Evolutionary Ecology of the coral genus Madracis - an illustration of the nature of species in scleractinian corals
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Coral reefs are, with tropical rain forests, the most diverse and productive eco-systems in the world (Lieth and Whittaker, 1975, Wanders, 1976) (Ray 1988). The reef framework, build by crustose coralline algae and corals, provides a habitat to thousands of other reef organisms. Because of their dominant functional role in one of the most fascinating ecosystems, corals have been studied since the mid 19th century (Darwin, 1962). From the start of coral research, the morphological species concept established itself for practical reasons and until recently this species definition has been widely used in all fields of coral research. In recent research coral species now show to be highly variable taxonomic units displaying a remarkable variation in morphological, ecological and, recently, genetic characteristics.

During the last two decades the development in diving and genetics stimulated a new era of coral research. The increasing number of genetic studies on coral systematics is mainly responsible for revealing the incongruence between previously morphologically defined and "true" evolutionary species. The uncertain status of the morphologically based species concept in stony corals (Scleractinia) results from large intra-specific variation. Studying the evolutionary behavior of coral species therefore requires insight in the variation present within species and answers the question whether a species-concept is possible at all in stony corals.

Stony corals (Scleractinia) are key organisms on reefs (Bak and Luckhurst, 1980) and primarily responsible for the enormous biodiversity. Firstly, they are a diverse group per se and, secondly, they provide the physical structure that houses the multitudinous groups of other coral reef dwellers. The many forms of stony corals display a bewildering range of morphological variation that has overwhelmed scientists since the early days of coral reef research (e.g. Wood Jones, 1907). Since the realization that different genetic components were responsible for some of the morphological variation (Stephensen and Stephensen, 1933), the modern view evolved that the morphology of a coral colony is an expression of genetic characters in response to the environment (e.g. Yonge, 1968). Coral species were subsequently described with regard for variation induced along gradients of environmental variation (e.g. Roos, 1970, Wijsman Best, 1972), but a remarkable range of variation remained unexplained (Potts, 1978). This variation regards ecological characteristics such as inter- and intraspecific aggression (Bak and Criens, 1981) as well as unexplained significant morphological variation within one species in the same habitat (Van Duyl, 1985).
Although both morphological and genetic studies provide insight in the status quo of the evolutionary relations between species, the underlying explanatory mechanisms are seldom considered. Reproductive isolation, genetic polymorphism/phenisms, niche diversification due to disruptive selection, ecological preferences and fitness-differences all influence the evolutionary trajectory of both syngameons and their component species, but such factors have received relatively little attention.

Our coral research group has been studying the reefs of Curaçao and Bonaire (Netherlands Antilles) for the last three decades (e.g. Bak, 1973, 1974, 1975, 1977, Bak and Engel, 1979, Bak and Luckhurst, 1980, Bak, 1983, Van Veghel and Bak, 1993, Meesters and Bak, 1993, Bak and Nieuwland, 1995, Meesters et al. 1996, 1997, Van Veghel et al. 1996, Nagelkerken and Bak, 1998, Bak and Meesters 1998, Gast et al. 1999, Meesters et al. 2001, Diekmann et al. 2001). Confronted with the taxonomical problems outlined above, our group started the first research project to study the species-problem in corals on the coral Montastraea annularis (Ellis & Solander), a dominant Caribbean reef building coral in 1990. Morphological characteristics in conjunction with ecological life history traits and genetic components (Van Veghel, 1994) were studied in three morphotypes of this species. Again, large variation in morphological characteristics showed up but explanatory mechanisms were hard to find. The data showed differentiation between morphospecies (e.g. in aggression), but there was no hard evidence that the three morphospecies were separate species.

