

Self Righting in the Free-Living Coral *Manicina areolata* (Cnidaria: Scleractinia): Morphological Constraints

AMY V. UHRIN^{1,2,5}, CHRISTOPHER L. SLADE³, AND JEFF G. HOLMQUIST^{1,4}

¹University of Puerto Rico, Mayagüez Campus, Department of Marine Sciences, P.O. Box 908, Lajas, PR 00667, U.S.A.

²current address: NOAA, National Ocean Service, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516, U.S.A.

³Florida Fish and Wildlife Conservation Commission, Florida Wildlife Research Institute, South Florida Regional Laboratory, 2796 Overseas Highway, Suite 119, Marathon, FL 33050, U.S.A.

⁴current address: University of California White Mountain Research Station, 3000 East Line Street, Bishop, CA 93514, U.S.A. and Marine Science Institute, University of California, Star Route 1, Box 198, Mammoth Lakes, CA 93106, U.S.A.

⁵Corresponding author: Amy.Uhrin@noaa.gov

ABSTRACT.—Free-living colonies of *Manicina areolata* (Cnidaria: Scleractinia) inhabiting shallow, high-energy environments, are frequently overturned by waves and currents and are able to right themselves by a variety of adaptations. Coral colony complexity and size may influence the ability to right. We experimentally tested the relationship between various coral morphological attributes (e.g., area, meander density, and shape) and time required for righting. The average time for righting was 116 h (S.E. \pm 28.7), with 86% of inverted colonies righting by the end of the 23 day experiment. Colony area was the only significant predictor of righting; large colonies were less efficient at righting. Effects of meander density and colony shape were minimal and were overwhelmed by the relatively strong influence of area. Although an increase in meander density may facilitate the process of sediment rejection in high energy environments it appears that the concomitant increase in area hinders the colony in terms of its ability to right.

KEYWORDS.—Scleractinia, *Manicina areolata*, righting, coral, behavior, Caribbean

INTRODUCTION

Free-living coral colonies with no stabilizing attachment to the substrate commonly inhabit turbid, shallow-waters (e.g., seagrass, sand, and rubble flats) where high-energy conditions (e.g., strong waves and currents) may overturn them (Hubmann et al. 2002). Free-living corals thrive in these environments using a variety of morphological and physiological adaptations. High resistance to physical burial was demonstrated in free-living species from the west coast of Florida (Rice and Hunter 1992). *Pavona* spp. from the Gulf of Panama (Glynn 1974) and colonies of *Siderastrea radians* in Barbados (Lewis 1989) develop spherical growth forms, which enable colonies to roll along the substrate when disturbed by physical or biological

agents, thus preventing burial. Others are able to exhume themselves when buried via polyp distension (Fabricius 1964; Hubbard 1972) and to actively shed sediment using tentacular action, ciliary beat, and mucus entanglement (Abe 1939; Goreau and Goreau 1960; Fabricius 1964; Hubbard and Pocock 1972). Corals that are either always or occasionally free-living, including species of *Isophyllia*, *Isophyllastrea*, *Cycloseris*, *Diaseris*, *Fungia*, and *Manicina*, are able to “right” themselves, i.e., return to an oral side up position, after being overturned (Abe 1939; Goreau and Goreau 1960; Fabricius 1964; Goreau and Yonge 1968; Hubbard 1972; Hoeksema 1988).

The key to the righting of *Manicina areolata* colonies after inversion lies in the inflation of the coenosarc (i.e., live tissue between adjacent calices) by ingestion of water through the stomodeum (i.e., mouth; Goreau and Goreau 1960; Fabricius 1964). The resulting swelling is presumably a re-

ms. received March 5, 2004; accepted March 31, 2005

action to contact of the polystomodal tissues with the substrate and the pressure of a colony's own weight when inverted (Fabricius 1964). The ingested water is flushed from the stomodeum in a stream directed against the sediment, undermining the colony on one side. This produces a rocking motion which continues until the colony is righted. However, not all colonies are able to fully right themselves once overturned; smaller colonies, with conical bases, often remain at an angle (Fabricius 1964; A. Uhrin pers. obs.).

