

Patterns of Oil-Sediment Rejection in Corals

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Abstract

The patterns of oil-sediment rejection of 19 Caribbean hermatypic corals are identical to their patterns of rejection of clean sediments. The rejection pattern is typical for coral species, and displays maximum and minimum rates dependent on the size and density of the oil-sediment particles. The viscosity of the oil determines the size of the oil-sediment particles. A coral's efficiency of rejection of sediment depends on the size and amount of the sediment particles. Oil drops ≥ 0.06 mm are removed by the coral's tissues. Physical contact with oil-sediment particles appears to be less harmful to corals than the toxic effects of oils.

Introduction

Because of the increasing interest in oil exploitation and the expansion and development of oil terminals in the vicinity of coral reefs, more information is needed on the effect of oil pollution on coral reefs. The subject has been studied by, for example, Connell (1970), Spooner (1970), Straughan (1970), Johannes (1972), Johannes *et al.* (1972), Fishelson (1973a, b), Eisler *et al.* (1974) and Loya (1975). These workers expressed their apprehension concerning the harmful effects of oil spills. Rützler and Sterrer (1970), Spooner (1970), and Shinn (1972) reported on the survival of coral reefs subjected to oil spills.

Waves and currents can bring oil and bottom sediments into contact. Gilmore *et al.* (1970) summarized that most of 36 major oil spills by tankers during 1956 - 1969 occurred within half a mile of the shore, during high winds (40% above gale-force) and heavy seas (40% of the waves over 3 m in height). Such conditions can result in the settling of oil-saturated material. Weathered crude oil, as tar balls, or sediment-bound oil are the primary types of oil pollution in coastal waters. Oil sludge accumulation can be expected around harbours, oil terminals and off-shore works (Gilmore *et al.*, 1970).

So far no attention has been paid to the effect of oil-sediment particles on

the living surfaces of coral colonies. We have attempted to determine the possible effect of oil-polluted sediment on coral colonies, using experiments with clean sediment as controls.

Although the influence of sediment on corals and coral distribution has attracted much attention, relatively few workers seem to have done experimental work on the sediment rejection capacity of corals. Within certain limits, hermatypic corals rid themselves of sediment by mucus secretion and ciliary action (Edmondson, 1928; Yonge, 1930, 1935; Marshall and Orr, 1931; Lewis, 1973). Yonge (1930, 1935) and Lewis and Price (1975) studied the patterns of ciliary currents. Large polyps are reported to be more effective in the rejection of accumulated sediments (Mayor, 1918). Some corals, such as the genus *Porites*, are more specialized in silt-removal (Manton and Stephenson, 1935). Only recently has the subject received appropriate attention - in the most quantitative studies so far and by means of a valuable new approach (Hubbard and Pocock, 1972; Hubbard, 1973). These authors quantified the cleaning capacity of corals subjected to several types of sediment and related the efficiency of the overall process to morphology and behaviour of the colonies. However, we were unable to use the factual data of their reports. Our preliminary tests on the sediment rejection of various species showed a very

Table 1. Rejection of oil-sand combinations by some hermatypic corals within 24 h (+) and not within 24 h (o). 1: 0.75 g sand + 1 cm³ oil; 2: 2 g sand + 2 cm³ oil; 3: 4 g sand + 3 cm³ oil

