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RUBBLE MOUNDS OF SAND TILEFISH *MALACANTHUS PLUMIERI* (BLOCH, 1787) AND ASSOCIATED FISHES IN COLOMBIA

Heike Büttner

ABSTRACT

A 6-month study consisting of collections and observations revealed that a diverse fauna of reef-fishes inhabit the rubble mounds constructed by the sand tilefish *Malacanthus plumieri* (Perciformes: Malacanthidae). In the Santa Marta region, on the Caribbean coast of Colombia, *M. plumieri* occurs on sandy areas just beyond the coral zone. The population density is correlated with the geomorphology of the bays; the composition of the material utilized depends on its availability. Experiments showed that debris was distributed over a distance of 35 m. Hard substrate must be excavated to reach their caves. In the area around Santa Marta the sponge *Xestospongia muta* was often used by the fish as a visual signal for suitable substratum. The rubble mounds represent a secondary structure within the "coral reef" ecosystem. These substrate accumulations create structured habitats in the fore reef, which are distributed like islands in the monotonous sandy environment and where numerous benthic organisms are concentrated. The tilefish nests attract other organisms because they provide shelter and a feeding site in an area where they would not normally be found. At least 32 species of fishes were found to be associated with the mounds. Some species lived there exclusively during their juvenile stage, indicating that the *Malacanthus* nests serve as a nursery-habitat. *M. plumieri* plays an important role in the diversification of the reef environment.

For several years artificial reefs and isolated structures, for example patch reefs and coral blocks, have been the subject of investigations of development and dynamics of benthic communities (Randall, 1963; Fager, 1971; Russell, 1975; Russell et al., 1974; Sale and Dybdahl, 1975). The importance of these structures is the provision of a habitat for many organisms in a monotonous environment. Thus they contribute to the diversification of the marine fauna. An artificial reef may provide different resources for various marine organisms: offering hard substrate for many organisms, which forms a source of nutrition for other animals. A complex structure of the substrate offers a habitat and refuge from predator attacks for numerous species, and serves as an orientation point for fishes during their foraging (Botero et al., 1980).

Malacanthus plumieri is a sedentary and strongly territorial species and lives in colonies on sandy bottoms (Baird and Baird, 1992). Each individual excavates and lives in a burrow. On top of the cave—a nearly horizontal tunnel—the fish accumulates a mound of coarse debris consisting of coral rubble, pelecypod shells and stones (Böhlke and Chaplin, 1968; Clifton and Hunter, 1972; Colin, 1973; Dooley, 1978). The burrow serves as a primary refuge from predator attacks (Baird, 1988; Baird and Liley, 1989).

Earle (in Clifton and Hunter, 1972) was the first to indicate that the mounds serve as habitats for small reef fishes in St. John, and Colin (1973) made similar observations in the Bahamas. I received a preliminary list of fishes living in the *Malacanthus* mounds on the Caribbean coast of Colombia in the Santa Marta area from Acero (personal communication). Schmitting-Falk (1990) mentioned that the mounds provide a suitable habitat for non-digging brachyuran crabs beyond the coral zone. In my investigation (Büttner, 1993) the associated fauna of the tilefish mounds was qualitatively and quantitatively studied to demonstrate the importance

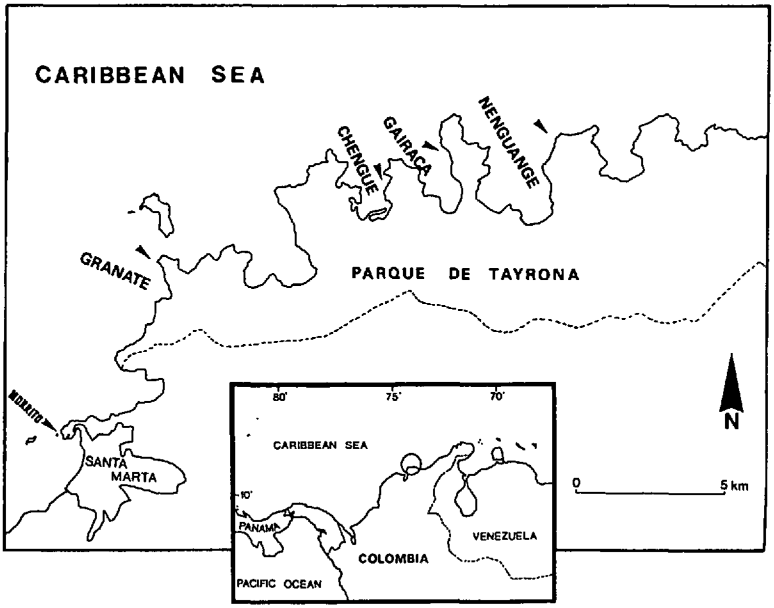

Figure 1. Map of the study area. Stations of observations and samplings around Santa Marta and in the Tayrona National Park.

of the biotope, constructed by the activity of only one organism, for the diversity within its environment.