Goreau and Goreau (1960) suggested that the high complexity of meander pattern (and thus a high surface area to volume ratio) of free-living meandroid forms, like *M. areolata*, enhances righting capability. The rate of increase in meander complexity with age tends to be faster in colonies of *M. areolata* in environments with high energy and fine grained sediment (Johnson 1988). Johnson (1988) and Hubmann et al. (2002) suggested that the pattern complexity in *M. areolata* is an adaptive character.

Colony size and meander complexity in *M. areolata* are positively correlated, although the relationship is not linear (Johnson 1988). Smaller colonies have faster righting times than larger ones (Fabricius 1964). However, Johnson (1988) suggested that the ability of an inverted colony to right is size-limited (i.e., larger colonies are less able to right), and there may be a negative relationship between pattern complexity and time required for righting (i.e., more complex colonies will right faster).

Based on Fabricius (1964), we hypothesized a positive relationship between *M. areolata* colony area and time required for righting (i.e., small colonies will right faster than large colonies). We likewise hypothesized a negative relationship between colony complexity (i.e., meander density), and time required for righting, based on the premise that increased meander pattern enhances the surface area to volume ratio thus facilitating righting. In addition, we examined the influence of colony shape on righting time.

MATERIALS AND METHODS

Thirty-six colonies of *M. areolata* were haphazardly collected from shallow seagrass (*Thalassia testudinum*) near La Parguera, Puerto Rico in October 1997. In the field, colonies were arbitrarily categorized by length: small (< 5.0 cm), medium (5.5-7.5 cm), or large (> 7.5 cm) to insure that a variety of sizes would be represented in the experiment. The arbitrary size categories were not used as predictor variables themselves. We collected equal numbers of colonies for each size category. Length and width for each colony (in plan view) were measured, while colony area (i.e., size) was estimated by multiplying the length and width of each colony, producing a slight overestimate of actual area. Because some colonies are elongate while others are circular, the ratio of length to width (from previous plan view measurements) was calculated as a proxy for shape. We placed colonies on the sandy bottoms of aquaria in an open seawater system (4 colonies per aquarium, randomly selected). Colonies acclimated for 6-14 days before onset of experimentation.

Yonge (1936) and Fabricius (1964) noted nocturnal activity in *M. areolata* including righting, horizontally-directed movements, and feeding. In addition, we previously conducted a pilot study where 10 of 12 overturned colonies righted during the night, so we began our manipulations at dusk. After the acclimation period, 6 randomly chosen colonies were manually overturned (i.e., oral surface down) every 2 hours beginning at 1800 h on 8 November 1997. We staggered the overturning of corals to incorporate diurnal variance. For the first 12 h (1800-0600), colonies were monitored every 10 min, recording any movement and during the following 12 h (0600-1800) we monitored at 20-min intervals. During the second night, colonies were observed every 30 min, whereas in the second day, we made observations every 2 hours. In the third night, observations were reduced to twice daily (sunrise and sunset), until day 23 at which point the experiment was terminated. We decided to reduce observation intensity because many coral

colonies righted within the first 24 h, and righting was slower thereafter. After the righting experiment, we measured meander complexity of each colony by placing a section of twine in the central, continuous valley system of each colony. Additional pieces of twine were placed in the valleys of branching lobes, and the aggregate length of twine was measured. When lobes were too short to permit the insertion of twine, we measured directly with a ruler. Since colony size and meander complexity are positively correlated (Johnson 1988), we used meander density (i.e., meander length per unit colony area) for our measure of complexity.

Data were tested for normality (Shapiro-Wilk) and homogeneity of variance (F_{\max} , SAS Institute 1999). Although Mallow's C_p statistic (SAS 1999) suggested that a single variable model was the best for these data, we assessed the following variables using simple and multiple regression (SAS Institute, 1999), the latter using area, meander density, and the ratio of length to width as predictor variables.

