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Function of funnel-shaped coral growth in a high-sedimentation environment

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ABSTRACT: Advantages and disadvantages of a funnel-shaped growth in 2 coral species (*Acropora clathrata, Turbinaria peltata*) in a high-sedimentation environment (Natal, South Africa) were observed in the field and modeled in a flow tank. Funnel-shaped growth serves different purposes in different hydrographic settings. In calm waters with little currents (in our case deep reef areas, 18 to 25 m) funnel-shaped colonies served as 'sacrificial sediment traps': all sediment trapped inside the funnel was directed towards the centre, where it was concentrated. There, tissues underwent necroses, but all other tissues remained sediment free and healthy. In areas with high currents (in our case shallower reef areas with high surge, 8 to 14 m) funnels tended to be self-cleaning. By a process of vortex shedding, mass replacement of fluid within the funnel also led to the removal of all sediment. Current speeds between 30 and 90 cm s^{-1} were enough to clean the funnels of 3 experimental grain sizes (coarse, fine, medium sand).

KEY WORDS: Coral · Sediment · Shape · Ecology · South Africa

INTRODUCTION

Coral shape generally reflects environmental conditions, high morphological plasticity allowing corals to adapt to local conditions (Hubbard & Pocock 1972, Jackson 1979, Nakamori 1988). Certain growth-form types are frequently associated with particular environments: for example, thinly branching species generally occur in areas of low wave energy, colonies under low light conditions are frequently sprawling or table-like, and many corals in turbid areas develop humps rather than flat growth forms.

In the Indo-Pacific, many lagoonal areas are dominated by funnel-shaped corals, which at times receive higher sediment pulses than more exposed areas. Off the east coast of South Africa, an area with high sedimentation rates, the funnel-shaped corals *Acropora clathrata* and *Turbinaria peltata* dominate wide areas in shallow and deep water (Riegl et al. 1995). This is at first sight counter-intuitive, as one would expect a funnel-shaped growth-form to be poorly adapted to an environment with high sedimentation. Although a funnel exposes a high surface area to solar radiation, it is likely to accumulate sediment. This potentially has adverse effects on colony health as coverage of coral tissue by sediment leads to bleaching and necroses (Riegl 1995, Riegl & Bloomer 1995).

We proposed 2 explanations for this apparent paradox. Our first hypothesis was that the funnel could serve primarily as a light- and food-gathering apparatus but also acts as a 'sacrificial sediment trap'. This means that it trades the advantages of high light-gathering power and better access to suspended resources (Jackson 1979) for the disadvantage of high sediment accumulation. However, the funnel may concentrate all settling sediment at its centre. If sediment slides off the tissues on the oblique wall, they will be kept clean for photosynthesis and prey-capture, while the tissue in the centre is sacrificed.

Our second, and alternative, hypothesis was that the growth-form itself helps to reduce the deposition of sediment by inducing vortices and leads to self-

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cleaning. In high surge, which is manifested at the seafloor as oscillating currents parallel to the substrate, the shape of the funnel may create vortices and turbulences, which could aid in emptying the funnel of sediment. Then funnel shape would have only advantages: high light- and food-gathering powers and a self-cleaning design.

We tested both hypotheses by field observations and experiments with models in a flow tank. The experimental approach in the laboratory simulated environmental conditions recorded on South African coral reefs and used the most common South African funnel-shaped corals *Acropora clathrata* and *Turbinaria peltata*.

MATERIAL AND METHODS

The study area was situated in the Maputaland reef system in northern Natal, South Africa (Fig. 1). The geomorphology of these reefs differs from that found on typical coral reefs (Ramsey & Mason 1991, Riegl et al. 1995). Reefs in the study area generally do not reach the surface (lying in minimum depths of 6–8 m) and therefore lack a typical reef crest, do not enclose a lagoon, and have no pronounced reef slope (mostly sloping at less than 10°). Major topographical features are gullies and associated drop-offs of up to 5 m, dissecting the reefs at irregular intervals and with an irregular orientation.