Coral species	Description ^a	Nco. ^c			Fco.			TJPco			Flr.			Lsr.		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1 <i>Stephanocoenia michelinii</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2 <i>Madracis decactis</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3 <i>Madracis mirabilis</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4 <i>Acropora palmata</i>	hor.-exp.	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
5 <i>Acropora palmata</i>	45°-exp. ^b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
6 <i>Acropora palmata</i>	vert.-exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7 <i>Acropora cervicornis</i>	exp.	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
8 <i>Agaricia agaricites</i>	hor.-exp.	+	o	o	+	o	o	+	o	o	+	+	o	+	+	o
9 <i>Agaricia agaricites</i>	45°-exp. ^b	+	+	o	+	+	o	+	+	+	+	+	+	+	+	+
10 <i>Agaricia agaricites</i>	vert.-exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11 <i>Siderastrea siderea</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12 <i>Porites astreoides</i>	45°-exp. ^b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
13 <i>Porites porites</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
14 <i>Diploria strigosa</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15 <i>Diploria strigosa</i>	not exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16 <i>Manicina areolata</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
17 <i>Manicina areolata</i>	not exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
18 <i>Colpophyllia natans</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
19 <i>Colpophyllia natans</i>	not exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
20 <i>Montastrea annularis</i>	hemisph.-exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
21 <i>Montastrea annularis</i>	flat-exp.	+	o	o	+	o	o	+	+	+	+	+	+	+	+	+
22 <i>Montastrea cavernosa</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
23 <i>Montastrea cavernosa</i>	not exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
24 <i>Meandrina meandrites</i>	hemisph.-exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
25 <i>Meandrina meandrites</i>	hemisph.-not-exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
26 <i>Meandrina meandrites</i>	flat exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
27 <i>Meandrina meandrites</i>	flat-not exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
28 <i>Dichocoenia stokesii</i>	exp.	+	+	o	+	+	o	+	+	+	+	+	+	+	+	+
29 <i>Dichocoenia stokesii</i>	not exp.	+	+	o	+	+	o	+	+	+	+	+	+	+	+	+
30 <i>Dendrogyra cylindrus</i>	45°-exp. ^b	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
31 <i>Mycetophyllia aliciae</i>	exp.	+	+	o	+	+	o	+	+	+	+	+	+	+	+	+
32 <i>Mycetophyllia aliciae</i>	not exp.	+	+	o	+	+	o	+	+	+	+	+	+	+	+	+
33 <i>Eusmilia fastigiata</i>	exp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

^aexp.: expanded; hor.: horizontal; vert.: vertical; hemisph.: hemispherical.

^bAngle of coral surface.

^cFor full description of oils see Table 2.

different pattern, e.g. *Meandrina meandrites*, a coral unable to remove any sediment in the experiments of Hubbard and Pocock, turned out to be a most effective sediment-rejector in our experiments. It is possible that stress or damage, to which corals are very sensitive (e.g. Kanwisher and Wainwright, 1967), influenced the actual results of Hubbard and Pocock.

We were compelled, because of lack of data in the literature, to determine the rejection pattern of oil-sediment particles by corals by comparison with their rejection patterns of clean sediments.

Materials and Methods

For the experiments we selected 19 hermatypic coral species (Table 1) displaying large variation in morphology, structure, and behaviour. All the species are common on the fringing reefs of the southwest coast of Curaçao. After collection, the corals were kept submerged in seawater and brought to the laboratory immediately. Previous experiments showed that corals can be kept healthy in the Caribbean Marine Biological Institute's running seawater system for many months.

The possibilities of adsorption of crude oil to the coral ectoderm and the

Table 2. Physical characteristics and abbreviations of oils employed in this study

Oil	Kinematic viscosity (cSt) 38°C	Specific gravity (15.6°/15.6°)
Nigerian crude oil (Nco)	5,7	0,871
Forcados crude oil (Fco)	7,2	0,871
Tia Juana Pesado crude oil (TJPco)	4066,0	0,985
Forcados long residue (Flr)	4000-5000	0,940
Lagomar short residue (Lsr)	15.000,0	1,014

reactions of corals to small oil drops introduced in the gastrovascular cavity were examined. We used small drops of Nigerian crude oil of approximately 0.06 mm diameter, and hollow needles directed by micromanipulators. Because these experiments had to be performed in stagnant water, *Acropora palmata*, *A. cervicornis*, *Porites astreoides* and *P. porites*, copious mucus secreters under such conditions, had to be excluded from these tests.

We used three types of sediment in the sediment-shedding experiments: sand, sand-oil combinations and carborundum powder. The sand was collected at the reef and had a mean diameter of 1200 μ (range 100 to 3000 μ). This sand was used to prepare the oil-sediment particles in combination with the following oils: Nigerian crude oil (Nco), Forcados crude oil (Fco), Tia Juana Pesado crude oil (TJPco), Forcados long residue (Flr) and Lagomar short residue (Lsr) (Table 2). The viscosity of these oils increases in this sequence at the temperature of the experiments (26° to 28°C). The resulting oil-sediment particles immediately sank in seawater.