A new paradigm to study coral evolution was brought forward by Veron (1995) suggesting that reticulate evolution operates in scleractinian corals. It would replace human defined units of morphological similar assemblages indicative of common descent, by genetically intergrading entities harboring different degrees of morphological or ecological variation. Such entities are not discrete through time or space and form a reticulate network because genetic exchange occurs between entities. Variation (morphologically and ecologically) is often maintained within such entities and seldomly results in speciation (Veron, 2000). At a higher level one finds “syngameons”, collections of entities that exchange genetic information, that are reproductively isolated from other such collections. A syngameon is useless for taxonomic purposes and exist because their component species cannot maintain variation over large environmental gradients. The relations within a syngameon are represented by genetic, not morphological identification (Veron, 2000). Ocean currents maintain genetic variation within syngameons and are primarily responsible for speciation events (Veron, 1995). Reticulate evolution provides an interesting conceptual model to study coral ecology and evolution. Supportive evidence is gradually forthcoming but still

With the possibility of these new insights and genetic techniques, the Caribbean coral genus Madracis was the second genus that was investigated by our group, in an effort to increase insight in the status and organization of coral species complexes. Madracis occurs worldwide and at least five morphospecies occur in the Caribbean (Wells, 1973a,b). Two studies were started simultaneously to quantify morphological, genetic and ecological variation of the five species comprising the genus: Madracis decactis, M. formosa, M. mirabilis, M. pharensis and M. senaria. Genetics and morphometrics were investigated by Onno Diekmann at the University of Groningen, the ecological and morphological characteristics were investigated by the present author at the University of Amsterdam and the Netherlands Institute for Sea Research. The thesis lying in front of you is the result of this study.

The genus Madracis (Pocilloporidae)
The genus Madracis (Milne Edwards and Haime, 1849) comprises 8 species worldwide. M. asanoi (Yabe and Sugiyama, 1941) is only found in the northwest Pacific and M. kirbyi (Veron and Pichon, 1976) occurs from the Pacific to the Red Sea. All other species occur in the Caribbean Sea with some species extending to North Africa, Brazil and the East coast of Florida. One of the Caribbean species, M. asperula, (Milne Edwards and Haime, 1850) is a deepwater species (>200m, Vermeij pers. obs.) and therefore not further included in this thesis. All other species, M. pharensis (Heller, 1868), M. senaria (Wells, 1973b), M. formosa (Wells, 1973b), M. decactis (Lyman, 1859) and M. mirabilis (Duchassaing and Michelotti, 1861) are systematically separated based on morphological characteristics of both the corallite and colony (Wells, 1973a, b). Although Madracis is potentially one of the most abundant genera in the Caribbean (average density on Curaçao: 9.2 colonies m\(^{-2}\); chapter 3), ecological studies on the members of this genus are extremely scarce. Most studies focused on the branching species M. mirabilis. These studies investigated the role of fragmentation in their life history (Bak and Criens, 1981, Bruno, 1998, Nagelkerken et al. 2000) or its feeding behavior (Sebens et al. 1996, 1997, 1998). Fenner (1993) mentions the uncertain distinction between M. pharensis and M. decactis as different species based on morphological criteria and suggest that the two morphospecies should be regarded as ecotypes.

The study on the phylogenetics of Madracis by Diekmann et al (2001) is the first serious attempt to explore the status of the various Madracis species. The phylogenetics relationships of the five Caribbean Madracis species were studied at the intra-individual, inter-individual and inter-
specific level using the ITS1-5.8S-ITS2 region of the ribosomal DNA cistron. Genetic variation between species was small and of the same order as within species (approx. 5%). Only two species formed monophyletic groups: *M. senaria* and *M. mirabilis*. All other species are closely genetically related. No genetic difference is observed between *M. pharensis* and *M. decactis*. Diekmann et al. suggest that introgressive hybridization occurs between the *M. formosa* group and
the *M. decactis/M. pharensis* group. The latter hypothesis corresponds to observations (Vermeij, Diekmann, Bak) that another undescribed morphotype exists that combines characteristics of *M. decactis* (10 primary septa) and *M. formosa* (branching morphology). We have described this morphotype as a new species: *Madracis carmabi* (see: chapter 10, this thesis). The phylogenetic relationships between the various species are shown in figure 1 (modified after Diekmann et al. 2001).