Two types of reef occur: deep, flat outcrops between 18 and 24 m depth (4-Mile Reef, Kosi Mouth Reef) and typical fossil dunes or shallow sand stone outcrops, from 8 to about 34 m depth (2-Mile Reef, 9-Mile Reef, Red Sands Reef). These outcrops can be divided into high lying, largely sediment-free areas and gullies with resident sediment and high resuspension and resettlement rates in surge conditions.

The area is characterized by high swells, predominantly from the south (Schumann 1988). Water velocities created by surge in 20 m depth ranged from 0.07 m s^{-1} in calm to over 1 m s^{-1} in medium swell conditions (authors' unpubl. data).

The most common funnel-shaped coral was *Acropora clathrata*, which dominated gully edges between 8 and 18 m, and elevated, flat parts of the reef between 18 and 25 m. *Turbinaria peltata* also occurred in the same habitat, though not as frequently (Riegl et al. 1995).

The following colony morphometrics were measured: maximum colony (= funnel) diameter, angle of opening, height of funnel edge above the substratum, thickness of the stem (Fig 2). Additionally, the presence of necrotic areas of tissue in the centre of the funnels (termed 'dead centres') was noted. Thirty specimens of each species were measured and 100 colonies were used to determine the frequency of necrotic funnel centres. Corals were sampled in all environments in which they occur. *Acropora clathrata* occurred both outside gullies as well as on gully edges. As visual inspection showed that colony morphologies did not differ between these habitats, data from all colonies were pooled irrespective from which habitat they were taken. *Turbinaria peltata* only occurred outside gullies, so all measured colonies stem from corresponding habitats.

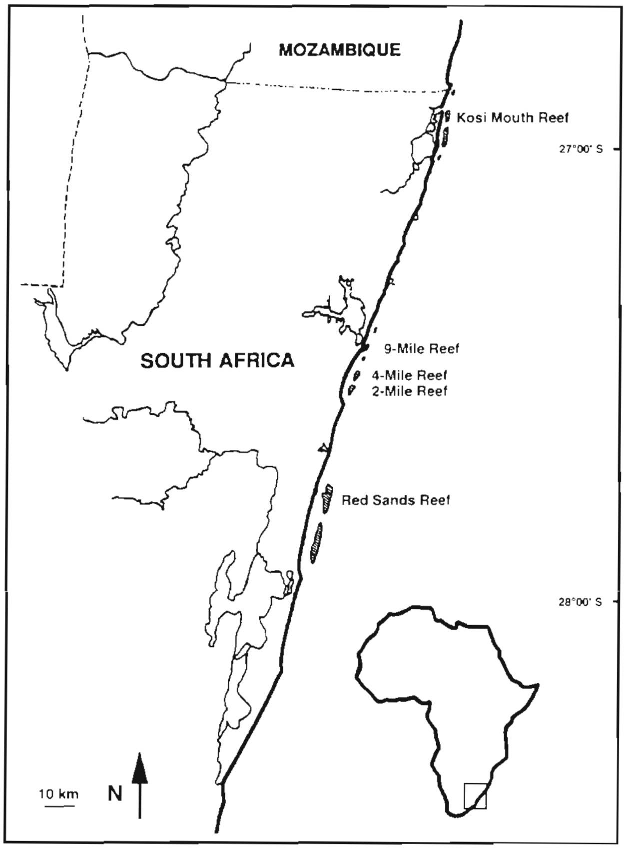

Fig. 1. The study area in Maputaland, northern Natal, South Africa. Funnel-shaped colonies were measured on 2-Mile, 4-Mile and 9-Mile Reefs

From 10 colonies of each species, all sediment found inside the colonies (in the funnel centre) was transferred into plastic bags for grain size analysis, which was performed using nested sieves at 1 ϕ intervals and a mechanical shaker (Dyer 1986). Sediment was collected from the substratum adjacent to the corals ('sediment on the reef'), and sediment traps were employed to provide a relative measure of sedimentation at specific sites. These traps comprised plastic tubes of 11 cm bore, which were 20 cm high (the average height of funnels), and projected vertically from rectangular vinyl containers of 20 × 10 cm that served to accumulate the sediment.

