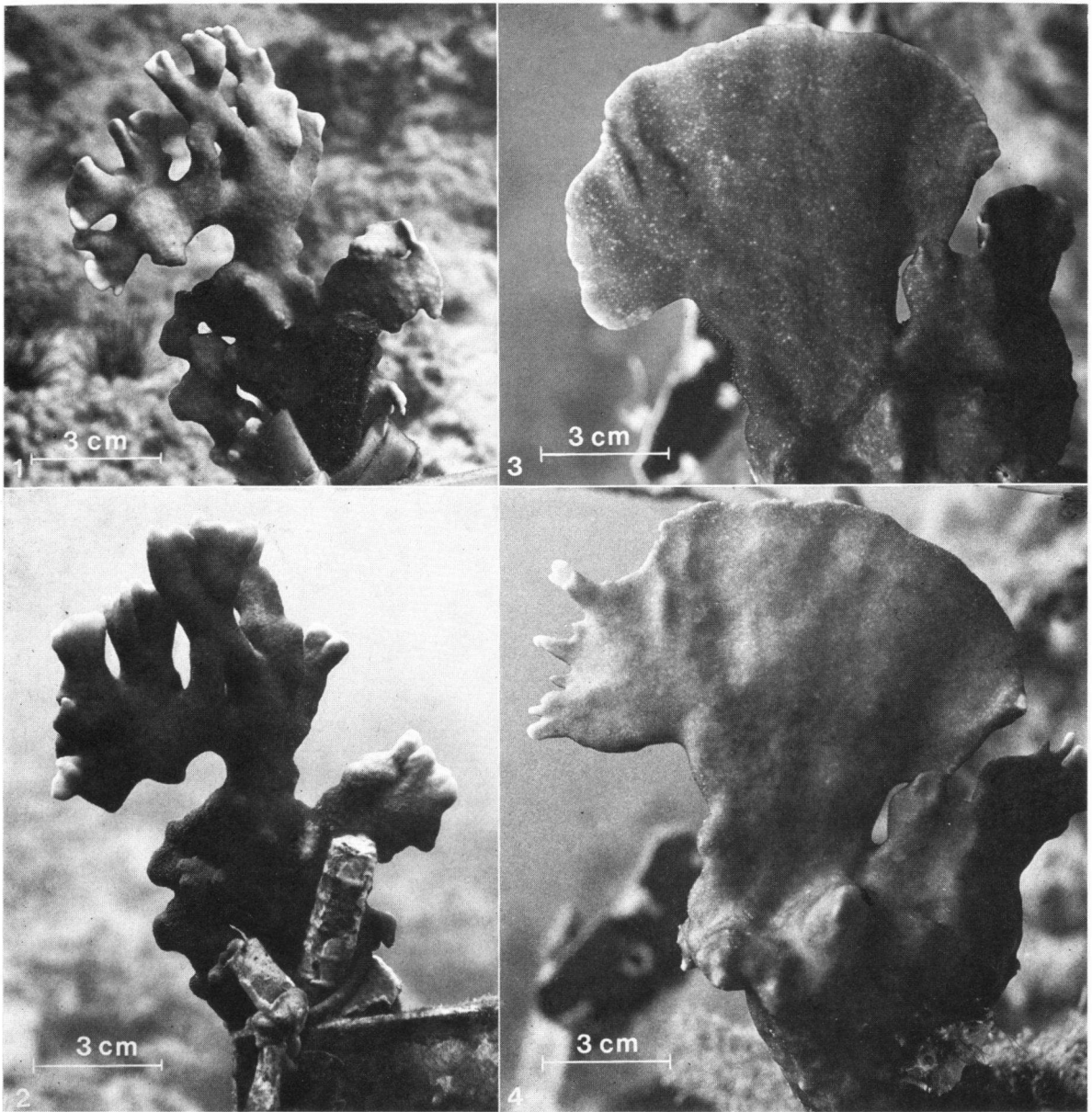
PLATE V

1, Branching colony, transplanted from 15 m to 1 m, date: 3 June 1976; 2, same colony, date: 8 December 1976; 3, bladed colony, transplanted from 5 m to 15 m, date: 13 April 1976; 4, same colony, date: 10 December 1976.

