

## Functional Morphology of Coral Shape and passive Hydrodynamic Self-Righting in Recent *Manicina areolata*

With 3 Figures and 1 Plate

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### Abstract

The scleractinian *Manicina areolata* is a common coral on Caribbean hard and soft substrata and was studied at Lee Stocking Island (Exuma Cays, Bahamas). It is not only found in reefal areas but also on bioclastic sand with seagrasses. The meandroid coralla typically grow to sizes of 2 to 10 cm and are morphologically variable. Growth form can vary from conical with round to oval cross-section to turbinate forms with few meanders and flat oval cross-section. The conical morphotype is usually attached to hard substratum, while the turbinate morphotype tends to live unattached, usually upright, in soft substratum. In infratidal areas, both attached and unattached turbinate forms were found in close vicinity, however, conical attached forms were rare.

Habitats with sandy softgrounds, where free-living turbinate morphotypes were common, were influenced by strong tidal currents with concurrent danger of burial or 'disorientation' of the coralla. Therefore, strategies are necessary for the corals to remain in the upright position. Besides a high self-cleaning potential (FABRICIUS 1964), the colony shape itself leads to passive cleaning and self-righting, which is achieved by the flat-turbinate morphology of the corallum, with a concave side and a flat to slightly convex opposite side, under high current speeds. The concave side, and particularly the median lobes formed by many meandroid coralla, are the critical morphological factors. Particularly the grooves formed inbetween the lobes channel currents in a way that scour underneath the coral and drag produced by the lobes act together to allow passive self-righting.

**Key words:** unattached Scleractinia, soft substratum, currents, coral, shape-selfrighting

### Introduction

The classical view of zooxanthellate corals is one of fixosessile organisms remaining firmly attached to the hard substratum all through their postlarval life. Fragments usually rapidly reattach, but in special instances can survive unattached as 'coralloliths' (GLYNN 1974, RIEGL et al. 1996). Among zooxanthellate corals, only the fungiids, mostly solitary corals, routinely remain unattached once the primordial polyp has broken off

the substratum. However, unattached life in soft sediment is the norm in many solitary corals, many azooxanthellate.

HOEKSEMA (1993) differentiated between forms that live in a 'loose' or 'semi-buried' way on or in the sediment. These corals are competent self-cleaners and polyps have various mechanisms for exhumation and regaining of a vertical position (PLUSQUELLEC et al. 1999, cum lit.). Also the skeletons are shaped and made in a way allowing them 'to swim' in the sedi-

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ment. Skeletons are laterally flattened discoidal (as in the Fungiids) or buoy-shaped or horn shaped. Comparable phenotypes have repeatedly evolved in Earth History, not only in Mesozoic and Cenozoic scleractinia but also in Paleozoic rugosan corals.

One of the few colonial species that is found as frequently attached as unattached is the Caribbean *Manicina areolata* which can either be attached or live 'semi-buried' in soft sediment (FABRICIUS 1964 cum lit.; JOHNSON 1992a,b; HOEKSEMA 1993, RONIEWICZ & STOLARSKI 1999; PLUSQUELLEC et al. 1999). According to the terminology of SEILACHER (1984) it

is a 'mud sticker' (although more frequently found on sand). This species is common and therefore an ideal object to study the advantage of morphological adaptations in unattached corals – both recent and fossil.

We investigated the behavior of both attached and unattached specimens in order to 1) understand the orientation of coralla in unattached and attached specimens in relation to currents 2) understand advantages of oral field morphology 3) investigate how 'mud sticking' specimens keep from being buried.

## Material and methods

### The corals

*Manicina areolata* (LINNAEUS 1758) occurs in the subtropical and tropical Atlantic from the shallow infratidal to about 20 m depth, but it is the most common unattached scleractinian on loose sediment. *Manicina* is a colonial species with a meandroid corallum up to about 10 cm diameter in the study area (text-fig. 1). Colony shape is dependent on the complexity of oral-field meanders. Colonies vary from a round-oval, only slightly arched oral field (morphotype A) to an almost flabellate, clearly elongate oral field (morphotype B). The distance between the apex (aboral pole) and oral field shows a tendency to decrease with age, what leads to a change from a 'horn' shape (morphotype A) (cf. Pl. 1) in younger specimens to a 'buoy' shape (morphotype B) in older ones.

FABRICIUS (1964) investigated morphotype A in detail regarding its survival strategies in sandy habitats. We therefore concentrated on morphotype B in this study.