In the laboratory, plastic models of the corals were built to a scale of 6:1, using the averaged values of colonies measured in the field. These models were tested in a unidirectional flow tank with variable water speeds, which was modelled on that illustrated in Denny (1988). Water was pumped around a closed circuit by propellors situated in the vertical leg of the return pipe. The working section of the tank was rectangular and constructed of acrylic. At its entry, a 'flow straightener' was built of soda straws, which made the flow through the experimental chamber uniform (Fig. 3). Water speed could be modulated from 30 to 90 cm s^{-1}. Specimens were attached to a Plexiglas specimen holder in a manner that allowed the specimen to be held upside-down or in a normal orientation, which allowed both the application of sediment into the funnel (in the normal orientation) as well as the injection of dye through the stem into the funnel centre, to visualize vortices and currents inside the funnel (when the specimen was held upside down). Streaklines were visualized using phosphorescent dye (Vogel 1983).

Three grain sizes of sand were used in the experiment: fine sand (ϕ +3 to +2, grain size 0.125 to 0.250 mm), medium sand (ϕ +2 to +1, grain size 0.250 to 0.500 mm), coarse sand (ϕ +1 to 0, grain size 0.500 to 1 mm). These sand fractions were obtained by sieving carbonate sand (obtained locally from the reefs) through a series of nested sieves at 1 ϕ interval. Constant quantities (dry weight 10 g) of sand were applied to the centre of the funnels in still water. Then, varying current speeds between 30 and 90 cm s^{-1} were applied for 10 min. After this time elapsed, all sand remaining in the funnels was collected, dried and weighed.

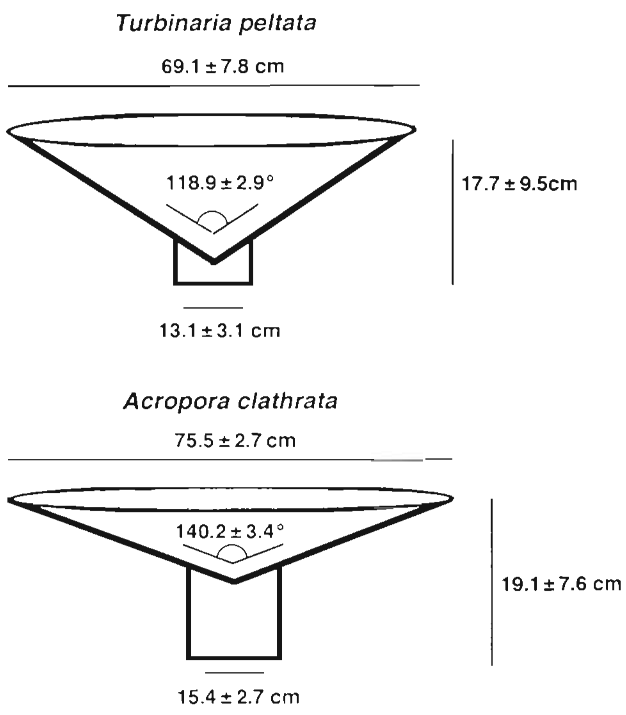

Fig. 2. Morphometric characteristics of all measured funnel-shaped colonies of *Turbinaria peltata* and *Acropora clathrata*. These measurements were used to build models at a scale of 1:6 for use in flow tank experiments

RESULTS

Morphometry of funnels, frequency of dead centres

Acropora clathrata funnels did not have thicker stems ($t = -1.3$, $p > 0.05$), were neither higher ($t = -1.1$, $p > 0.05$) nor wider ($t = -0.7$, $p > 0.05$), but had a significantly greater angle of spreading than those of *Turbinaria peltata* ($t = -4.3$, $p < 0.001$; Fig. 2). In deep water (greater than 18 m), 58% of all funnels had dead centres, while this was only the case for 17% in shallow water. In *T. peltata*, 50% of all colonies had a dead centre, while only 43% of all *A. clathrata* suffered that condition, primarily those in deep water. *T. peltata* was only frequent in deep water, therefore no such differences were evident.