In this paper I submit detailed information about the distribution pattern of the sand tilefish in the Santa Marta region and the fish community associated with the rubble mounds. The study considers the synecological aspects of the community to assess its function. Hence it contributes to the ecological investigations within the program: "Ecosistemas Marinas" of the INVEMAR (Instituto de Investigaciones Marinas de Punta de Betín) carried-out along the Caribbean coast of Colombia.

Methods

Study Site.—The field study was carried out from February to July 1991 on the Caribbean coast of Colombia in the Santa Marta region (11°12'N, 74°13'W). In this region sandy areas just beyond the coral-zone are typical locations for the occurrence of the sand tilefish. Sublittoral areas in the Tayrona National Park were chosen for the investigation, where the bays are flanked by coral formations, and in the region Northeast of Santa Marta around the Punta de Betín peninsula (Fig. 1). All observations and samplings were made during scuba-diving expeditions.

Fieldwork.—A total of 33 burrows in different locations were selected and marked with buoys. I measured the size (length × width × height), the depth, and noted the condition (occupied or abandoned) of the burrows. The remarkable nature of the tilefish mounds necessitated different methods to record the associated fauna. The composition and density of the species of the ichthyofauna was estimated by repeated observations and counting. Furthermore typical behavior relative to the substrate was recorded. Sampling was necessary to identify the cryptofauna. Rubble samples of 3–4 liters were taken and the individuals were examined in the laboratory. The pebbles were sorted with respect to size and quality to understand the correlation between the species composition and density of the community to the substrate.

Two dummy mounds were constructed to evaluate the colonization process of the different organisms in relation to the structures. Material of different quality was used to investigate the influence of the substrate on the colonizers. A mound of stones (69 × 53 × 17 cm) was constructed at Punta de

Betín and another mound of dried mound material (66 × 61 × 20 cm) was placed within a *Malacanthus*-population in Nenguange.

Laboratory.—The nutrition spectrum was analysed to examine predator-prey relations, competition for food, and use of nutritional resources as well as adaptations to the biotope. The species were grouped in feeding classes according to Randall (1967) and my own examinations. The classification was based on the highest percentage of the stomach content.

The species were identified and quantified in terms of relative abundance (dominance), frequency of occurrence (presence) and species diversity in order to describe the fish community.

RESULTS

Malacanthus plumieri: *Presence in the Study Area; Size and Distribution of the Mounds; Burrow Construction.*—In the study area *M. plumieri* has been found at depths of 7.5 to 45 m. The horizontal distribution is restricted to a maximum distance of 40 m from the reef.

The average size of the investigated mounds was 133 × 102 × 22 cm (max. 208 × 198 × 17 cm; min. 85 × 67 × 15 cm). The form of the mounds differed: the higher ones were often pyramid shaped, others covered a wider area but were lower.

Some digging sites and collapsed burrows were observed. Frequently a sponge was integrated in the rubble mound. Besides *Neofibularia nolitangere* (Duchassaing and Michelotti) and *Ircinia strobilina* (Lamarck), a tube of *Xestospongia muta* (Schmidt) was often situated on top of the entrance to the cave. The sponge only colonizes on hard substratum. It is possible that it functions as a visual signal for the sand tilefish indicating that suitable substrate for burrow construction is available. The nature of the substrate is obviously an important factor in cave excavation. *M. plumieri* needs a roof construction on the sandy substrate to prevent the cave from collapsing.

During several dives at the Morrito, individuals were observed actively excavating the cave and accumulating coarse debris. By undulating its whole body, the fish first forms a depression in the sand. If hard substrate is encountered, the fish continues to dig by pushing its snout against the substrate, and performing further undulating movements. Furthermore the fish picks up small fragments and drops them at the top of the cave. When the cave is nearly completed, *M. plumieri* looks for coral and shell debris in the surrounding area. It carries them to the building site and drops them there. The fish are selective. One young specimen (20 cm TL) was observed picking up fragments again and again. It examined them and used only selected fragments for its nest. The pebbles used were smaller than in the other mounds. It is possible that because of its body size the fish could not carry larger ones.

Due to the water current and the sedimentation rate, abandoned nests were covered with sand. Occupied burrows are maintained by the activity of the fish which continually brings new debris. Mounds which were damaged by samplings were completely reconstructed within four weeks. During this time one fish carried a volume of about 3 liters of material. The condition of the nest shows if it is abandoned or occupied. The entrances of abandoned nests are blocked with clastic material. Occupied burrows have an area of loose sand around the entrance.