Based on the same study, the divergence between the various species is estimated at 4.8-12 million years (Diekmann et al. 2001) which corresponds to the estimated fossil age. Both *M. decactis* and *M. mirabilis* are known from the Cretaceous (15-11Ma ago; Budd et al. 1994, 1995, Swedberg, 1994). All other species are not known from the fossil record except for one description of *M. pharensis* (1.5 Ma ago; Budd and Johnson, 1999). Because the morphological characters used for species discrimination overlap between species (Vermeij, Diekmann, Bak; pers. obs., Zlatarski and Estalella, 1982, Fenner, 1993), it remains unclear whether the absence of species in the fossil record is a taxonomic artifact or a valid indication that the undescribed species developed only recently (< 12 Ma).

**Thesis outline**

After a general introduction to scleractinian corals (*Chapter 2*), the genus *Madracis* is introduced. In spite of its abundance the coral genus *Madracis* has received no previous attention in comparative ecological studies. We therefore started with the distribution of the species on the reef. The size frequency distribution of all species was compared over a reef slope till a depth of 60m and related to abiotic factors (*Chapter 3*). Population structure and depth distribution proved to be highly species specific and variation between species was twice as large as variation related to environmental factors. In contrast to population structure, colony density depends on environmental structuring. Life-history strategies differ between species sharing identical colony morphology. At both ends of a species depth distribution (i.e. in marginal habitats) the size frequency distribution changed similarly in all species, because relatively large colonies dominated the population. Two new statistics are introduced (the Gini-coefficient and range standardization of size data) to analyze changes in coral size frequency distributions and characterize populations growing under marginal conditions. We show that ecological characterization based on population size structure is an additional tool besides morphological and genetical characterizations to describe differences between potential species in coral biology.
An integration of existing (Bak and Meesters, 1998, 1999, Meesters et al. 2001) and new statistics (from Chapter 3) to analyze size frequency distributions in corals revealed interesting relations in 19 Caribbean coral species (Chapter 4). The statistics that we used are applied after log transforming the original size data. Log transformation increases the number of size classes for small colonies. It makes size class representative of the number of growth steps leading to a certain colony size. This allows for a better comparison between species and greater insight in processes affecting colony size in the early stages of colony growth. Species with small colony size (e.g. Madracis species) show a relative low proportion of large colonies in a population compared to species whose colonies grow large (e.g. Montastraea species). We show that this range mirrors separation in reproductive strategies. Brooding species are characterized by small colony size and overdominance of small colonies in the population. Spawning species show the opposite pattern. Secondly, the variation in coral populations decreases with decreasing abundance. This indicates that population’s size frequency distributions become more uniform in marginal habitats. In general, populations growing in marginal habitats are characterized by a coefficient of variation (CV) higher than 0.5.

After addressing the nature of species specificity in population structure we wanted to explain the differences in depth distribution between the various species. Light has always been regarded as a major factor influencing the depth distribution and morphology of corals (Roos, 1967, van den Hoek et al. 1978, Titlyanov, 1981, Graus and Macintyre, 1982, Falkowski et al. 1984, Chalker et al. 1988, Nakamori, 1988, Graus and Macintyre, 1989, Haramaty, 1997, Kaandorp, 1999, Muko et al. 2000). The effect of light has often been assumed but seldomly studied. We related the light that colonies of all Madracis species receive to their distribution on the reef and to morphological characteristics (Chapter 5).

It was observed that species differ in their behavior towards and we observed three possible strategies: (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. Furthermore, we illustrate that the function of light variation as a temporal or positional cue decreases with depth and that changes in transparency (i.e. increasing $k$') mainly affect on the distribution of corals at greater depth.