Sediment on the reefs and in the funnels

Maximum sedimentation levels, as measured in sedimentation traps on the reefs under conditions of high surge (water speed > 0.7 m s^{-1}) were 107 mg cm^{-2} h^{-1} in sandy gullies and 43 mg cm^{-2} h^{-1} on elevated, relatively sediment free parts of the reefs. This

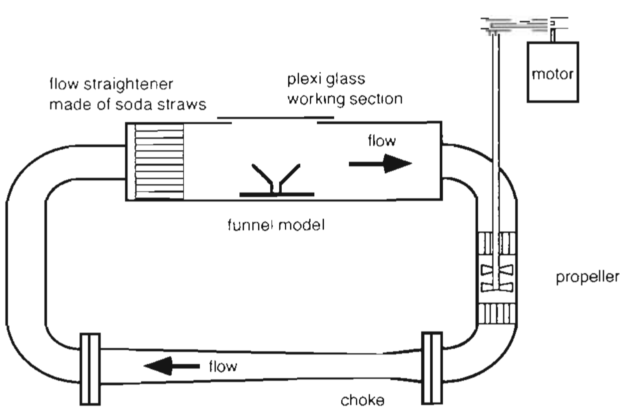

Fig. 3. Schematic drawing of the flow tank set-up. Modified from Denny (1988)

was mainly due to resuspended sediment which resettled in the adjacent areas. Suspended sediment loads 40 cm above the substrate were 389 mg l^{-1} in sandy gullies and 112 mg l^{-1} on elevated parts of the reefs.

Grain sizes of sediments collected on the reef, in traps near the funnel-shaped colonies and inside *Acropora clathrata* and *Turbinaria peltata* colonies are given in Fig. 4. The sediment traps collected mainly small grains which are easily resuspended in moderate surge. Small grain sizes also predominated in the funnels of *A. clathrata*. In *T peltata* some very large granules were present. The grain size distribution of sediment in the funnels differed significantly between the 2 species (chi-square: 387.1, df: 5, $p < 0.001$).

Turbinaria peltata funnels collected higher amounts of sediment (7.03 ± 5.4 SD g) than *Acropora clathrata* (0.6 ± 0.7 SD g) but differences were not significant ($Z = 1.33$, $p > 0.05$).

Flow tank experiments

Dye paths indicated a narrowing of streaklines above the funnel and the formation of turbulences and vortices inside the funnel, originating on the up- and downstream funnel edges. These turbulences were caused by vortices created at the funnel lip.

All dye injected into the center of the funnel was quickly sucked away. At the slowest current speed (30 cm s^{-1}), the dye took a circular path through the funnel, indicating the existence of a large vortex which remained for a relatively long time within the funnel. At high current speeds (90 cm s^{-1}), all dye was quickly sucked outside the funnel in the direction of the current, remaining only in a turbulent area on the downstream funnel wall (Fig. 5). These patterns were similar for the models for the models of both *Acropora clathrata* and *Turbinaria peltata*.

Removal of sediment from the funnels followed the same path as the dye. All sediment was quickly dis-