Material Composition of the Malacanthus *Mounds.*—No detailed information exists about the composition and the origin of the utilized material although Clifton and Hunter (1972), Colin (1973) and Clark et al. (1977) touched on this topic. One subject of this investigation was to analyse and compare the material components of different *Malacanthus* mounds. The investigation revealed that the composition varies within the different bays and the specific location. Altogether

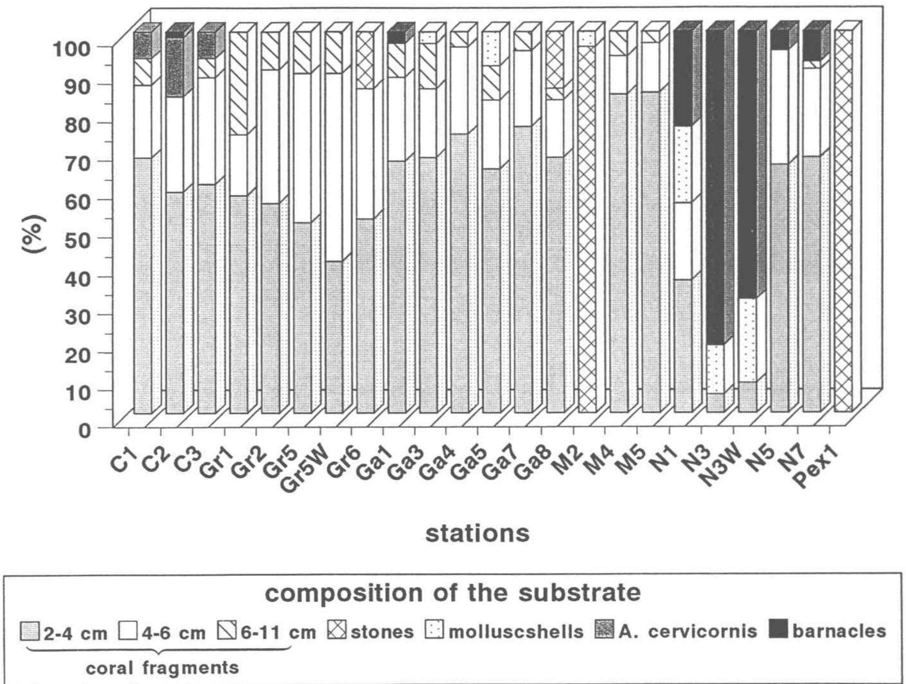

Figure 2. Composition of the material of different *Malacanthus* mounds.

the following components were found: stones, coral fragments, mollusc and star barnacle shells. Depending on the age of the hard substrate, the fragments were overgrown by different organisms: calcareous algae, green-, red-, and brown algae, foraminifers, bryozoans, hydroids, tunicates, tube-building polychaetes, vermetids, balanids and sponges. The structure of the surface varied accordingly. Figure 2 shows the percentage of the material composition of different tilefish mounds. With few exceptions, the samples were similar. The principally utilized materials were coral fragments of 2–4 cm length and width. In addition, sampling showed that there were strata within the mounds. Smaller fragments were found in the center while the material was larger at the periphery.

At the base of the Punta de Betín peninsula, at a depth of 7 m, the mounds were mainly constructed with stones, presumably because the sand bottom is bounded by a zone of rocky-debris. The structure of the material utilized provides a spacious interstices system. In Chengue, a distinct relationship between the *Malacanthus* mounds and the substrate available in the surrounding area, could be observed. Within these mounds the fragments of *Acropora cervicornis* (Lamarck) were conspicuous. *A. cervicornis* dominates the reef formation along the northern flank but most of the colonies are dead. The study site in Nenguange was located at the base of a steep slope of a single rock in an offshore location. Here the rubble mounds displayed widely varying compositions. At the base of the rock, the mounds were constructed exclusively from balanid shells. The rocky intertidal zone provides an ideal substrate for star barnacles, and their shells broken by the strong wave movement, are a building material used with preference by *M. plumieri.* In contrast nests further from the rock contained only few balanid shells, and were dominated by coral fragments.

Table 1. The fishes associated with the rubble-mounds constructed by the sand tilefish *M. plumieri*. Number of individuals in order of decreasing abundance (N), percentage of number of individuals (%), frequency of occurrence over the 31 investigated mounds (Oc), status in the biotope and feeding class.