The oil particles vary in size and consistency depending on the viscosity of the oil. In the experiments the following particles were formed: (1) sand grains coated with oil and small clods up to 0.5 cm in diameter (Nco and Fco); (2) a more viscous mass that can disintegrate (TJPco and Flr); (3) a solid oil-sand combination of high viscosity (Lsr).

Ciliary currents were traced with carborundum powder. This powder was also used to test the silt rejection capacity of the coral species. Actual silt clouds the water to such a degree that the corals become invisible. We studied contrast-stained sections of *Madracis mira-*

bilis to determine the position and densities of cilia.

The various sediments were brought upon the surface of the corals through a vertical tube (3 cm diameter) held close to the coral surface so that the sediment rain evenly covered a 3 cm-diameter circle on the colonies. We used the following quantities of sediment: (1) sand - 0.75 g, 1.5 g, 3 g; (2) sand-oil combination - 0.75 g + 1 cm³, 2 g + 2 cm³, 4 g + 3 cm³; (3) carborundum powder - 0.75 g. The rejection efficiency or capacity was defined as the time necessary to clean the colony surface of sediment. This time, as well as the shedding behaviour, was recorded. Time was rounded to the nearest hour. Preliminary experiments showed the rejection behaviour to be very consistent, nevertheless, each experiment was performed twice on two different colonies of the same habitus and habitat. Thus, the data obtained are the means of 4 observations. Because the morphology of the living coral surface varies greatly depending on the degree of expansion of the polyps, and because this phenomenon is often synchronized with the day-night rhythm, experiments were performed by day as well as by night.

Results

We could find no evidence of adsorption of oil to living coral tissue. There was no active ingestion of oil drops by the corals. If drops were introduced into the gastrovascular cavity they were invariably extruded through the stomodaeum. Colonies with a common gastrovascular cavity also extruded oil drops through surrounding stomodaea. Addition of zooplankton (*Mysis* sp., *Artemia* sp.) to the seawater did not change this pattern. Oil drops became frequently trapped in tentacular cavities, to be subsequently expelled through the stomodaeum. When oil drops arrived on the peristome they were removed by ciliary currents and by tentacular and polypal movements. This resulted in the oil drops ascending to the water surface. When a species was a relatively active mucus secreter (Table 3), oil drops could be trapped in mucus for up to 5 h under the experimental conditions. Apart from these physical phenomena, of course, chemical activity of the oil may damage corals (e.g. Reimer, 1975; Elgershuizen and de Kruijf, 1976).

We found rejection efficiency to be correlated with the size (Fig. 1) and density of the particles (Fig. 2). The rejection of sand and oil-sand particles shows a similar pattern (Figs. 2, 3).

Table 3. Data on morphology and behaviour relevant to sediment rejection of various coral species. +++: Very marked; ++: obvious; +: present; -: insignificant; s: small (<4 mm); m: medium (4-8 mm); l: large (>8 mm); fe: most colonies fully expanded; pe: most partially expanded; fpe: 10% or fewer partially expanded; cc: colonies contracted (after Porter, 1974); tc: total colony reacts; pc: part of colony reacts; iac: increasing response until certain fixed area of colony reacts (after Horridge, 1957)