In one colony incrusting dead coral from 5 m some delicate outgrowths developed. These results seem to indicate that *Millepora* is quite capable to survive in turbid conditions.

CONCLUSIONS AND DISCUSSION

Some relations between the growth form in *Millepora* and the environment were found in this study: finely branched forms appear in deeper, quieter waters, sturdy forms in more turbulent waters, incrusting forms in turbid places as well as in extremely turbulent places. These adaptations in *Millepora* to environmental factors, especially water movement and light conditions have been described in scleractinian coral species as well (Yonge, 1963; Roos, 1964, 1967, 1971;

PLATE VI

1, Bladed colony, transplanted from 5 m to 1 m, date: 4 May 1976; 2, same colony, date: 9 June 1976; 3, same colony, date: 25 August 1976; 4, same colony, date: 9 December 1976.

Milliman, 1973). In the sites with strong current the abundance and co-existence of several growth forms of *Millepora* was highest, from which can be concluded that *Millepora* is extremely rheophilic.

The coexistence of different growth forms, however, is only to a certain extent explained by differences in ecological conditions. The various growth forms have wide and overlapping ecological amplitudes, which appears most clearly in optimal biotopes for *Millepora*. In contrast with these observations are the results of the transplantation experiments. Some bladed colonies started to resemble boxwork, when transplanted to the optimum depth of boxwork and most colonies transplanted to the optimum depth of the
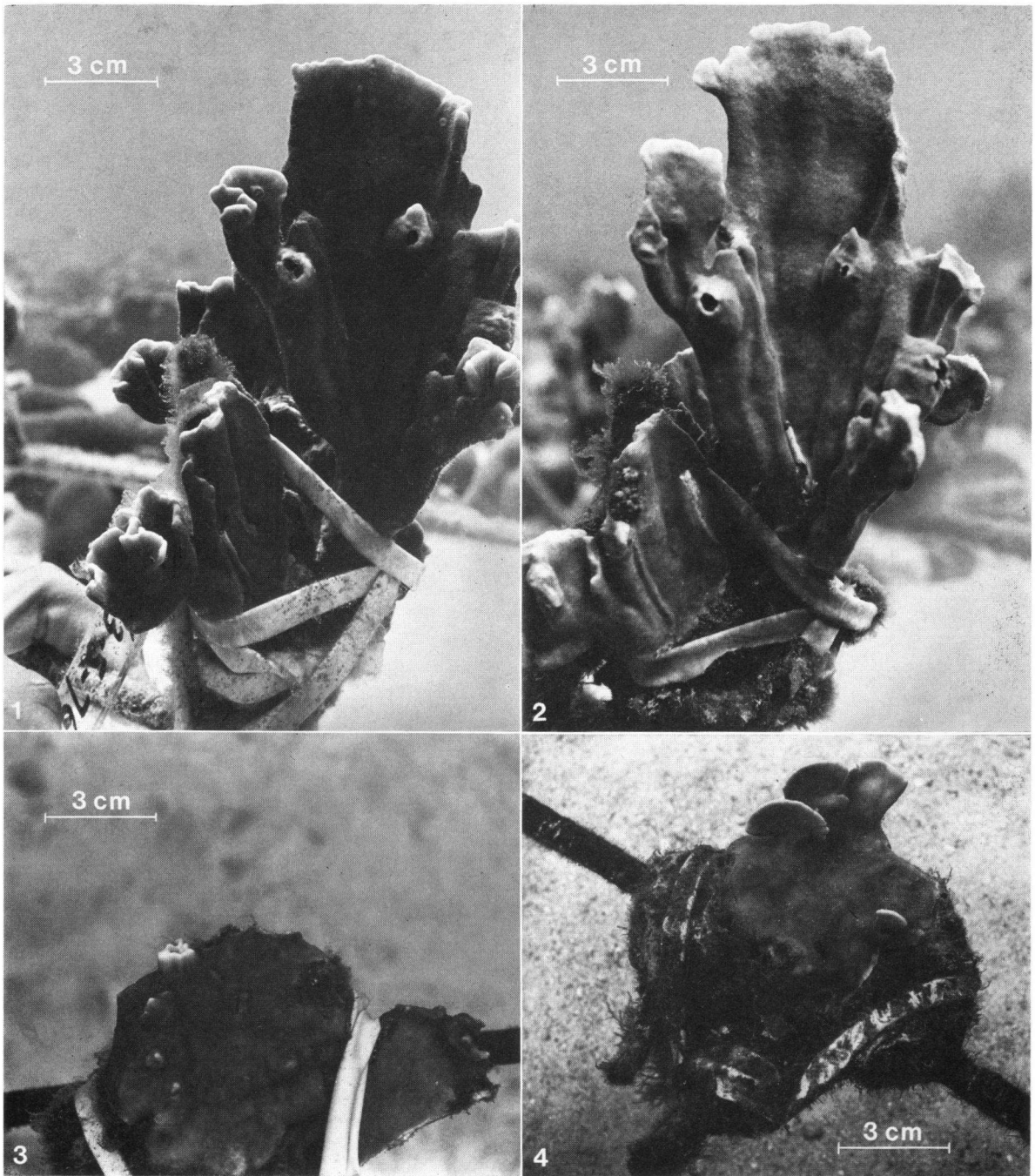
PLATE VII