Species	N	%	Oc	Status	Feeding mode
Stegastes partitus (Poey)	469	34.30	100	r	p + h
Chromis insolata (Cuvier)	242	17.70	55	r	p
Gnatholepis thompsoni Jordan	138	10.10	87	r	d
Apogon spp.	109	8.00	26	r	c
Centropyge argi Woods & Kanazawa	106	7.80	58	r	d + h
Haemulon sp.	76	5.60	23	t	c
Serranus baldwini (Evermann & Marsh)	62	4.50	81	r	c
Paranthias furcifer (Valenciennes)	30	1.30	16	v	p
Synodus synodus (Linnaeus)	14	1.02	39	v	c
Holacanthus tricolor (Bloch)	14	1.02	26	v	d + c
Apogon maculatus (Poey)	12	0.87	13	r	c
Canthigaster rostrata (Bloch)	12	0.87	32	v	o
Apogon pseudomaculatus Longley	11	0.80	16	r	c
Apogon quadrisquamatus Longley	9	0.65	13	r	c
Coryphopterus sp.	9	0.65	16	r	d
Scorpaena sp. 1	8	0.58	25	v	c
Chromis cyanea (Poey)	8	0.58	7	t	p
Ephinephelus fulvus c.f.	7	0.50	20	v	c
Opistognathus aurifrons Jordan & Thompson	6	0.43	17	r	p
Lycodontis moringa (Cuvier)	5	0.36	16	v	c
Chaetodon sedentarius Poey	5	0.36	13	t	c
Equetus lanceolatus (Linnaeus)	4	0.29	10	v	c
Serranus chionaraia Robins & Starck	3	0.22	3	r	c
Acanthurus bahianus Castelnau	2	0.15	3	t	h + d
Muraena miliaris (Kaup)	2	0.15	7	v	c
Pareques acuminatus (Bloch & Schneider)	2	0.15	7	v	c
**Scorpaena isthmensis* Meek & Hildebrand				r	c
**Scorpaena* sp. 2				r	c
**Scorpaenodes tredecimspinosus* (Metzelaar)				r	c
**Pseudogramma gregoryi* (Breder)				r	c
**Priolepis robinsi* Garzon & Acero				r	c
**Quisquilis hipoliti* (Metzelaar)				r	d

Presence (Oc)	Status	Feeding mode
0–25% rare	r: resident	c: carnivorous
25–50% occasional	v: visitor	d: detritivorous
50–75% common	t: transient	h: herbivorous
75–100% abundant		p: planktivorous

* Exclusively in samplings, not included in the quantitative survey.

Description of the Associated Fish Community.—During the study 32 species of 15 families were recorded at the nests of *M. plumieri* (Table 1). The following species which were observed in more than 75% of the *Malacanthus* mounds were considered as "abundant": *Stegastes partitus, Gnatholepis thompsoni,* and *Serranus baldwini. Chromis insolata* and *Centropyge argi* were "common" dwellers, and were recorded in more than 50% of the mounds. The classification of these species result from diurnal observations; cryptic and nocturnal forms were not included. Supplementary sampling also allowed the classification of the following species as "abundant": *Pseudogramma gregoryi* and apogonids. Species classified as "occasional" occurred regularly in 25–50% of the mounds. These species included *Scorpaena* sp. 1, *Canthigaster rostrata, Synodus synodus,* and *Holacanthus tricolor.* Most of the observed species were "rarely" present.

Differences regarding the relative abundance of single species were observed according to the number of individuals and species in the mounds. Dominant species were *St. partitus, Ch. insolata, G. thompsoni, Apogon* spp., *Ce. argi,* and *Haemulon* sp. They accounted for 84% of the total number of individuals. The remaining species were represented by only a few individuals.

Table 1 shows a lack of correspondence between the rank position by relative abundance (dominance) and frequency of occurrence (presence) for most species. Some species were observed in nearly every mound, but were represented by only a few specimens.

The status of the fishes in the biotope was classified according to occurrence, age structure and behavior of individuals at the *Malacanthus* mound. Resident species actually live within or are otherwise intimately associated with the rubble mounds. Species whose individuals remain for a couple of days or weeks and then move on are classified as visitors. Transients pass through the area and stay for only a short period. In the Santa Marta region, nearly 60% of the encounted ichthyofauna could be identified as residents (Table 1), based on the simultaneous occurrence of adults and juveniles and their frequent presence in the *Malacanthus* nests. The pomacentrids *Ch. insolata* and *St. partitus* occurred only as juveniles. It is assumed that the rubble mounds of *M. plumieri* serve as a nursery habitat for these species, whereas the adults have other habitat requirements. Ten species (=31%) were judged to be visitors. They were observed temporarily, but regularly. *Ephinephelus fulvus* c.f., *Paranthias furcifer,* and *H. tricolor* were only observed as juveniles. It is possible that the interstices of the pebbles are only used as a refuge during their juvenile stage, because the cavities become too narrow for adults. For the cryptic living Muraenidae, the mounds may provide refuge and food. It may be assumed that the voracious *Sy. synodus,* and the sciaenids *Equetus lanceolatus,* and *Pareques acuminatus* stay in the tilefish nests for the same reason. Four species classified as transients, were observed only sporadically. They have other habitat requirements and used the mounds coincidentally as a resting and feeding site during their wanderings.

Many species showed a preference for different areas of domicile in the *Malacanthus* mounds (Fig. 3). The nocturnal apogonids move only in the shadow of the cavities. *Ps. gregoryi* and the small *Scorpaena* sp.2 live exclusively cryptically. *Se. baldwini* prefers the sandy area near the edge of the mounds and is an aggressive species that does not permit other specimen to dwell close by. *Ce. argi* looks for shelter in the rubble interstices and emerges only for short periods. *St. partitus* and *Ch. insolata* move above the cupola of the mounds and slip into the cavities when attacked. *Sy. synodus* and the gobies *Coryphopterus* sp. and *G. thompsoni* use the adjacent sand area, and look for shelter under separate fragments. *Ca. rostrata, Eq. lanceolatus* and *Pa. acuminatus* dwell outside the mound substrate. The yellowhead jawfish, *Opistognathus aurifrons,* which lives in selfmade vertical burrows, shows an affinity to the *Malacanthus* nests, as it often excavates these burrows at the periphery of the rubble mounds.