Characteristic	Species and code nos.							
	<i>Stephanocoenia michelinii</i> (1)	<i>Madracis decactis</i> (2)	<i>Madracis mirabilis</i> (3)	<i>Acropora palmata</i> (4,5,6)	<i>Acropora cervicornis</i> (7)	<i>Agaricia agaricites</i> (8,9,10)	<i>Siderastrea siderea</i> (11)	<i>Porites astreoides</i> (12)
Colony form	massive	clavate	ramose	palmate	ramose	plating	massive	plating
Surface form	cerioid	cerioid	cerioid	plocoid	plocoid	meandroid/reticulate	cerioid	cerioid
Elevation of surface coenosarc	+					+	+	
Polypal column raising above coenosarc		+	+					+
Expanded tentacles raising above coenosarc	+	+	+	+	+	+	+	+
Tentacle length (mm)	2-3	2-4	2-6	1-3	1-3	1-3	1-2	1-2
Maximal length sweeper tentacles (mm)	6		8			12		
Bi/trifurcate tentacles							+	
Polyp diameter	s	s	s	s	s	s	s	s
Diurnal activity	fe	pe	fe	fe	fe	fpe	fpe	pe
Nocturnal activity	fe	fe	fe	fe	fe	fe	fe	fe
Reaction on sequential mechanical stimuli	pc	iac	iac	iac	iac	pc	pc	tc
Ciliary currents	++	++	++	+	+	++	++	+
Mucus secretion trapping sand as globules				+	+	+		
Mucus secretion trapping sand as threads	+			+	+		+	+
Mucus secretion trapping sand in film				+	+			+
Mucus secretion trapping carborundum	+	-	-	+++	+++	++	+	+

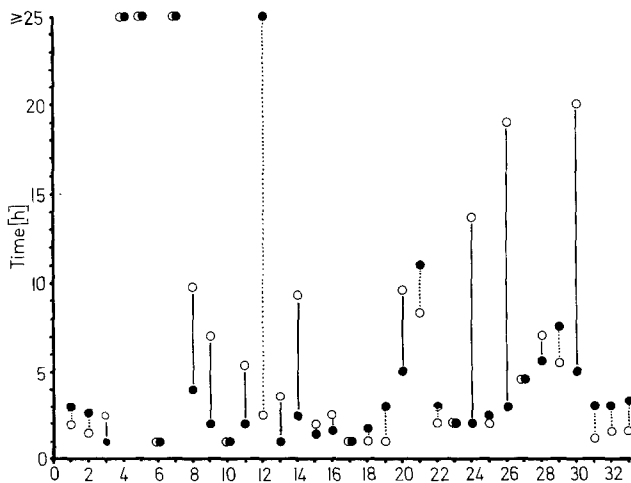


Fig. 1. Rejection times of equal quantities of sand and carborundum powder by various coral species (For explanation of species code numbers see Table 1). Filled circles: 0.75 g sand; open circles: 0.75 g carborundum powder. Dashed lines indicate a better efficiency for carborundum, continuous lines indicate better efficiency for sand

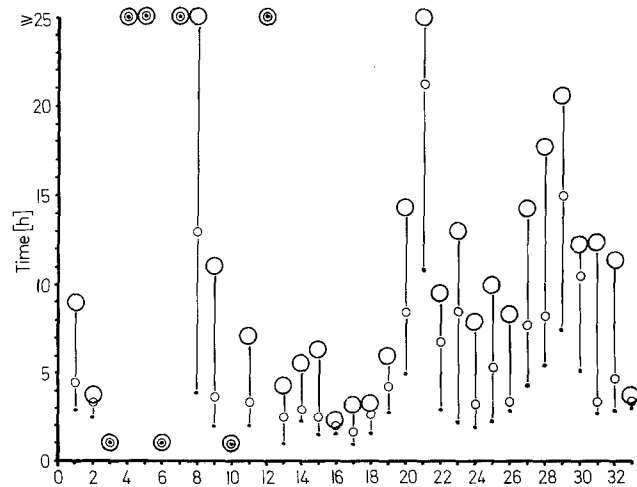


Fig. 2. Rejection times of different amounts of sand by various coral species (code numbers as in Table 1). Dots: 0.75 g sand; small open circles: 1.5 g sand; large open circles: 3.0 g sand