RESULTS

Colony area ranged from 135 to 10,192 mm^2 with a mean area of 2770 mm^2 (S.E. \pm 322). Meander density values ranged from 0.051 to 0.131 mm/mm^2 with a mean of 0.087 mm/mm^2 (S.E. \pm 0.00365). Time required for righting averaged 116 h (S.E. \pm 28.7), but half of the 36 colonies righted within the first 24 h. Many of these colonies were small, but some large colonies righted rapidly as well (Fig. 1). At the other extreme, five relatively large colonies failed to right within the 23 d allotted for the study. Necrotic areas appeared where the tissue of these colonies was in direct contact with the substrate. After 6 months, these five colonies had still not righted and had died. None of these colonies were small (Fig. 1). Colony area and meander density positively correlated ($r^2 = 0.88$; $p < 0.0001$), and there was also a significant, positive linear relationship between area and righting time ($r^2 = 0.38$; $p = 0.0002$; Fig. 1). Meander density ($r^2 = 0.06$; $p = 0.17$) and length:

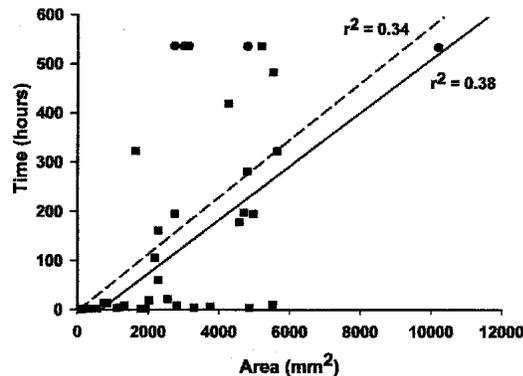


FIG. 1. Relationship between *Manicina areolata* colony area and righting time after colony inversion. Circles represent colonies failing to right during the 23 d experiment. These colonies were arbitrarily assigned the maximum time allocated for the experiment. The dashed line indicates the resulting area-time relationship from inclusion of these colonies in the analysis. The solid line and associated squares represent the relationship when non-righting colonies were excluded.

width ($r^2 = 0.02$; $p = 0.45$) were not significant predictors of righting (Figs. 2, 3), while multiple linear regression, including all predictor variables, offered little improvement over area alone ($r^2 = 0.37$; $p < 0.002$).

DISCUSSION

Righting in response to overturning appeared to be common in *M. areolata* (86%

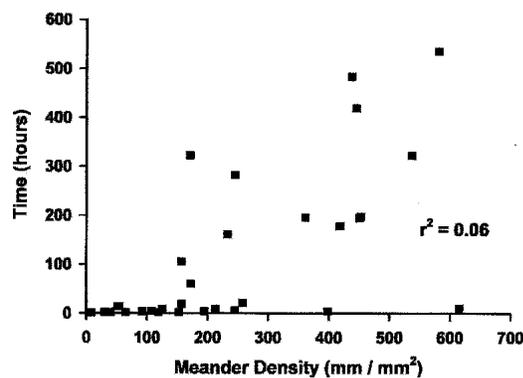


FIG. 2. Relationship between *Manicina areolata* meander density and righting time after colony inversion. The colonies failing to right (i.e., circles in Fig. 1) were not used in this analysis because complexity measurements for these colonies were not recorded.

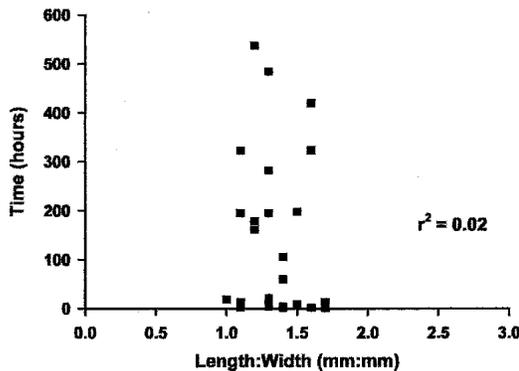


FIG. 3. Relationship between length:width (i.e., shape) and righting time after colony inversion.

righting rate). Ruiz-Zárte et al. (2000) observed 100% righting in 36 overturned colonies in the Mexican Caribbean. High rates of righting were also reported in free-living fungiid corals from the Indo-Pacific (Hoeksema 1988). Inverted corals would be expected to right quickly in order to avoid potentially negative effects. Inversion can lead to tissue necrosis (Fabricius 1964; A. Uhrin pers. obs.) and cause mouth blockage (Hoeksema 1988), which may inhibit ingestion. It is possible that inversion could lead to self-shading, and thus a loss of symbiotic algae. Colonies of *M. areolata* exposed to light stress (i.e., reduced light) lose zooxanthellae (Yonge and Nicholls 1931; Goreau and Goreau 1960; Ruiz-Zárte et al. 2000).