Table 2 shows the compilation of measurements of the structure of the associated fish community. The average number of species observed per nest was seven (range 3–14). The number of individuals per mound averaged 44 (range from 5–117). The Shannon-Weaver index for species diversity ranges from 0.72 to 2.11. Evenness values are relatively high with an average of 76%.

The material composition of the different mounds showed clear differences according to the quality of the hard substrate and the size of the interstices system. Considerable variety in the number of species and individuals at particular sites could be observed (Fig. 4). The mounds in Nenguange, mostly constructed with

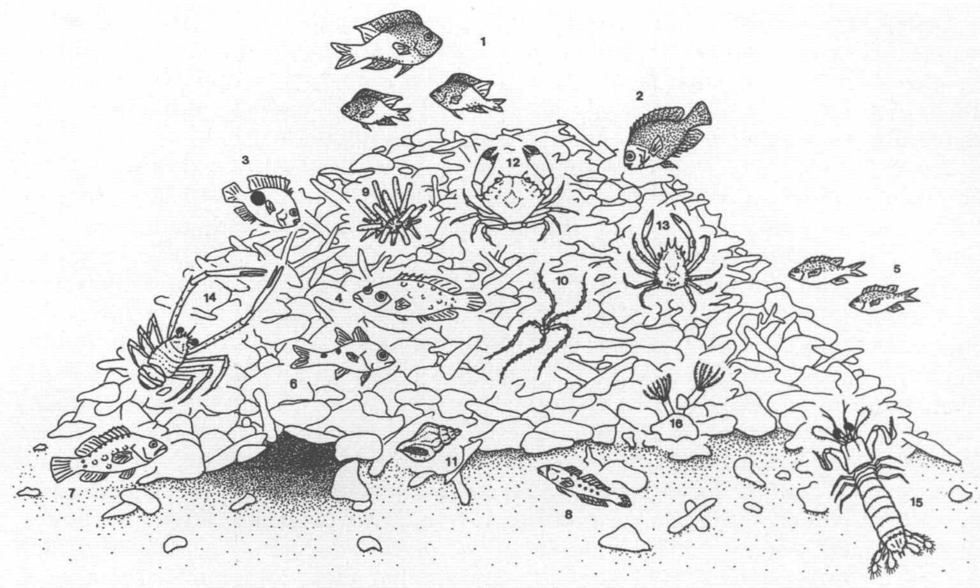

Figure 3. Schematic illustration of a *Malacanthus*-nest with some characteristic species of the associated fauna. 1. *Stegastes partitus,* 2. *Centropyge argi,* 3. *Holacanthus tricolor* juv., 4. *Pseudogramma gregoryi,* 5. *Chromis insolata* juv., 6. *Apogon* sp., 7. *Serranus baldwini,* 8. *Gnatholepis thompsoni,* 9. *Eucidaris tribuloides,* 10. Amphiuridae, 11. *Cantharus karinae,* 12. Xanthidae, 13. Majidae, 14. *Munida angulata* c.f., 15. *Odontodactylus brevirostris,* 16. Sabellidae.

star barnacle shells, had fewer species and lower abundances. The interstices-system was very narrow and provided only limited shelter for fishes.

A total of 66% of the associated fishes were carnivorous (Table 1). The rich cryptofauna in the mounds of *M. plumieri* is an attractive food source for predatory species. *Apogon* spp. and *Ps. gregoryi* were present in abundance, were cryptic and fed on the cryptic crustaceans. *Sy. synodus, Eq. lanceolatus,* and *Pa. acuminatus* occurred with only a few individuals, foraging at the periphery of the mounds. Sporadically relatively large individuals of *Scorpaena* sp.1 were found lying in ambush on the substrate waiting for prey. In addition there were herbivorous and detritivorous species (18%), which feed on algae and deposition material. *Ce. argi* and *H. tricolor* left the sheltering cavities for only short periods to pick food from the substrate. The planktivorous species (16%) used the cavities of the pebbles during their foraging in the water as a shelter site when attacked. *St. partitus, Ch. insolata,* and *Pa. furcifer* live in groups and remained above the mounds snapping for plankton. The substrate character of the *Malacanthus* mounds creates a variety of nutritional sources. Three main sources can be distinguished: a) Material stemming from outside the biotope, containing detritus

Table 2. Compilation of measurements of associated fish community structure

	Maximum	Minimum	Mean
s (number of species)	14	3	7
n (number of individuals)	117	5	44
H' (diversity)	2.11	0.72	1.45
J' (evenness)	98	46	76