The study area was in the Exuma Cays (Bahamas) near Norman's Pond Cay where unattached morphotype B corals

are found in subtidal (2-5m depth) *Thalassia* seagrass meadows within strong tidal current settings (DILL 1991).

To understand the hydrodynamic behavior of unattached coralla and to experimentally verify our hypotheses, we built a simple flume consisting of two, 2.5 m long, inclined raceways with a water intake on the higher side and an outlet on the lower side (HUBMANN et al. 2001). By changing the inclination of the raceways, current velocity could be modulated. One raceway was filled with coarse grained sand, the other one with medium grained sand in order to learn about grain-size-specific behavior of the corals. Fluorecin dye traces suggested that flow within the raceways was reasonably laminar before impinging on the corals. 10 colonies were used with each grain size for replication of the experiments. Corals were oriented in alternation with their oral fields or their apices into the current. Since the produced currents (comparable to those in the study site, i.e. 10-100 cm.sec<sup>-1</sup>, DILL 1991) are strong enough to entrain sediment, it was possible to see the coral's defences against burial. In order to investigate active 'digging out' behavior, corals were totally buried in the sediment without any current and left for 12 hours.

## Results

Ten colonies were oriented with their oral fields into the current and 10 against the current. No differences were found in the coral's active or passive behavior in relation to different grain sizes. Therefore we discontinued testing with different grain sizes.

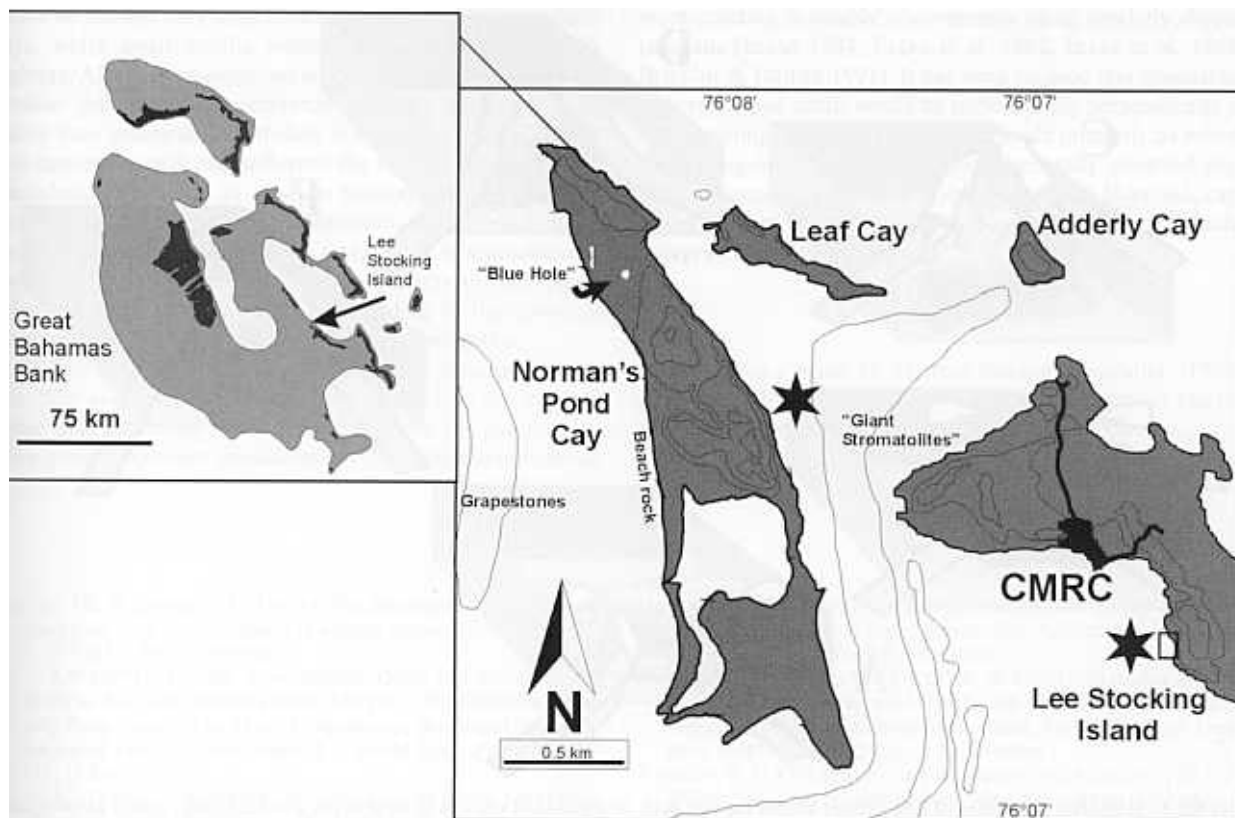
*M. areolata* exhibited 'passive digging' behavior. During the entire experiment in the flume, the corals never inflated their oral fields for active self-cleaning. It was, however, clearly visible that ciliar activity was used to clear away sediment particles.