The presence of species that deal with enormous amounts of light in shallow water vs. species that survive under extreme low amounts of light in deep water (133m; 0.26% surface light; see Chapter 5) suggests the presence of various adaptational processes. Fluorescent particles in coral tissue have been proposed to play a role in photoprotection and as a feature to assist zooxanthellae photosynthesis (Salih et al. 1998), but much is still unknown about the natural occurrence of fluorescence in corals. To determine possible functions of fluorescence we quantified fluorescence patterns in of all Madracis morphospecies and various colormorphs of $M. pharensis$ over a 60m depth gradient (Chapter 6). The number of colormorphs (in total 25 were discovered) decreased exponentially with depth. The decrease in colormorphs corresponds to decreasing available light and we suggest that colormorphs evolved as a photoprotective mechanism to change light of short wavelength (i.e. UV) to less damaging, longer wavelengths. At the same time, green fluorescence was observed in corals growing under low light conditions. The emitted green fluorescence corresponds to the excitation wavelength of zooxanthellate pigments. Green coral fluorescence results in extra light to increase photosynthesis of the endosymbiotic algae in low light environments.

Another aspect of the existing problems in the species distinction was the absence of objective methods to describe complex morphological growth forms. We applied X-ray computer tomography techniques, i.e. CT-scanning, to investigate morphological variation between and within species (Chapter 7). We explore the possibilities of three-dimensional analyses to increase the amount of information that can be obtained from a single structural object, using Madracis mirabilis as a model. Although problems still exist in reducing complex forms to simple wire-skeletons by using thinning algorithms, the methods presented provide a new powerful technique in analyzing the nature of morphological variation in corals.

The observation that genetic exchange takes place in Madracis (Diekmann et al. 2001) corresponds with the suggestion of Veron (1995) that reticulate evolution operates in corals. Species complexes are clusters consisting of component species that exchange genes to a variable degree through time and across space. To determine whether temporal reproductive isolation and species specific differences in reproductive behavior exist in Madracis we studied gametogenesis on a monthly basis.
and coral larvae (planulae) release on a daily basis (Chapter 9). We included all Madracis morphospecies in this 13 months study period. We found that 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 were similar between species and differences between species were only found for oocyte number and size. We found that life-history elements including reproductive characteristics showed trade-offs between the closely related species, e.g. for oocyte number and size. We propose the hypothesis 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 histological slides, we hypothesize that the term “brooding” does not apply for Madracis species and propose the term “quick-releasing” as its alternative. When compared with other Pocilloporidae, members within the same taxonomical level show large similarities in their reproductive behavior. The differences between taxa become smaller, but more variable towards the lowest taxonomical level, i.e. the species level. The final reproductive strategy of a species is therefore an integrated characteristic composed of elements typical for each taxonomical level the species nests in. The differences between our species are only found at the lowest taxonomic level and therefore very subtle.

After fertilization, colonies of all species released planulae from April to December. Spawning intensity fluctuated highly at a daily scale. In general, planulae release followed one month after gamete maturation. Because of the direct relation between water temperature and gamete maturation, planula release relates to seawater temperatures of the previous month. Species and even color morphs of the same species differ mainly in the number of planulae released per surface area. Additionally, Madracis senaria differs from all other species since it releases planulae according to a lunar cycle. Also, M. senaria releases large amounts of planulae (>1000) during the Caribbean mass spawning in October and November (Van Veghel, 1994, de Graaf et al. 1999), whereas all other species release planulae gradually and in a non organized pattern. We explain how the traditional division of reproductive strategies into “brooders” and “spawners” does not reflect reality of reproductive strategies on the reef and propose a subdivision for the brooding strategy: organized mass release or gradual release in low numbers without an organizational pattern. The latter strategy, characteristic for most Madracis species, is hypothesized to be evolutionary advantageous because (1) it reduces risk of predation, (2) allows the allocation of more
energy towards colony survival and (3) prevents the potential effect of catastrophic mortality.

It happened that during this study a group of planulae settled in a test tube that we used to catch them. In this group several planulae metamorphosed and started calcification. Other planulae transformed into polyps and moved freely over the substratum. We give a short overview of our observations on this undescribed behavior, which allows corals to explore their settlement location by active movement (Chapter 10).

In the course of our research we encountered a Madracis morphospecies that differs from all the original species descriptions (Wells, 1973a, b). At first, we regarded this morphotype a new Madracis decactis form. After closer inspection and consulting the genetical evidence (Diekmann et al. 2001) we found that this morph is likely to have arisen through (potentially recent) hybridization of M. decactis and M. formosa. We described it as a new species based on its unique combination of a branching morphology and corallites containing 10 septa. The species was named after the marine biological institute at Curaçao: Madracis carmabi (Chapter 11).