<i>Porites porites</i> (13)	<i>Diploria strigosa</i> (14,15)	<i>Manicina areolata</i> (16,17)	<i>Colpophyllia natans</i> (18,19)	<i>Montastrea annularis</i> (20,21)	<i>Montastrea cavernosa</i> (22,23)	<i>Meandrina meandrites</i> (24,25,26,27)	<i>Dichocoenia stokesii</i> (28,29)	<i>Dendrogyra cylindrus</i> (30)	<i>Mycetophyllia aliciae</i> (31,32)	<i>Eusmilia fastigiata</i> (33)
ramose cerioid	massive meandroid	plating meandroid	plating meandroid	plating/massive plocoid	massive plocoid	massive/plating meandroid	massive plocoid	columnar meandroid	plating meandroid	ramose phaceloid
+	+	+	+	+	+	+	+	+	+	+
2-4	2-6	2-7	5-10	1-3	15-30 80	5-15	2-6 8	6-15	2-6	10-20
s	m	m-1	m-1	s-m	1	1	m-1	m	+	+
fe	fpe	cc	cc	fpe	fpe	cc	cc	fe	l	l
fe	fe	fe	fe	fe	fe	fe	fe	fe	cc	pe
iac	pc	pc	pc	pc	pc	pc	pc	pc	pc	pc
+	++	+++	+++	++	++	++	++	++	++	++
	+	+		+			+		+	
+	++	-	-	-	+	-	+	+	++	-

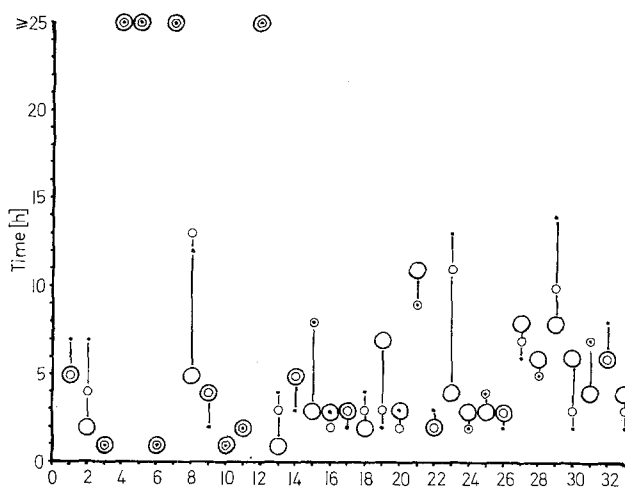


Fig. 3. Rejection times of different sand-oil combinations by various coral species (code numbers as in Table 1). Data on Nigerian crude oil and Forcados crude oil as well as Tia Juana Pesa-do crude oil and Forcados long residue have been combined, since their very similar kinematic viscosity at 26° to 28°C results in particles of the same type, that are rejected over the same time period. Dots: 0.75 g sand + 1 cm³ Nco or Fco; small open circles: 0.75 g sand + 1 cm³ TUPco or Flr; large open circles: 0.75 g sand + 1 cm³ Lsr. (For description of oils see Table 2)

Different rejection strategies are used for particles of different sizes. Our study on the reaction of coral colonies to either sand, oil-sediment particles or carborundum powder shows the reaction to be intimately linked to the specific morphology of the coral colonies. Relevant data are shown in Table 3. Because the morphology of the colonies is important at least at three levels (colony as a whole, colony surface, and calical morphology), the impact of sediment on corals depends on a diverse set of morphological factors. On the first level, the effect of colony shape on sediment rejection is illustrated by the difference in rejection efficiency of *Agaricia agaricites* colonies in different positions (Fig. 2: 8,9,10). Experiments on *Montastrea annularis* (Fig. 2: 20,21) and *Meandrina meandrites* (Fig. 2: 25,27) show the difference between hemispheric and horizontally plating colonies. On the next level, colony surfaces, these can be cerioid, plocoid or meandroid. This is of importance in sediment removal (see Hubbard, 1973), e.g. long meandroid valleys (Fig. 2: 14-19) are more advantageous than short reticulate valleys (Fig. 2: 8,9). On the last level, calical morphology, this affects the mobility of polyps.