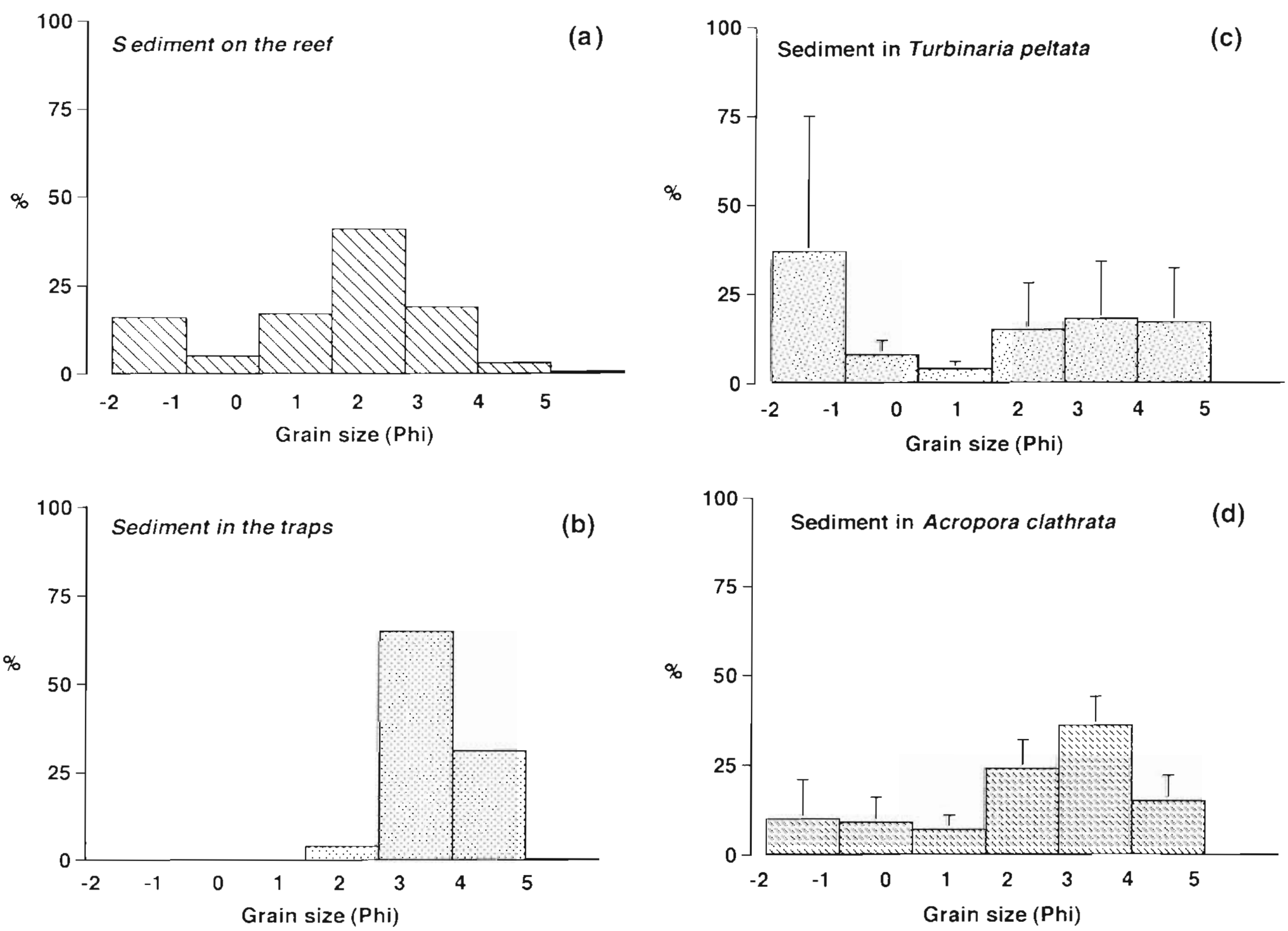

Fig. 4. Natural grain size distribution of sediments (a) on the sea-floor among the measured coral colonies, (b) in sediment traps, (c) in *Turbinaria peltata*, and (d) in *Acropora clathrata*