### Observations

Passive digging behavior utilized flows around the oral field (text-figs. 2, 3): When corals were oriented with their oral field into the current, streamline partitioning on the oral field's inner edge led to the creation of vortices in front of the oral field, thereby leading to the erosion of sediment (text-fig. 3A: 2, 3). The corallum then fell into the pit created underneath this stable vortex (text-fig. 3A: 3, 4), which raised the aboral apex. This in turn led to increased shed-eddy and vortex generation

with subsequent sediment erosion near the aboral pole (text-fig. 3A, 4-7). The erosion of sediment by the strong vortices near the aboral pole led to the generation of a pit into which the corallum slid. This in turn led to an increasingly upright position of the corallum (text-fig. 3A: 8, 9). The fact that the oral field was now oriented into the current led to increased hydrostatic pressure and increased drag while erosion near the aboral pole continued (text-fig. 3A: 9). Drag and pressure on the oral pole combined with the aboral pole sliding into the pit generated by the lee vortices finally pushed the coral upright (text-fig. 3A: 10, 11). The new position of the corallum now allowed more laminar flow around it and vortex generation in the lee decreased, causing the 'leeward pit' to be filled-in and thus a consolidation of the corallum's new position (text-fig. 3A: 11).

Passive digging behavior of coralla oriented with their aboral (pointed) sides into the current was observed as follows (text-fig. 3B): Streamline separation and vortex formation led to vortices in the lee of the corallum (in front of the now downstream oral field) with resultant strong sediment erosion and pit formation (text-fig. 3B: 1). The oral field slipped into this pit (text-fig. 3B: 2 – 4) which caused the coral 'to stand on its



Text-fig. 1. Study area in the vicinity of Norman's Pond Cay and Lee Stocking Island in the Exuma Cays, Bahamas. The position within the Bahamas is indicated by an arrow in the overview chart. CMRC = Caribbean Marine Research Center. Star indicates the position of study area.

head' (text-fig. 3B: 5, 6). Increased drag on the upward pointing aboral pole toppled the coral, which now rested with its oral field pointing into the current. Now the same process as described above was repeated (text-fig. 3A).

The experiments in the flume showed also that the shape of the corallum, in particular the degree of meandrization and the shape of the aboral pole (whether pointed or blunt, straight or bent) had an important influence on the coral's hydrodynamics and, in consequence, passive digging abilities. In particular young coralla tended to be elongate in the oral-aboral axis with short meanders. This is an advantageous shape to lie on the sediment or to firmly stick within it.

Older coralla tended to form irregular lobes (Pl. 1). These lobes can funnel currents and influence vortex generation. In particular the formation of two lateral lobes with a cen-

tral, dividing constriction appeared as a highly advantageous growth-form. In such a case, the current hitting the oral field was funneled through the central constriction to flow along the corallum to hit the aboral pole (text-fig. 3 B). If this was upward turned, as is frequently the case in nature, this led to a maximization of the leeward, aboral vortices and following sediment erosion and subsequent rapid self-righting of the coral.