The same three levels mentioned above can also be distinguished in the active

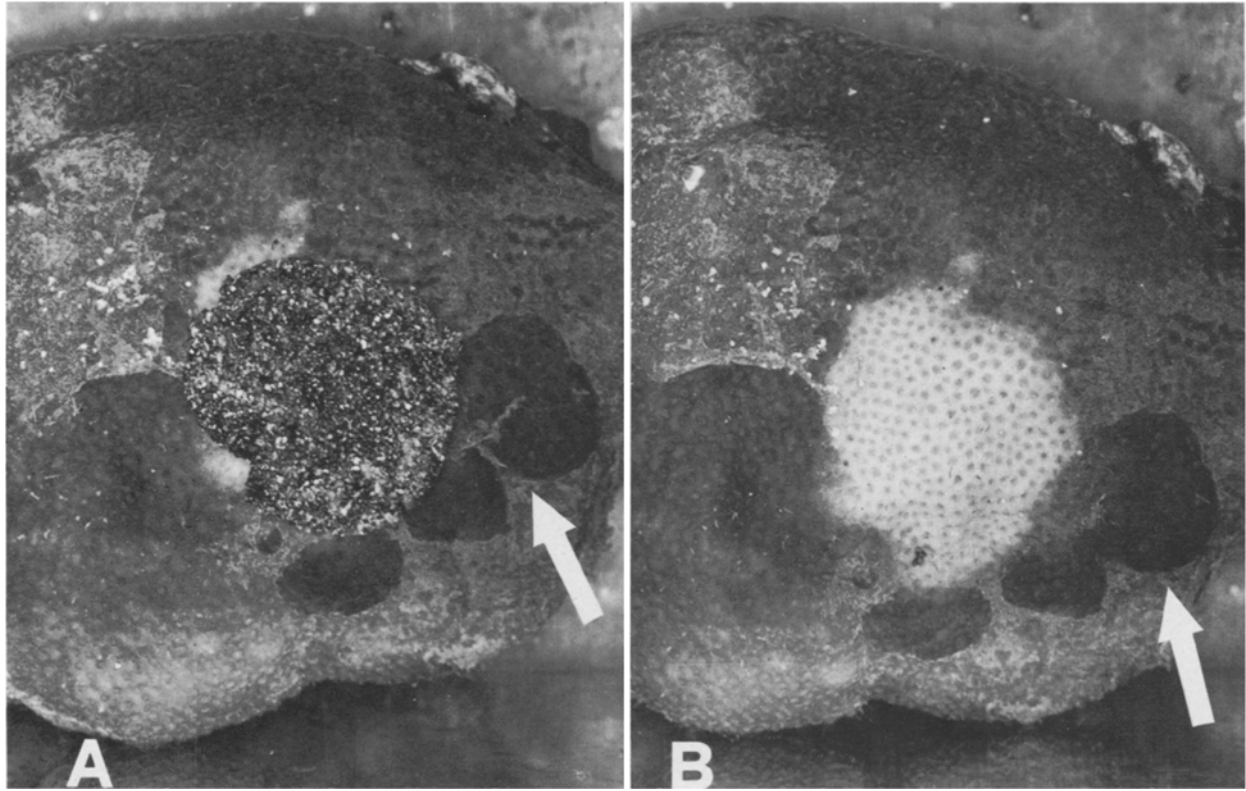


Fig. 4. *Porites astreoides*. Failure to reject oil-sand combinations. (A) Combination of 0.75 g sand + 1 cm³ Forcados long residue remains 48 h on surface of the coral. (B) This has resulted in death of the underlying living tissue. Note in (A) and (B) that the whole living tissue is covered by mucus sheets except for a small area (arrowed)

behaviour of the living tissue. In the active reaction of corals, the degree of cooperation between various parts of the colony is very important. The immediate contraction of the polyps upon contact with sediment particles enhances the instability of the sediment. Subsequent expansion of the polyps removes many particles. This behaviour is, for example, displayed by the long and mobile polyps of *Madracis mirabilis*. In this branched coral, a combination of advantageous features on the different levels results in immediate rejection of all particles larger than carborundum powder (No. 3 in Figs. 1,2,3); carborundum powder is removed by ciliary currents. In *M. mirabilis*, cilia are present in greatest numbers on the stomodaeum, the tentacles and the column wall. Tracing currents with carborundum showed the only inwardly directed current to be on the stomodaeum. On the column wall the currents move upwards, and on the tentacles towards the tips. Consequently, by bending of the tentacles the carborundum is directed towards the stomodaeum. The different effects of expansion of the tissues and polypal movements that are important in the re-

moval of larger particles (ranging from sand to sand-Lagomar short-residue combinations, 3 cm in diameter) and of the ciliary currents that remove carborundum powder are clearly visible in *Diploria strigosa* and *Meandrina meandrites*. When the tentacles of these species are expanded, the directions of the ciliary currents are obstructed and the rejection of carborundum powder is delayed (Fig. 1: 14, 15,24,25).