1, Boxwork colony, transplanted from 1 m to 5 m, date: 18 May 1976; 2, same colony, date: 8 December 1976; 3, colony, incrusting dead coral, control colony of 5 m, date: 29 March 1976; 4, same colony, date: 7 December 1976.

branching form started to resemble this form. From this it can be concluded that the growth form is induced by the factor depth (in which both water movement and light are included), and that the adaptability of *Millepora* to various con-ditions on the reef is very high.

To which extent Boschma (1948a) has taken into account the adaptibility of growth forms in *Millepora* may be apparent from the following. He stated (: 71): "There are a number of species
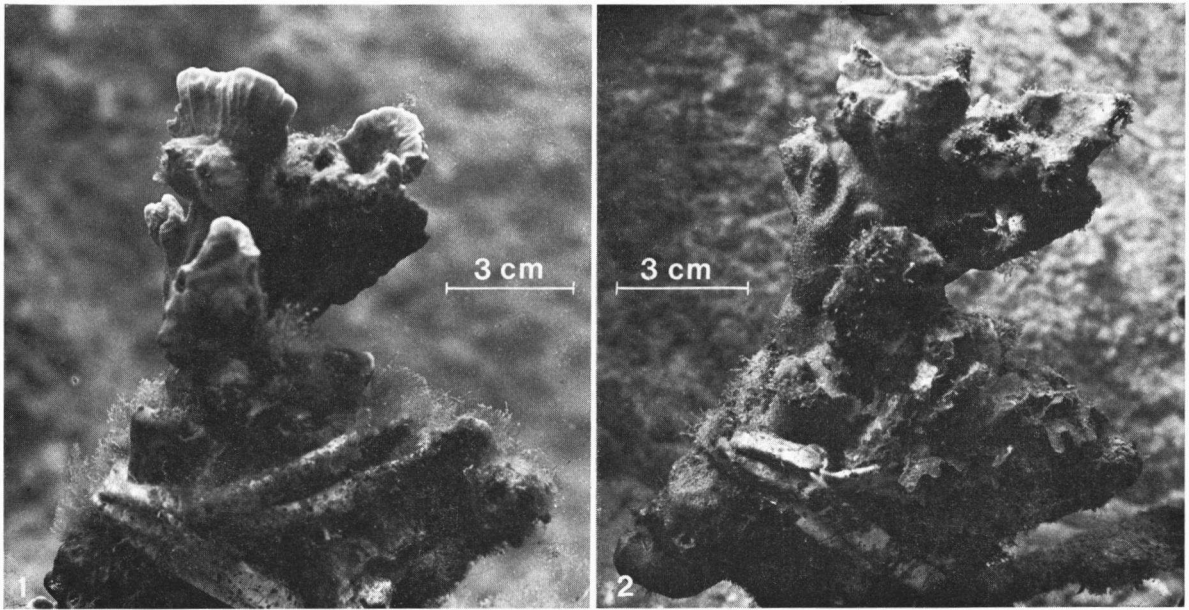
PLATE VIII