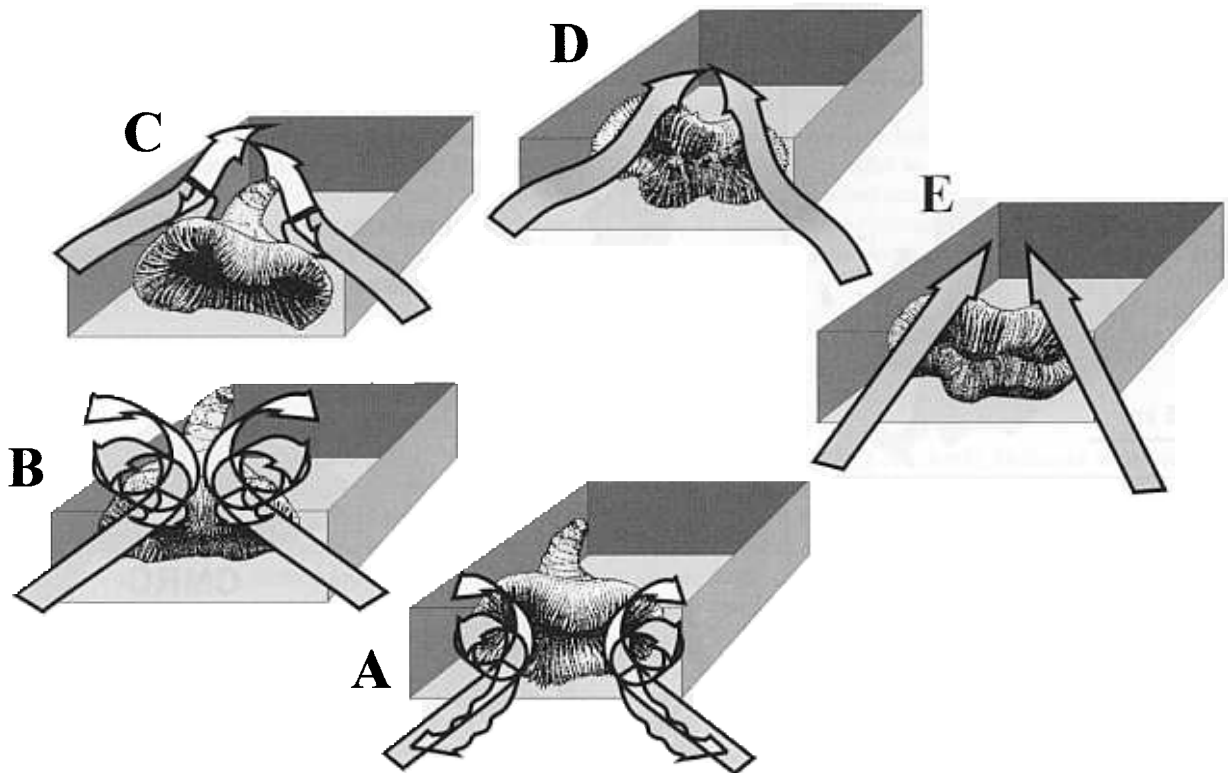
In older coralla, oral-aboral distance shrinks, while the width of the oral field increases which leads to increased buoy shape. This in turn gives higher stability on the substratum and large colonies can only be displaced by catastrophically strong currents. Large corals also reacted more actively to sediment by inflation of the polyp or cilial activity than smaller corals.

## Discussion

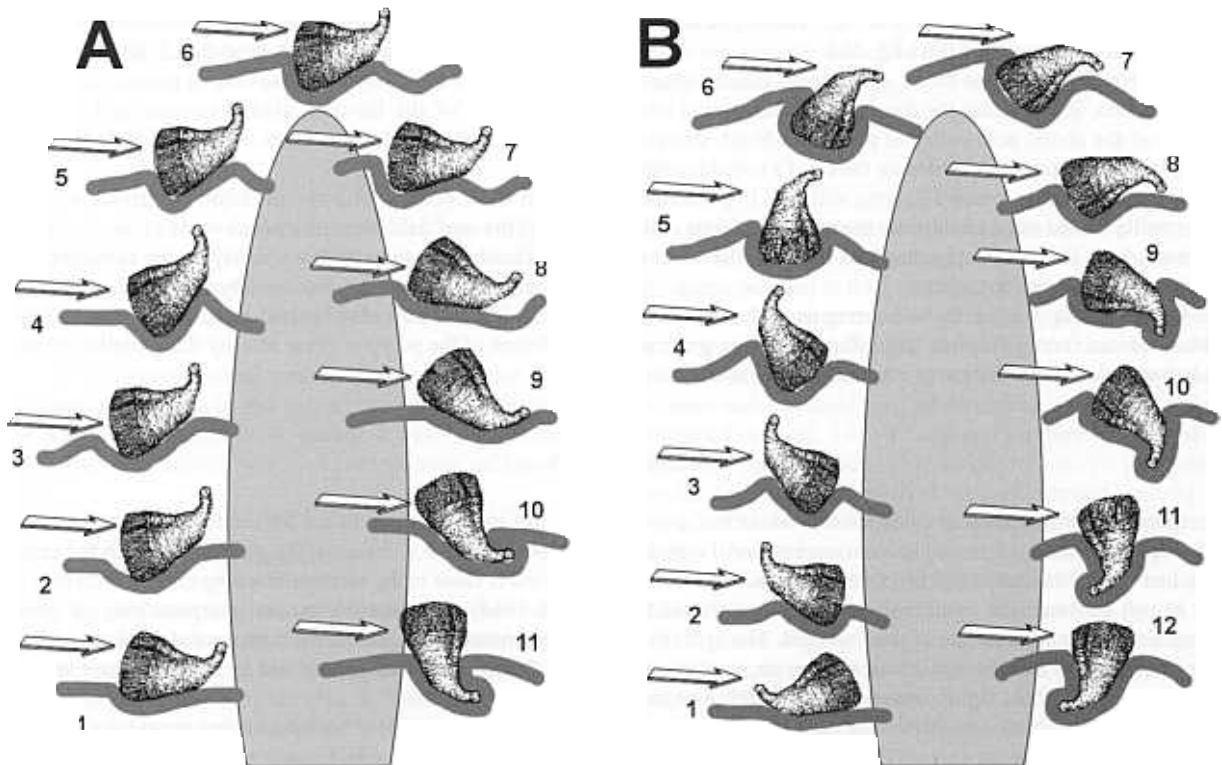
The experiment provided clear evidence that *Manicina areolata* is capable of both active and passive orientation of coralla in attached as well as unattached life forms. Unattached coralla living in soft substrata are capable of active and passive self-righting, i.e. upward orientation of the oral field. The hydrodynamic properties of morphotype A allow lying on, or sticking in the substratum without significant energy expenditure on the coral's side (i.e. soft body activities). The coralla's shape allow "automatic" self-righting in case of dislocation, disorientation (i.e. turning upside-down) or even transport in currents.