Mucus is also an important component of the sediment-rejection mechanism. In *Porites astreoides*, the copious secretion of mucus that is not constantly removed from the colony surface and the small size of expanding polyps are prominent features. Mucus sheets, that can cover colonies of this species, may be induced on contact with sediment and are responsible for the trapping of sediment. This form of mucus secretion is very common *in situ* as well as in the laboratory. In the absence of these sheets, which are removed by water movement, small amounts of only very fine sediment can be rejected (Fig. 1: 12). Oil-sand particles that remain on the colony surface longer than two days cause the death of the

underlying coral tissue (Figs. 3: 12, and Fig. 4).

Agaricia agaricites is an example of a species depending on strong ciliary currents for sediment rejection. Probably the rapidly retractable tentacles are only important in feeding. The strong ciliary currents can, combined with a raising of the coenosarc, remove even fairly large oil-sand particles. In this species small particles, such as carborundum powder, are trapped in mucus. These particles can be retained longer at less ciliary active parts of the tissue, resulting in death of small edges of valleys.

Table 1 shows the capacities of oil-particle rejection of the various corals within 24 h for 0.75 g sand + 1 cm³, 2.0 g sand + 2 cm³, 4 g sand + 3 cm³ of the tested oils. In all the coral species, the capacity to remove particles from the surface of the colony depends on size and density of the particles. This means that in the case of oil-sediment particles, removal depends on the viscosity of the oil. The possible effect of this phenomenon is demonstrated in Table 1 by the inability to reject some oils by *Agaricia agaricites* (8), *Montastrea annularis* (21), *Dichocoenia stokesii* (28,29) and *Mycetophyllia aliciae* (31,32). Low-viscous oil-sand particles were lethal to these 4 species, especially in large amounts. *Acropora palmata* (4,5), *A. cervicornis* (7) and *Porites astreoides* (12) are, without help of wave action or currents, unable to remove particles of any size.

We did not find any specific reaction of the corals to oil-sand particles. The rejection mechanisms used in oil-sand particle removal are the same, and apparently function in the same manner, as those used in the rejection of clean sediments.

Discussion

The effect of the morphology of corals on the stability of coral-covering sediment was studied by Hubbard and Pocock (1972) and Hubbard (1973). We found the behaviour of the living polyps to be so influential in rejection processes, that the increase in rejection efficiency suggested by Hubbard (1973) in a series from cerioid, plocoid to meandroid surfaces is decisively deranged. In our experiments there also appeared to be no linear relation between rejection capacity and diameter of the calices or number of calices per surface unit.

A sediment rain on an expanded coral surface results in contraction of the

polyps. This is not the case with very fine sediment, e.g. carborundum powder. Contraction phenomena as responses to food particles have been described by, for example, Bullock and Horridge (1965) and Porter (1974). Contraction as a reaction to stress was described by Horridge (1957). In the present study, we observed that contraction as a reaction to contact with non-food particles occurs with the stomodaeum closed. This results in a pattern of ciliary currents from the mouth towards the periphery of the peristome. Reversible currents, that were related with reversible movement of cilia, were found by Yonge (1930), Abe (1938) and Sorokin (1973); we did not find such reversible currents. The present observations on *Madracis mirabilis* revealed that a displacement of the outer edge of the stomodaeum can suggest reversible currents. When this outer edge of the stomodaeum, i.e., the only area covered with cilia producing an inward current, moves into the polyp during food ingestion, the edge of the mouth is covered with more peripheral tissue. This tissue indeed exhibits ciliary currents towards the periphery of the peristome. Tentacle activities are amply discussed by Lewis and Price (1975). Stress can result in extrusion of mesenterial filaments (Goreau *et al.*, 1971; Lang, 1971, 1973). In our experiments we only saw this happen as a reaction to the introduction of oil drops in the gastrovascular cavity.