In our experiment, the positive relationship between colony area and righting time was consistent with previous results (Fabricius 1964; Johnson 1988; Ruiz-Zárte et al. 2000). Larger, rounded colonies may have more difficulty righting, because only a relatively small percentage of the colony's stomodeal area is in contact with the substrate. If enough stomodeal area is not in contact with the substrate, the amount of ejected water may be insufficient to facilitate the undermining of a colony and subsequent righting. However, even if a substantial proportion of the stomodeal area is in contact with the substrate, the heavy weight of a large colony may be difficult to overcome (Ruiz-Zárte et al. 2000). Johnson (1992) found that the increased mortality rate for large *M. areolata* colonies in the

Panamanian Caribbean may be due to difficulties in righting after inversion. On the other hand, in small, overturned colonies, a large percentage (often 100%; A. Uhrin pers. obs.) of the surface area, and hence stomodeal area, is in contact with the substrate. In this case, water expulsion can lead to rapid undermining of the sediment and subsequent righting. The shape of the base of a colony may also play a role in facilitating righting (Fabricius 1964; Hoeksema 1988). In our experiment, larger, dome-shaped colonies had flat bases whereas many smaller colonies had conical bases. This latter base shape may aid in righting by counteracting colony weight (Fabricius 1964). In contrast, the high center of gravity associated with the dome-shape exhibited by colonies of some *Fungia* spp. may actually aid in righting (Hoeksema 1988). In many cases, it may be more critical for smaller colonies to right rapidly because of the potential for smothering. A large colony is not at immediate risk, because only a small percentage of the colony's surface area is in direct contact with the substrate when inverted (A. Uhrin pers. obs.).

The lack of a relationship between meander density and time required for righting was contrary to our hypothesis. Meander density effects on righting were minimal and overwhelmed by the relatively strong influence of area. High meander densities were associated with larger sizes, thus, large colonies were less efficient at righting. Although an increase in meander complexity (i.e., meander density) may facilitate the process of sediment rejection in high energy environments (Goreau and Goreau 1960; Johnson 1988; Hubmann et al. 2002), it appears that the concomitant increase in size (i.e., area) hinders the colony in terms of its ability to right. The tradeoff is that, once a colony reaches a given size, the susceptibility to being overturned may be reduced, and therefore more energy may be devoted to sediment rejection. Examination of the prevalence of overturning of *M. areolata* colonies in the field, as a function of colony size, in addition to flume experiments where colonies can be exposed to increasing current speed, would be useful in determining size thresholds. Effects of

colony weight, height, and volume on righting in *M. areolata* warrant further investigation as well.

Meandroid growth forms, like *M. areolata*, exhibit a type of intratentacular budding (i.e., parent polyp divides into two or more polyps) whereby polyp formation occurs only at the ends of valleys (Veron 1993). This type of growth results in colonies that are initially elongate when small. These small (i.e., younger), elongate colonies might be expected to right faster than large (i.e., older), more circular colonies because of lessened resistance to righting via either coral activity or waves and currents. High rates of inversion and righting were observed for elongate colonies of *Fungia scutaria* (Hoeksema 1988); however, our data indicate that shape (approximated as length:width), does not play a role in the righting ability of *M. areolata*, at least in a laboratory setting.

The active movements of *M. areolata* (i.e., righting and lateral displacement) may serve as survival strategies and dispersal mechanisms for this species. Righting enables *M. areolata* to colonize and thrive on unstable substrates and in areas of high water motion, niches not commonly exploited by larger, reef-building coral species. Because dispersal is restricted by larval brooding and rapid larval settlement, it has been suggested that populations of *M. areolata* are self-seeding (Johnson 1992). Transport of these corals by currents may facilitate local dispersal.