An important parameter for the functioning of this passive rotation is the coral's specific weight, which in the case of *Manicina* is close to the surrounding aragonitic sediment (FABRICIUS 1964). For paleobiological interpretations of similar coral phenotypes (i.e. Paleozoic horn corals) the density difference of coral and sediment, caused by the corallum's anatomy is of relevance.

JOHNSON (1988) linked increasing meander complexity to the maintenance of a high surface area-volume ratio, necessary for efficient sediment rejection (GOREAU & GOREAU 1960). Our results are consistent with this observations inas-



**Text-fig. 2.** Simplified illustration of flow vectors around the oral field. A: creation of vortices in front of the oral field (blue, yellow arrows), and erosion of sediment (red arrows). B: due to erosional effects in front of the coral the corallum falls into a depression created underneath the vortices causing erection of the aboral apex. Red arrows indicate hydrostatic pressure pushing the coral into a 'standing' position. C: the 'standing' position is unstable, the coral is pushed over and vortex generation with subsequent sediment erosion (red arrows) near the aboral pole lead to sediment erosion there. D: erosion of sediment behind the coral's oral field generates a pit into which the corallum slides. E: the coral is oriented with its oral plane normal to sediment surface causing more laminar flow (blue arrows).



**Text-fig. 3.** Cartoon of the self-righting behaviour of *Manicina* colonies in a flume channel. Further explanations in the main body of the text. A: Oral field oriented into the current. B: Oral field oriented downcurrent.

much we showed only large coralla to be active sediment shedders, while small coralla seemed to rely on passive self-righting. Also, our observations support JOHNSON's (1988) suggestion that meander complexity may be environmentally rather than genetically controlled, since sedimentation regime and current strength may influence the formation and shape of meanders, particularly in small to medium sized coralla. We also support JOHNSON's (1988) statement that self-righting is limited by the coralla's size, and that growth is semi-determinate with larger coralla having more difficulty to right themselves. For them, better sediment shedding in the upright position, aided by a meandroid shape, is advantageous.

The fact that we demonstrated here that *Manicina* coralla can 'flip over' while being oriented parallel to the current, rather than just being rolled perpendicular to the current may have some important considerations for paleoenvironmental

reconstruction in muddy environments using similarly shaped rugosans (ELIAS 1984, ELIAS et al. 1987, ELIAS et al. 1988, BOLTON & DRIESE 1991). It has been claimed that orientation of horn-shaped corals would be preferentially perpendicular to the prevailing currents, since coralla would primarily be rolled. If 'flipping-over' was indeed a more generally observed phenomenon among corals with a similar shape as *Manicina*, care has to be taken when using corallum-orientation as an aid in the interpretation of paleo-currents.

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*Plate 1*

Skeletons of morphotype A *Manicina areolata* (Linnaeus 1758) from the east side of Norman's Pond Cay in the Exuma Cays, Bahamas (23°46,72N / 76°07,68W). Remarkable is the morphological variability of coralla.

Fig. A – E lateral views,

Fig. A' – E' oral view of coralla. Note increasing complexity of lobe arrangements.