1, Boxwork colony, transplanted from 1 m to station *b* (depth 5 m), date: 30 March 1976; 2, same colony with ampullae, date: 10 December 1976.

in *Millepora*, each of which is so strongly variable that under the influence of external conditions it may assume a form which is more or less typical for another species." However, some pages earlier he stated (: 48): "But these changes in form, as they are caused by external influences, manifest themselves within certain limits. Every species of *Millepora* has its range of variation, but notwithstanding that it keeps certain characters of its growth form which as a rule are suffiently distinct to warrant a reliable specific identification." The results of the transplantation experiments are not in agreement with the last quoted statement, but indicate that the growth form of *Millepora* is more variable than Boschma supposed.

The following example shows that taxonomic treatment of growth forms is not consistent. In the Indo-Pacific as well as in the Atlantic region bladed *Millepora* corals occur in two growth forms: purely bladed and boxwork, but with many intermediate forms. Whereas the Indo-Pacific forms are considered as one species (*M. platyphylla*), the Atlantic ones are treated as two different species (*M. complanata*, *M. squarrosa*). In my opinion this is not justifiable, as long as identification is merely based on the growth form.

Certain Atlantic forms generally treated as *M. squarrosa* might however be the shallow-water form of *M. complanata*. The existence of many intermediate forms points in this direction. When I started the transplantation experiments I was convinced that the shallow boxwork form was *M. squarrosa*, for it fully agreed with the description of Boschma (1948a). Later, however, I studied the four specimens of this species in the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH, coll. no. 8513, 8514, 8515 and 10557, the last specimen identified by Boschma), and they were clearly different from the boxwork forms found in Curaçao and Bonaire. The museum specimens differed in: general appearance, the ratio size gastropores/size dactylopores (the gastropores being at least twice as large as the dactylopores), the number of dactylopores surrounding each gastropore, the degree of isolation of the cyclosystems, formed by the gastropores and dactylopores, and finally in texture of the surface. The surface of the museum specimens was much smoother than in the boxwork forms previously identified by me as *M. squarrosa*.

Concerning the occurrence of *M. squarrosa*, Boschma (1962) writes that this species is of a

much rarer occurrence than *M. alcicornis* and *M. complanata*. Although *M. squarrosa* is officially known from Pernambuco (Brazil), Puerto Rico, Barbados (Boschma, 1962) and St. Eustasius (collection RMNH, det. Dr. J. van der Land), which means that it has a rather wide geographical distribution in the Western Atlantic region, only a few specimens have ever been observed. It might be that *M. squarrosa* does not even occur at Curaçao and Bonaire, and that the boxwork form is always erroneously considered to belong to this species. If this is the case *M. squarrosa* turns out to be a rather rare species, conform the observations of Boschma (1962), and all bladed (including the thin bladed boxwork, thick bladed boxwork and boxwork dwarf form) colonies treated in this paper should be identified as *M. complanata*, unless additional information about the above-mentioned characters points to a real specific status of the *squarrosa* form described in this paper.

A preliminary investigation of the sizes of the pores indicated that no differences between the boxwork and bladed forms exist, whereas these forms together differ significantly from the branching forms. Therefore a re-examination of the characters mentioned, including the size and shape of the ampullae (although not always present) seemed worth while after the present study. This may reveal characters which are of greater taxonomic significance than Boschma (1948a) supposed. The results of this study will be discussed in a future paper.

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