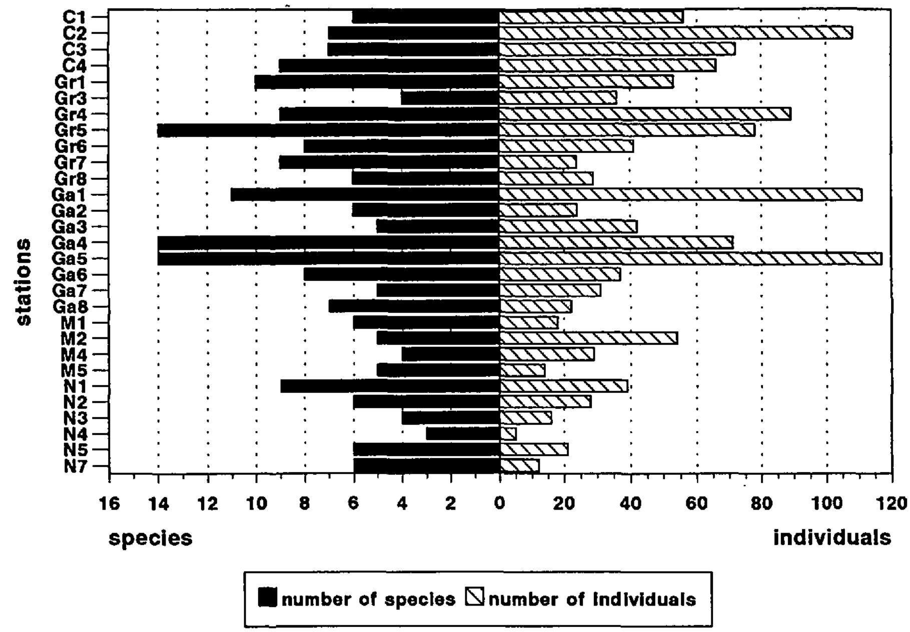

Figure 4. Number of species and individuals at different *Malacanthus*-mounds.

and plankton. It sinks down from the upper levels of the water and is carried with the current. Some of this material accumulates in the crevices and interstices of the hard substrate. b) The zoobenthos which provides a nutritional source for predators in the biotope. The relationship between predator and prey means that trophic biological dependencies exist between some species. c) Material which can be found directly on the substrate. It consists of overgrowing algae, sessile animals (sponges, bryozoans, balanids etc.) and deposition material (detritus) which is produced by the community of the tilefish mounds.

Dummy Experiments.—Dummy mounds were constructed to determine the interval of time in which the offered substrate is colonized by organisms. Different material was utilized to determine the influence of the structures on the colonizers.

PUNTA DE BETÍN (Pex1). The stone mound was piled up at a depth of 20 m and at a distance of 10 m off the reef. During six dives within 136 days, a total of nine fish species with 23 individuals were recorded. Figure 5 shows the number of species and individuals in relation to the time interval. A distinct maximum occurred at 38 days. Thereafter the number of species and individuals decreased continuously. The main function of the stone mound was seemingly to provide a center of attraction for fishes looking for shelter in the crevices within the monotonous sandy environment. Within a short time (15 days) several fishes had immigrated from the coral zone.

Due to the high sedimentation rate in Punta de Betín, the mound was soon covered with sand and thus in the course of time lost its attraction for fishes. The reduction of free space resulted in an emigration of species. However, decimation by predators could not be excluded.

NENGUANGE (Nex2). Here the rubble mound was constructed of dried sampling material and was smaller than the *Malacanthus* mounds in the surroundings. 14 days after construction a total of four fish species with six individuals was ob-

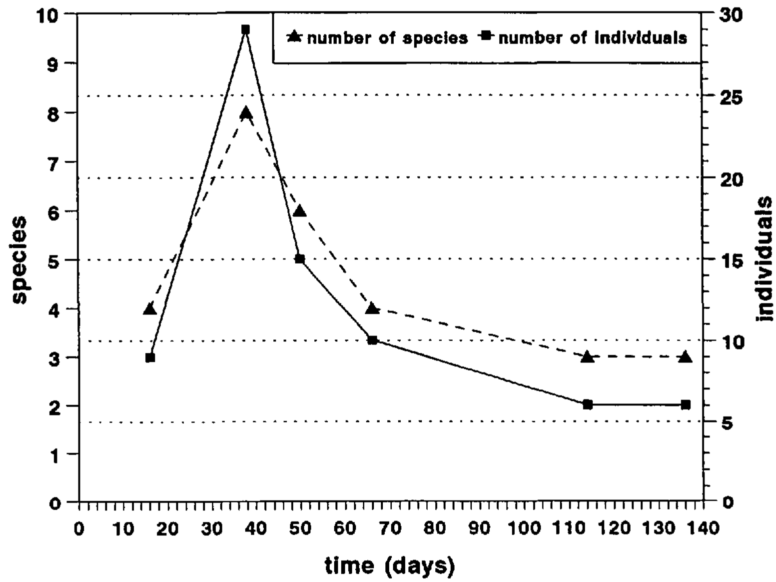

Figure 5. Number of species and individuals of fishes in relation to the observation interval at the dummy mound in Punta de Betin.