So far, the data accumulated defined 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 (Diekmann et al. 2001), who showed that both species are monophyletic. The relation of M. formosa with all other species is shortly discussed (Chapter 11) since ecological and genetical data (Diekmann et al. 2001) suggest that it shares genetic information with M. decactis through introgressive hybridization resulting in a new species. One relation remains at this point unclear: that between the genetic similar species M. pharensis and M. decactis. We therefore focused on possible underlying mechanisms that could maintain such a species complex (Chapter 12). We found a sigmoidal relation between the proportion of nodular colonies, M. decactis, in the species complex and the availability of horizontal substrate at 23 sites. The pattern for encrusting colonies, M. pharensis, is opposite. Encrusting colonies are 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 (Hillborn and Mangel, 1997) indicated that the polymorphism model described the observed relation best. We show that underlying genetic variation for colony morphology responds to habitat complexity and that populations can become fixed for one morphotype. This occurs when costs for maintaining tolerance to environmental variation (i.e. habitat heterogeneity) do not outweigh the negative costs from fitness reduction resulting from expressing the wrong morphotype.
We explain how high wave energy reef communities are overdominated by *M. decactis*, because such reefs are characterized by levels of habitat heterogeneity that are too low to maintain both morphotypes. We then show how the degree of separation within *M. pharensis*/*M. decactis* communities is determined by habitat complexity, even at the scale of islands (i.e. 10 km scale).

*M. pharensis* populations at many sites on Bonaire and Curaçao revealed a high degree of similarity in their size frequency structure. Since variation in size frequency structures is an important informative characteristic (see: Chapter 3 and 4), we quantified the relative influence of several spatio-temporal factors leading to size variation in coral populations (Chapter 13). The age of a population, i.e. the time that elapsed after the start of initial settlement, was the factor that contributed most to the size variation in coral populations. At the age of ≥5 years, *M. pharensis* populations obtain a specific size distribution which is similar over large spatial scales. Because of the constancy in its size distribution, we propose that the population composition of *M. pharensis* has the characteristics of a stable state, i.e. resilience or resistance to environmental heterogeneity combined with an identical size structure. This study is one of the first to argue for the presence of stable states at the population rather than at the community level.

As part of the previous study we investigated population development of *M. pharensis* populations that developed on artificial substrates during a period of three years (Chapter 14). The dynamics of these populations showed all aspects of a clonal life-history strategy: fusion, fission, partial mortality and rapid early growth. It is commonly assumed that whole colony mortality is the dominant structuring factor in juvenile coral populations. Our results show that other life-history elements contribute to population structure besides mortality, e.g. 13% of the colonies present on the settlement racks after 2 year (n= 74) resulted from colony fission.

Since we used the same methodology at the same site (Van Moorsel, 1989), we could compare settlement rates (recruits m$^{-2}$) for various species with the rates found by Van Moorsel in 1980. We found an extreme decrease in settlement rates of 13 scleractinian coral species (Chapter 14). Depending on species, settlement rates decreased between 1600 to >10000% between the periods 1979-1981 and 1999-2001. This decrease exceeds natural yearly variation in settlement rates, that differs by a factor 3 (Hughes et al. 1999, van Moorsel 1989). We propose two processes to cause the decrease: (1) algal overgrowth of suitable settlement positions and (2) reduced fecundity in the parental population due increased environmental stress. Reductions in the size of open populations due to natural events or human impacts would be readily reversible if a virtually inexhaustible supply of recruits exists. Our data
show that such influx of settling individuals has been greatly reduced over the last two decades. This highlights the influx of settlers as a crucial factor in the population dynamics of corals. It furthermore indicates that widely used indicators for coral reef health, especially the percentage of coral cover, do not reflect critical processes that determine population survival. Identification of these processes is essential to manage coral reef ecosystems effectively and understand the ecological response of coral populations in stressed environments.

CITED LITERATURE


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