Righting behaviors are characteristic in a number of other reef flat inhabitants including echinoderms and strombid gastropods (Hyman 1955; Reese 1966; Berg 1974, 1975). The righting behaviors of several species of asteroids and echinoids are well-documented, particularly responses to environmental stress (Diehl et al. 1979; Himmelman et al. 1984; Stickle et al. 1990; Watts and Lawrence 1990; Lawrence and Cowell 1996). Environmental modification can have a direct impact on organism physiology which often translates into behavioral changes (Eisler 1979). For example, increased righting times (Himmelman et al. 1984; Watts and Lawrence 1990; Lawrence and Cowell 1996) and decreased feeding

activity (Forcucci and Lawrence 1986; Watts and Lawrence 1990) resulting from aerial exposure and changes in temperature and salinity have been observed for asteroids and echinoids. The righting response of *M. areolata* may be similarly affected. Changes in marine invertebrate behaviors such as feeding, swimming, phototaxis, valve pumping rates, and righting have been explored as bioindicators of toxic stress (Lang et al. 1980; Sanders 1984; Rada 1992; Bourdelin 1996). The righting response of *M. areolata* and similar corals might also serve as an indicator of ecosystem stress, a concept that requires further investigation.

Acknowledgments.—We thank A. Bowden-Kerby, C. Eckrich, M. Nemeth, A. Ortiz, H. Ruíz, B. Roque, M. Shärer, J. Schmidt-Gengenbach, E. Weil, and P. Yoshioka for helpful discussion and J. Schmidt-Gengenbach for German translations. This work was supported by U.S. Army Research Office grant DAAH 04-95-10308 to J. Holmquist. The views contained in this manuscript do not necessarily reflect the view of NOAA.

LITERATURE CITED

- Abe, N. 1939. Migration and righting reaction of the coral, *Fungia actiniformis* var. *palawensis* Döderlein. *Palao. Trop. Biol. Stn. Stud.* 4:671-694.
- Berg, C. J. Jr. 1974. A comparative ethological study of strombid gastropods. *Behaviour*. 51:274-322.
- Berg, C. J. Jr. 1975. Behavior and ecology of conch (Superfamily Strombacea) on a deep subtidal algal plain. *Bull. Mar. Sci.* 25:307-317.
- Bourdelin, F. 1996. Physiological responses of the tropical mussel, *Modiolus auriculatus* – a possible biological monitor in French Polynesia. *Mar. Pollut. Bull.* 32:480-485.
- Diehl, W. J. III, L. McEdward, E. Proffitt, V. Rosenberg, and J. M. Lawrence. 1979. The response of *Luidia clathrata* (Echinodermata: Asteroidea) to hypoxia. *Comp. Biochem. Physiol.* 62A:669-671.
- Eisler, R. 1979. Behavioural responses of marine poikilotherms to pollutants. *Phil. Trans. Roy. Soc. B.* 286:507-519.
- Fabricius, F. 1964. Aktive Lag.—und Ortsveränderung bei der Koloniekoralle *Mamicina areolata* und ihre paläoökologische Bedeutung. *Senck. leth.* 45:299-323.
- Forcucci, D., and J. M. Lawrence. 1986. Effect of low salinity on the activity, feeding, growth and ab-