After contraction, the corals react with expansion of the tissues. The surface is cleaned by ciliary currents and movements of the tentacles, the polypal column and the coenosarc. Mucus can promote the rejection of sediments (Yonge, 1930; Lewis, 1973) if the mucus sediment fraction is transported over the coral surface by currents. We found that generally mucus secretion causes a delay in the cleaning of coral surfaces. Especially small particles (carborundum powder) become trapped in mucus, which can result in prolonged presence of the sediment on colonies. In this study, lethal effects of mucus-trapped sediment occurred in *Porites astreoides* and *Agaricia agaricites*. Mucus can enter food chains by feeding of zooplankton and fish (Johannes, 1967; Coles and Strathmann, 1973). It is possible that minute oil particles are thus ingested. Blumer (1972) suggested the possibility of uptake of persistent oil components in the lipid pool of the sea. Adsorption and phagocytosis of such particles has been studied in Protozoa (Andrews and Floodgate, 1974). The coral species we tested refused to ingest very small oil parti-

cles. It is important to note that oil or oil-sand particles never induced an obvious increase in mucus secretion compared with the secretion resulting from clean sediment.

The relation between rejection efficiency and density of sediment particles has many varieties of the following patterns: Rejection can be immediate, it can take a certain time, or it may not occur. Also rejection can, with increasing amount of sediment or with increasing size (related to oil viscosity) of the particles, become either more rapid, more delayed, or be linearly related; this can result in either a shortening or prolonging of the time needed for complete rejection. Generally, the natural rejection patterns are combinations of the above-mentioned possibilities. Such a combined pattern can display maximum and minimum efficiencies. An example is *Montastrea cavernosa* (No. 22 in Figs. 1 and 3). This coral removes large oil-sand particles (3 cm diameter) easily by movements of the tentacles and polyp expansion. Small oil-sand particles (e.g. 1 mm diameter) fall between the polyps and must be rejected by ciliary movements. However, still smaller particles (0.1 mm diameter) are transported much more easily by the cilia. Thus, maximum efficiencies occur where a part of the complex rejection mechanism has a maximum impact on particles of a certain size. When the components of a rejection mechanism have relatively little impact on particles of a certain size, this results in minimum rejection efficiency. It should be noted that in some species the patterns by day and night (which depend on the varying expansion of the living tissue) can be very different (e.g. *Diploria strigosa* Fig. 3: 14,15).

The success of the sediment rejection mechanism in corals greatly depends on their habitat. Amount and size of particles, as well as water movement, are important variables *in situ*. But while the consequence of strong water-movement for an ineffective sediment remover such as *Acropora palmata* in its high-energy habitat is clear, the alternative approach, to relate sediment rejection mechanisms to coral distribution on reefs, appears much more difficult. In lagoons and inner bays, sediment can apparently limit the distribution of coral species (Roy and Smith, 1971; Bak, 1975). On the open reef, too many factors operate together, and apart from certain areas where sediment rain and shifting sand are decisive environmental factors, sedimentation cannot be related directly to coral distribution (Ott, 1975). However, the effect of sediment on coral distri-

bution is very decisive during and in the first months after coral settlement (Bak and Engel, in preparation), at least at the microhabitat level.

Conclusions

In 19 hermatypic coral species the efficiency of removal of oil-sediment particles was the same and performed by means of the same rejection mechanisms, as when they were covered with clean particles of the same size and/or quantity. The size of particles and the amount of sediment can limit the efficiency of rejection mechanisms. *In situ* water movement, however, can counteract such limits imposed on sediment rejection of coral species.

Patterns and efficiency of sediment rejection are specific to the various coral species. Generally, the relationship between efficiency of rejection and size and amount of particles displayed maximum and minimum rates.

Oil drops of ≥ 0.06 mm in diameter do not adhere to living coral surfaces and are not ingested. Probably the water-soluble toxic fraction of oils in seawater is more harmful to corals *in situ* than physical contact with oil-sediment particles.

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