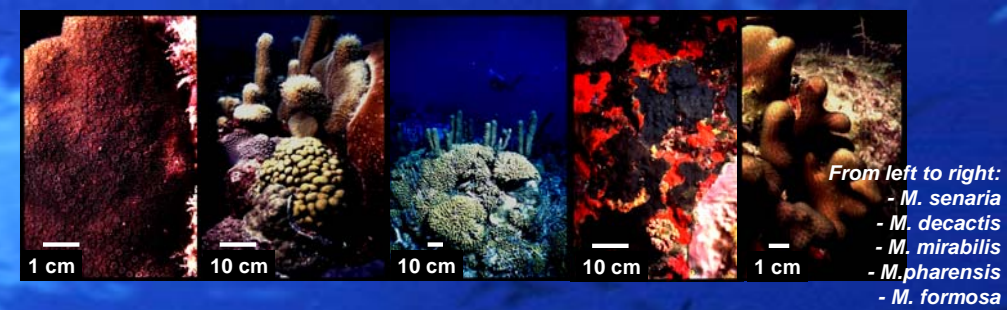


# EVOLUTION AND ECOLOGY OF CLOSELY RELATED *MADRACIS* SPECIES

## an illustration of the nature of species in scleractinian corals

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### I. Introduction

To understand variation between coral species we looked at ecological variation in six closely related *Madracis* morphospecies, whose taxonomical status is uncertain at present. We studied the interaction between environmental factors and species life-history strategies (e.g. reproductive isolation, distributional patterns, morphological variability, ecological characteristics) to understand the evolutionary organization in the genus.

### II. How do coral species differ?

**Population structure.** The colony size frequency distribution of all species is compared over a reef slope till a depth of 60m and related to local abiotic factors. Population structure (Fig. 1) and depth distribution prove to be species specific. Variation between species is twice as large as variation induced by environmental factors. In contrast to population structure, colony density depends mainly on local environmental factors.

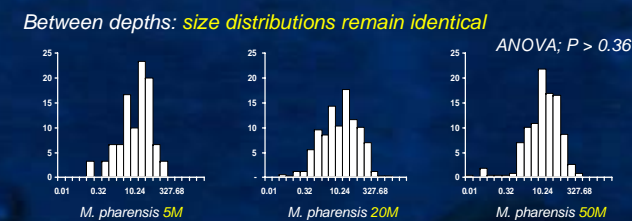
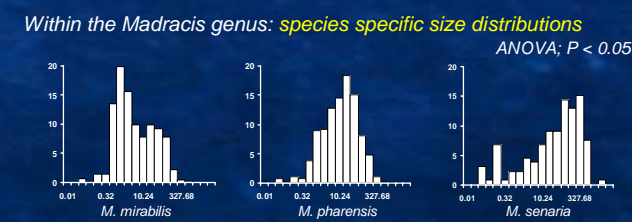


Fig. 1 The size frequency distribution of *Madracis* morphospecies is species specific and is stable over a 60m depth range.

Size variation in coral populations decreases with decreasing abundance. In general, populations growing in marginal habitats are characterized by a coefficient of variation (CV) higher than 0.5 (Fig. 2).

**Light.** The distribution of colonies relates to the light they receive at a small spatial scale (<10cm) and we find three ecological strategies towards light: (1) Species strive for maximum light capture and occur above a threshold light value. This limits their distribution towards greater depths. Such species are found in shallow (<15m) water and their morphological variation is not related to variation in the light they receive. (2) Species strive for maximum light capture but occur below a threshold light value. They occur only on deeper parts (>30m) of the reef slope and their morphological variation is also unrelated to variation in the light they receive. (3) Species occur in low light habitats. They are found over the entire reef slope (5-60m) if cryptic habitats are provided through structural complexity. Light has a structuring effect on the morphology of such species. Variation in light received by colonies within one depth is identical to the light variation received between depths. This makes depth a useless proxy for light in these species.

**Tissue fluorescence.** Tissue fluorescence (Fig. 3) characterizes the 3<sup>rd</sup> strategy. It serves as a photoprotective adaptation in shallow water and aids in photosynthesis at greater depth. Fluorescence emits wavelengths (512-620nm) corresponding to the excitation wavelengths of photosynthetic pigments of the symbiotic zooxanthellae.

### Reproduction: Gametogenesis and Spawning

To determine if differences in reproductive behavior or reproductive isolation exists in *Madracis*, we have studied gametogenesis on a monthly basis and coral larvae (planulae) release on a daily basis. All species are hermaphroditic brooders and show similar patterns in gamete development. Temporal reproductive isolation is absent in the genus and all species show gamete-maturation in relation with increasing seawater temperature, with mature gametes present from August to November. Gametogenic pathways are similar between species and differences between species are only found for oocyte number and size. We propose that the size and number of oocytes is related to the distance to be traveled by planulae to sustain gene-flow and prevent population inbreeding. Secondly, based on the absence of planulae in thousands of fertile polyps (histological analyses), we hypothesize that the term "brooding" does not apply for *Madracis* species and propose the term "quick-releasing" as its alternative. All species release planulae from April to December. Planulae release follows one month after gamete maturation. Species and colormorphs of the same species differ mainly in the number of planulae released per surface area. *Madracis senaria* differs from all other species and released planulae according to a lunar cycle (Fig. 4). Also, *M. senaria* shows unique "mass release" of planulae (>1000) during the Caribbean mass spawning, whereas all other species release planulae gradually and in a non organized pattern. The traditional division of reproductive strategies into "brooders" and "spawners" does not reflect reality of reproductive strategies and we suggest a subdivision for the brooding strategy: organized mass release or gradual release in low numbers without an organizational pattern.