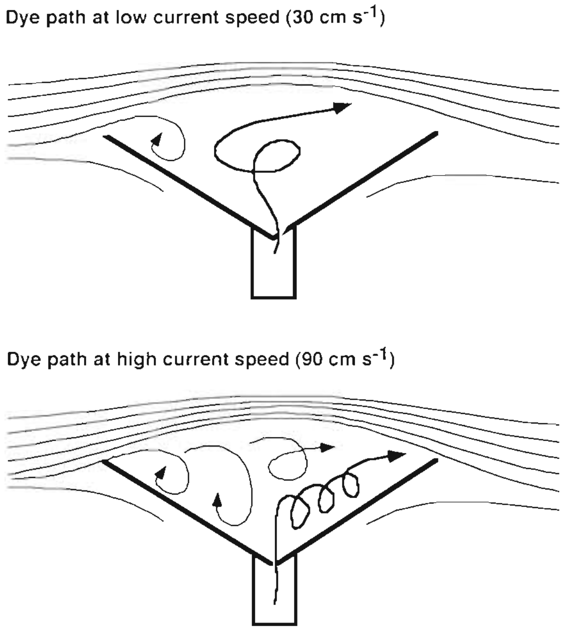

Fig. 5. Paths of streaklines passing over the funnels and of dye injected through the centre of the funnel. Streaklines show a narrowing over the funnel, indicating acceleration. In slow current speeds, dye follows a vortex and remains longer inside the funnel than in high current speeds, when dye is immediately sucked out of the funnel

placed from the funnel center to the turbulent area on the downstream funnel wall, from where it slid in small portions over the edge. In the *Acropora clathrata* models, sediment removal increased quickly from nil to almost total between current speeds of 30 and 40 cm s^{-1}. In *Turbinaria peltata* models, full removal of all grain sizes occurred only at a speed of 75 cm s^{-1} (Fig. 6).

DISCUSSION

A funnel-shaped form provides a coral with numerous potential advantages. By growing upwards into the water column, the corals enter a spatial refuge (Buss 1979), which is less crowded than the substratum and where it has better access to light and suspended food (Jackson 1979). On the other hand, in areas where sedimentation is high, these advantages may have to be balanced against the possible disadvantage of increased sediment accumulation inside the funnels. Mechanical implications of this growth form have been discussed by Vosburgh (1982) in relation to hydrodynamic exposure but not sedimentation.

Our first hypothesis was that a funnel shape accumulates sediment but concentrates it at the centre, while the walls of the funnel escape smothering and survive. Sediment will naturally build up in the funnel centre because of gravity and ciliary action. If this sediment is not removed, it will smother the central area, leading to bleaching and necroses (Riegl 1995, Riegl & Bloomer 1995). On the other hand, the funnel walls will remain free of sediment, which would otherwise interfere with prey capture and photosynthesis. Thus the centre acts as a 'sacrificial sediment trap'.

This situation was observed in deep water (18 to 25 m), where water movement due to wave action is low. The centres of about 60% of all funnel-shaped corals in deep water accumulated sediment and were dead. The sediment building up in these funnels was comparable in size composition to that deposited on the reef, whereas sediment in the traps, which collected much of the easily suspended sediments, was predominated by fine particles (Fig. 4).

Our second (alternative) hypothesis assumed that funnel-shaped corals exploit vortices and turbulences