served: *St. partitus, Se. baldwini, A. quadrisquamatus,* and *G. thompsoni.* The second observation, carried out 47 days after construction showed only two individuals of *Se. baldwini.* By this time a high substrate loss had occurred; from the initial rubble mound only a few fragments remained in place. On one side the substrate was covered by sand and on the other side the pebbles had been "stolen" by *Malacanthus.* The observation of the surrounding tilefish mounds showed that some individuals made use of the artificially created rubble mound to maintain and extend their own nests. As they were bleached during drying, the stolen fragments could be identified by their pale colour. Several fragments were found in mounds at a distance up to 35 m.

These results demonstrate, that the colonization by fishes depend on the size of the mounds and subsequently on the available space, as well as on the substrate structure.

Discussion

Malacanthus plumieri and its Mounds.—Due to its nature as a builder of burrows, *M. plumieri* is not only of interest for the ethology and ichthyology, but also for geological studies. The fact that *M. plumieri* roofs its cave with a mound of rubble has paleobathymetric importance (Clifton and Hunter, 1972; Clifton, 1973). They discovered that the fish collects material at distances up to 12 m to rebuild a partly destroyed rubble mound. As a representative of the reef fauna, *M. plumieri* contributes significantly to the transport and distribution of sediments in the reef environment. The restricted experimental conditions must be taken into consideration when interpreting the distance of 12 m. Using dummy mounds the present study demonstrated that debris travelled up to a distance of 35 m. My assumption is that sand tilefish remove the fragments up to 35 m, although no explicit observation could be made to ascertain that an individual carried debris 35 m. Possibly *M. plumieri* steal from each others mounds, thus distribute the material. In the Santa Marta area the extension of *Malacanthus*-colonies requires that the fish moves longer distances as the sandy area is only sparsely covered with potential building material such as coral fragments and mollusc shells. Collecting material more than 10–30 m away from the mound and rebuilding it after disturbances, indicates that the sand tilefish expends much time and effort for the construction and maintenance of its rubble mound. According to Baird (1988) each individual lives in its own burrow, and the defence and maintenance of the burrow ensures refuge from predators at all times. Due to intraspecific aggressive behavior the members of a colony avoid conflicts among individuals in neighboring territories. Furthermore it is apparent that the rubble mounds serve as an orientation and marking point. However this function alone could also be accomplished by lower mounds. During this investigation, conspicuous size differences between the tilefish mounds were noted. Sometimes pairs of *M. plumieri* could be observed entering nests, and in these particular cases the rubble mounds were higher than usual. Possibly, the mounds had an additional function as social signals (attraction), for the purpose of reproduction. Further investigations are needed to determine this conclusively.

In the bays of the Tayrona National Park the distribution of the *Malacanthus* nests is restricted to a maximum distance of 40 m off the coral zone. As a consequence of the narrow continental shelf and the geomorphology of the bays, suitable substrate and building material is limited. The tilefish populations in the Santa Marta region do not attain the size in Glover's Reef (Belize) described by Baird and Baird (1992). It seems that the availability of building material and the conditions of the sand substratum are limiting factors for the colonization by *M. plumieri.* Clark et al. (1977) also assumed that sediment depth influences the dispersion pattern of the sand tilefish. Hard substrate, which has a stabilizing function, is necessary for the construction of the cave. As the rubble mounds in the study area are often constructed around a sponge of the species *Xestospongia muta,* it is feasible to postulate that *M. plumieri* utilizes the sponge as a visual orientation, signalizing suitable conditions for burrow construction. Furthermore it is also possible that the sponge reinforces the "roof," thus helping to prevent collapse of the burrow.

Opinions on material composition differ. Colin (1973) suggested that the sand tilefish prefers coral fragments of *A. cervicornis.* Clifton and Hunter (1972) assumed that the fish may selectively collect shells and irregular fragments in preference to *A. cervicornis* rods, to pile up its mounds. This study shows that the composition depends primarily on the availability of material in the environment. Indeed, *M. plumieri* selectively collects material, but can not be too specific, as it is dependent on the supply of material. These findings are probably applicable to other areas. The utilization of large or small fragments is determined by the body size of the individual and its ability to carry such fragments. The observed strata within the mounds—smaller fragments in the center, larger ones on the outside—could be explained by the continuous building activity of the fish as it grows.

The typical behavior of *M. plumieri* with its characteristic mounds, creates a habitat for benthic organisms on the sandy area in the fore reef. As rubble mounds are built on top of the cave, distinct biotopes are created in the monotonous sandflat. This substrate accumulation provides a habitat for numerous benthic organisms, which could otherwise not live in this zone. Observations and dummy experiments show that *M. plumieri* is important for the spatial structuring of the habitat. Continuous enlargement of the mound by bringing new material prevents a reduction of the available space due to sedimentation and other disturbing influences. This activity has a stabilizing function for the benthic community by creating and maintaining of the habitat.