- sorption coefficient of *Luidia clathrata* (Echinodermata: Asteroidea). *Mar. Biol.* 92:315-321.
- Glynn, P. W. 1974. Rolling stones among the scleractinia: mobile coralliths in the Gulf of Panama. *Proc. 2nd Int. Coral Reef Symp.* 2:183-198.
- Goreau, T. F., and N. L. Goreau. 1960. The physiology of skeleton formation in corals. III. Calcification rate as a function of colony weight and total nitrogen content in the reef coral *Manicina areolata* (Linnaeus). *Biol. Bull.* 118:419-429.
- Goreau, T. F., and C. M. Yonge. 1968. Coral community on muddy sand. *Nature* 217:421-423.
- Himmelman, J. H., H. Guderley, G. Vignault, G. Drouin, and P. G. Wells. 1984. Response of the sea urchin, *Strongylocentrotus droebachiensis*, to reduced salinities: importance of size, acclimation, and interpopulation differences. *Can. J. Zool.* 62:1015-1021.
- Hoeksema, B. W. 1988. Mobility of free-living fungiid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. *Proc. 6th Int. Coral Reef Symp.* 2:715-720.
- Hubbard, J. A. E. B. 1972. *Diaseris distorta*, an "acrobat" coral. *Nature* 236: 457-459.
- Hubbard, J. A. E. B., and Y. P. Pocock. 1972. Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. *Geol. Rundsch.* 61:598-626.
- Hubmann, B., W. E. Piller, and B. Riegl. 2002. Functional morphology of coral shape and passive hydrodynamic self-righting in recent *Manicina areolata*. *Senck. leth.* 82:125-130.
- Hyman, L. H. 1955. *The Invertebrates: Echinodermata*. New York: McGraw-Hill.
- Johnson, K. G. 1988. Size, meander pattern, and behavior in the Caribbean free-living meandroid coral *Manicina areolata* (Linnaeus). *Proc. 6th Int. Coral Reef Symp.* 3:403-408.
- Johnson, K. G. 1992. Population dynamics of a free-living coral: recruitment, growth, and survivorship of *Manicina areolata* (Linnaeus) on the Caribbean coast of Panama. *J. Exp. Mar. Biol. Ecol.* 164:171-191.
- Lang, W. H., R. B. Forward Jr., D. C. Miller, and M. Marcy. 1980. Acute toxicity and sublethal behavioral effects of copper on barnacle nauplii (*Balanus improvisus*). *Mar. Biol.* 58:139-145.
- Lawrence, J. M., and B. C. Cowell. 1996. The righting response as an indication of stress in *Stichaster striatus* (Echinodermata, Asteroidea). *Mar. Fresh. Behav. Physiol.* 27:239-248.
- Lewis, J. B. 1989. Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. *Coral Reefs* 7:161-167.
- Rada, J. L., N. Zabala, G. deMahieu, J. Rodriguez-Grau. 1992. Applicability as an early warning system of several behavioral bioindicators of toxic stress on the mangrove associated bivalve species *Isognomon alatus*. Abstracts 13th Annu. Meet. Society of Environmental Toxicology and Chemistry.— Abstracts, Cincinnati (USA), 8-12 November 1992.
- Reese, E. S. 1966. The complex behavior of echinoderms. In *Physiology of Echinodermata*, ed. R. A. Booloottian, 157-218. New York: Interscience.
- Rice, S. A., and C. L. Hunter. 1992. Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. *Bull. Mar. Sci.* 51:429-442.
- Ruiz-Zárate, M. A., J. Espinoza-Avalos, J. P. Carricart-Ganivet and D. Fragoso. 2000. Relationships between *Manicina areolata* (Cnidaria: Scleractinia), *Thalassia testudinum* (Anthophyta) and *Neogoniolithon* sp. (Rhodophyta). *Mar. Ecol. Prog. Ser.* 206: 135-146.
- Sanders, I. M. 1984. Sublethal effects of copper on juveniles of the queen conch *Strombus gigas* Linné. *J. Shellfish Res.* 1:31-35.
- SAS Institute, Inc. 1999 SAS Version 8.0. SAS Institute, Cary, North Carolina.
- Stickle, W. B., L. L. Liu, and D. W. Foltz. 1990. Allozymic and physiological variation in populations of sea urchins (*Strongylocentrotus* spp.). *Can. J. Zool.* 68:144-149.
- Veron, J. E. N. 1993. *Corals of Australia and the Indo-Pacific*. Honolulu: University of Hawaii Press.
- Watts, S. A., and J. M. Lawrence. 1990. The effect of temperature and salinity on righting, feeding and growth in the seastar *Luidia clathrata* (Say). *Mar. Behav. Physiol.* 17:159-165.
- Yonge, C. M. 1936. Studies on the biology of Tortugas corals: 1. Observations on Meandra areolata Linnaeus. *Carn. Inst. Wash. Pap. Tortugas Laboratory* 29:187-198.
- Yonge, C. M., and A. G. Nicholls. 1931. Studies on the physiology of corals. V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. *Sci. Rep. Gr. Barrier Reef Exped.* 1928-1929 1:177-211.