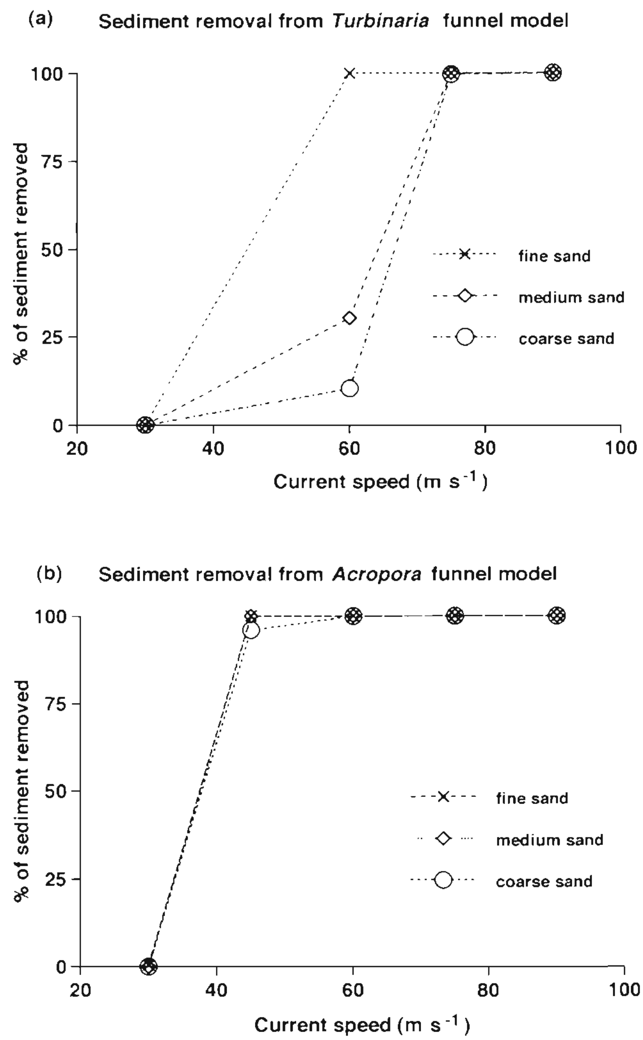

Fig. 6. Removal of sediment from models of the funnels of (a) *Turbinaria peltata* and (b) *Acropora clathrata*

in order to flush sediment out of the centres. At the funnel lip, vortices would be formed which periodically become unstable and are shed. This leads to bulk replacement of water within the funnel in the course of which sediment is sucked out of the funnel. Our simulations in a flow tank support this hypothesis as they show a vortex with longer remaining time within the funnel than at high speeds. Also the direction of water replacement is mirrored by that of sediment replacement (Fig. 7).

We also observed the results of this effect in the field. In comparison with calmer, deeper areas, funnel-shaped corals in shallow areas (8 to 14 m) with regular high water-motion had only half as many colonies with necrotic centres, a sign that funnels were more frequently emptied. In such environments corals exploit all the advantages of funnel shape: high light- and food-gathering capacity, growth into a less crowded environment, and self-cleaning during high water movement.

The shape of the funnels also proved to be important. *Acropora clathrata*, which built the flatter funnels, accumulated less and smaller grain size sediment. Inside the *Turbinaria peltata* funnels, an important proportion of the sediment consisted of large-size granules while fewer smaller grain sizes were present. The relatively high proportion of large granules in *T. peltata* funnels suggests that these were washed into the funnels in storms and could not be washed out again under normal conditions. *A. clathrata* funnels were obviously flat enough to allow exportation of the larger grain sizes, and more closely approached the size-spectrum of particles recorded in sediment traps. The accumulation of fine sediment in the sediment traps reflects the fact that small particles are most likely to be suspended in the water column. The higher amount of sediment collected in *T. peltata*, coupled with the higher frequency of dead centres, indicates that higher, but rarer, flow speeds are necessary to clean this funnel type. Therefore, of the 2 investigated species, *T. peltata* appears to use the 'sacrificial sediment trap' option more often than the flatter *A. clathrata*.

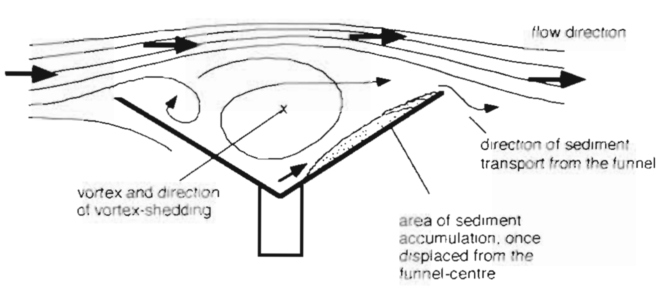

Fig. 7. Model explaining the hypothesis that sediment is removed from the funnel during the course of repeated vortex shedding. Vortices form inside the funnel, become unstable and are shed downstream. This leads to sediment transport during bulk replacement of liquid in the process of vortex shedding, first to the downstream funnel wall, then outside the funnel

CONCLUSION

Funnel-shaped growth in 2 species of South African scleractinia in a high-sedimentation environment had 2 effects: in areas of low water motion, it served as a sacrificial sediment trap, which collected all sediment at the base of the funnel where underlying tissues died, but all other tissues were kept sediment-free and able to capture prey and photosynthesize. In areas of high water motion, the funnel shape created vortices which in a process of vortex shedding and ensuing repeated mass replacement of fluid inside the funnels also emptied the coral colonies of accumulated sediment. Both strategies appear successful, as funnel-shaped colonies are dominant in areas of high and low water motion in South Africa.

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