**Preliminary conclusion.** Our data defines *M. mirabilis* and *M. senaria* as "true" species, since they differ in ecological characteristics and morphology from all other species. This suggestion is furthermore supported by genetical studies (Diekmann, et al., 2001), which show that both species are monophyletic.

*M. formosa* relates to *M. decactis* through hybridization resulting in a new species: *M. carmabi*. The new species shares morphological characteristics with *M. decactis* (10 septa) and *M. formosa* (branching

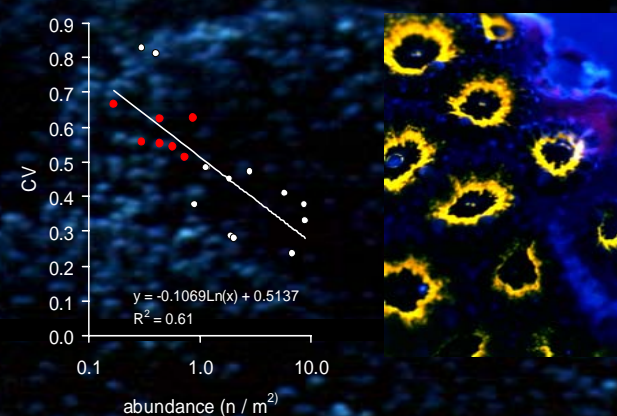


Fig. 2 The relation between the coefficient of variation (CV) and abundance. Red markers indicate populations growing in marginal habitats.

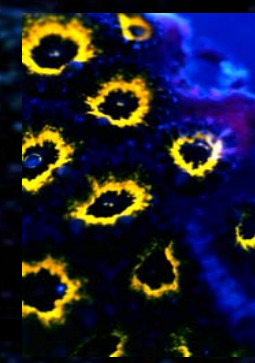


Fig. 3 Fluorescence in a *M. pharensis* colony at 60m induced with a regular commercial black light (Philips).

morphology) as well as intermediate ecological characteristics (depth distribution). The status of two species remains unclear: that between the genetic similar species *M. pharensis* and *M. decactis*.

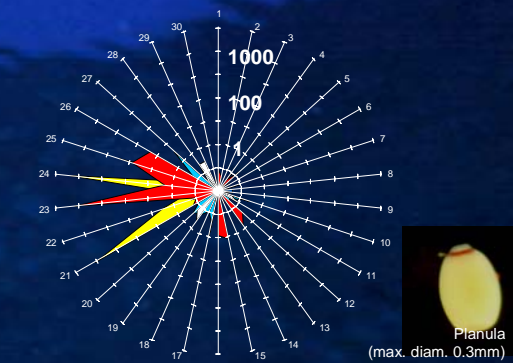


Fig. 4 The timing of larval release of *Madracis senaria* in relation to lunar day (numbers 0-30). The different colors in the graph correspond to different lunar cycles (blue, lunar cycle (LC) 937, [20-09-98/ 19/10/98]; yellow, LC 938, [20-10-98 -18-11-98]; white, LC 949, [09-09-99 - 08-10-99]; red, LC 950, [09-10-99 - 07-11-99]).

**Polymorphisms.** Encrusting colonies are (sigmoidally) increasing with the increasing availability of vertical surface. Three possible mechanisms are explored to describe this relation: a classical polyphenism, a switching polyphenism *sensu* Moran (1992) and a polymorphism. Maximum likelihood analysis indicates that the polymorphism model describes the observed relation best. We show that underlying genetic variation for colony morphology responds to habitat complexity at a small spatial scale (i.e. reef) and that populations become fixed for one morphotype if the habitat is dominated by either vertical (<33%) or horizontal surfaces (<30%).

### III. Conclusion

At present, *M. mirabilis* and *M. senaria* represent discrete evolutionary units to study coral ecology, morphology or genetics. Since they do not relate to other species, they are useless to describe speciation processes. The other four morphospecies show interspecific overlap in morphological, genetic and ecological characteristics. Therefore they provide a much better opportunity to study organizational processes in coral evolution. We found indications of two of such organizational processes in *Madracis*: introgressive hybridization and the controlled expression of genetic polymorphisms. More precisely, the *M. pharensis*/*M. decactis*-complex is a genetical polymorphism. Introgressive hybridization between *M. formosa* and the *M. pharensis*/*M. decactis* complex resulting in a new species: *Madracis carmabi*. The participation of *M. decactis* in both processes clearly illustrates the dynamic nature of coral evolution and the presence of **syngameons**. The evolutionary status of coral morphospecies can therefore not be determined *a priori* because of differences in their ecological and evolutionary dynamics.

### References

- Diekmann OE, Bak RPM, Stam WT and Olsen JL (2001) Molecular genetic evidence for reticulate speciation in the coral genus *Madracis* from a Caribbean fringing reef slope. *Mar Biol* 139:221-233
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