Patterns of Community Structure.—The present study has shown that the tilefish mounds offer in terms of both time and space, a substantial base for the existence of a complex benthic community. A variety of features are of importance. The substrate accumulation on the plane sand bottom extends the habitat in the vertical relief. A characteristic structure is created, depending on the size and quality of the utilized material, which determines to a large extent the composition of species of the community (Mac Arthur et al., 1962; Büttner, pers. obs.). In this study particular attention has been given to the relationship between substrate character and dwellers. I found that the substrate structure influenced the composition of species. The characteristic interstices system of the rubble mounds determines the potential organisation of the community, whose capacity is limited by the available space, while the composition of species is determined by the size of the interstices. The mounds constructed by *M. plumieri* are conspicuous within the biotope and form a particular type of microhabitat. They become a place of concentration, and a center of activity for benthic organisms. The species inhabiting the tilefish mounds are characterized by their preference for coarse debris, and they may be found elsewhere in the biotope coral reef where this type of substrate exists. Nevertheless as a consequence of the combination of ecological factors (e.g., complex substrate structure, isolated location) it is highly possible that there is a characteristic composition of species associated with the tilefish nests. A recurring pattern of species composition and dominance structure at the different mounds was observed.

The following were the typical species found in the fish community associated with the sand tilefish nests in the Santa Marta region: *Apogon* spp., *Serranus baldwini, Centropyge argi, Stegastes partitus, Chromis insolata, Pseudogramma gregoryi* and *Gnatholepis thompsoni.* All these species were resident and were characterized by their "common" presence in the rubble mounds. In Jamaica, Colin (1973) found the following species associated with *Malacanthus* mounds: *Serranus tortugarum, Stegastes partitus, Apogon quadrisquamatus* and *Centropyge argi.* He concluded that the material was of significance: "None of these species is exclusively associated with such mounds, but the size of material selected by the sand tilefish for mound construction may be attractive to these species as the size indicated." All these species except *S. tortugarum* were also observed in Santa Marta. It is to be expected that the nests of *M. plumieri* also provide a suitable habitat in other areas for species preferring rubble-biotopes. In addition to dead coral fragments, Erhardt and Werding (1973) also designated the coral *Eusmilia fastigiata* Pallas as a preferred habitat for *Ce. argi* in Santa Marta. Rivera (1991) pointed out, that in the Santa Marta area *Ce. argi* is only found with high abundance in the tilefish mounds. My additional observations revealed that this species is very rarely present in the rubble of the reef. Presumably the interstices system of the rubble mounds provides an ideal habitat for specialized species like *Ce. argi. M. plumieri* maintains this interstices system due to its continuous building activity. Such a system could not exist without the influence of the fish because the sedimentation would rapidly destroy it.

In addition, some fish have a preferred place of domicile within the tilefish mounds. Hence two groups of associated fishes could be distinguished: planktivore species which forage in the water column and merely seek for shelter in the mounds (e.g., *St. partitus* and *Ch. insolata*) and benthic species which are closely associated with the substrate and generally stay in the interstices or whose habitat is exclusively cryptic (e.g., *Ps. gregoryi, Ce. argi* and *Apogon* spp.). A fine-scale spatial structure results as a consequence of preferred places of domicile.

Food supply is a further limiting factor to composition of species and individual density of the community. The mounds constructed by *M. plumieri* provide a feeding site and a source of nutrition for the associated species. Three main sources can be distinguished: 1. material which comes from outside the biotope; 2. the zoobenthos itself; and 3. material which can be found directly on the hard substrate. The variety of food resources enables many species to coexist. Trophic dependencies exist between some organisms of the associated fauna, for example predator-prey relationships. Thus the sensitivity of species towards the presence of other species, is also a component in the structuring of the community.

Several fishes occur exclusively as juveniles and the mound serves as a nursery habitat. The body size of several species limits the shelter function of the rubble mounds to their juvenile stage. For other species food supply and territory size are important factors. *Malacanthus* nests enable some species to pass their first post larval phase sheltered from predators. Without this habitat, a higher loss to predators in the adjacent reef is to be expected, which would result in another population structure. Thus, the tilefish mounds may be important for the dynamics and structure of the fish- and invertebrate fauna of the adjacent reef.

The examinations in Santa Marta clearly demonstrate that *M. plumieri* has an important function within the coral reef ecosystem. I predict similar results for other mound-building malacanthids. Clark and Ben-Tuvia (1973) found that in the Red Sea, *M. hoedtii* Bleeker pile up rubble mounds on the top of their caves in a similar way to *M. plumieri.* Congeners in the Pacific, the Indian Ocean and in the Red Sea probably have a corresponding function for the diversification within the reef environment.

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ADDRESS: *ZMT (Zentrum Für Marine Tropenökologie), Klagenfurter Strasse GEO, D-28359 Bremen, Germany.*