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The ecology of *Millepora*

A review

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Abstract. Attention is drawn to the lack of quantitative ecological information on the calcareous hydrozoan *Millepora*. In spite of their abundance and geological importance on reefs, little attention has been paid to the millepores compared to the dominant corals. The literature on distribution and abundance on reefs is reviewed and attention is drawn to sources of bias in reported estimates of *Millepora* abundance. *Millepora* is shown to have many of the same parasites and predators as scleractinians. The sparse data on growth and production are reviewed and compared with that of corals. The physiological and ecological responses of *Millepora* to storms and other disturbances appear to be similar to those of the scleractinans but the millepores have escaped attack by the starfish *Acanthaster* and appear to be immune to the common diseases of corals. The morphological similarities and ecological differences between millepores and scleractinians are discussed in terms of life-history strategies.

Introduction

The calcareous hydrozoan *Millepora* is one of the most conspicuous of the skeleton-forming animals on coral reefs. Swimmers on reefs soon learn to recognize and avoid the "fire-coral" because it can inflict painful stings. Accounts of the distribution of hermatypic corals often include one or more of the species of *Millepora* which are nearly ubiquitous on reefs. Several species of millepores may be locally abundant (Goreau 1959; Loya and Slobodkin 1971; Fishelson 1973a; Sheppard 1982; Done 1983) and important framework builders, second only to the hermatypic corals (Stoddart 1971; Zankl and Schroeder 1972; Loya 1976; Adey 1977; Adey and Burke 1977; Dustan 1985). In spite of their abundance and geological importance, the less diverse, less spectacular and unpleasant millepores have received little direct attention compared to the pre-eminent corals. Most ecological accounts document the distribution of millepores incidentally in describing the zonation and abundance of reef corals (e.g. Manton and Stephenson 1935). A notable exception to this paucity of interest in *Millepora* was the work of H. Boschma who reviewed early research on the genus (Boschma 1948) and subsequently made a major contribution to the systematics of millepores (Boschma 1949a, 1950, 1951, 1961, 1962, 1966). However, there still remain unresolved taxonomic problems (de Weerdt 1981) which inhibit advances. The difficulty is that there are variable phenotypic forms of each species but no morphological characteristics of taxonomic value, other than growth forms of the coralla, have been recognized. The problem has recently been commented on by Stearn and Riding (1973) and by de Weerdt (1981, 1984).

The purpose of this review is to focus attention on *Millepora*, to gather the recent information on the ecology of *Millepora* from disparate sources, and to broaden interest and stimulate further study. It is not intended that the review should be a complete record of all references to millepores but rather that it should include those of comparative value over a wide geographical range and of quantitative ecological importance.

Distribution and abundance on reefs

The genus *Millepora* occurs worldwide throughout tropical seas as a regular component of coral reefs and millepores are found in depths of from less than 1 m to about 40 m. Early reports on the distribution of *Millepora* on reefs have been summarized by Boschma (1948). From most accounts, robust, bladed or platelike colonies are commonest on the surf-swept edge of reefs and on shoals and ledges where there is strong, turbulent water movement (Darwin 1842; Forbes 1885; Crossland 1927, 1928; Gardiner 1931; Sewell 1935, 1936; Abe 1937). Elsewhere on reefs, delicately branching, upright forms and thin, leafy colonies flourish in lagoons and sheltered deeper waters (Crossland 1928; Umbgrove 1928; Yonge 1930; Gardiner 1931; Scheer 1972). Simple encrustations of

Table 1. Distribution of *Millepora* spp. on coral reefs

Species locality	Growth form	Depth in m, reef zone	Water movement	References
M. complanata Lamarck. Caribbean, American seas	Vertical plates, blades	0.5–10. Surf zone, reef crest, seaward reef flat, inner spur and groove zone	Strong to heavy wave action, surf, turbulent water movement and swell	Adey (1975), Adey et al. (1977), Cairns (1982), Dustan and Halas (1987), Geister (1975), Goreau and Goreau (1973), Kuhlmann (1974), Mergner (1972), Morelock et al. (1977), Ramsaroop (1982), Raymont et al. (1976), Rützler and Macintyre (1982), Scatterday (1974, 1977), Squires (1958), Stearn and Riding (1973)
M. platyphylla Hemprich and Ehrenberg, Moorea, Red Sea, Madagascar, Mauritius, Seychelles Reunion	Blades, plates, fans, branches	0–10. Surf zone reef crest, spur and groove zone, seaward reef flat	Strong to heavy wave action, surf, turbulent water, swell	Barnes et al. (1971), Done (1982), Galzin and Pointier (1985), Harmelin-Vivien (1985), Loya and Slobodkin (1971), Maragos (1974a,b), Mergner (1971), Morton (1974), Odum and Odum (1955), Pichon (1971), Rosen (1971), Stoddart (1973), Taylor (1968)
M. dichotoma Forskal. Red Sea, Seychelles	Fans, branches, vertical plates with cross walls	0–5. Reefs crest, inner and outer crest below algal ridge	Turbulent swell and breaking waves	Loya and Slobodkin (1971), Mergner (1971, 1977), Stoddart (1973), Taylor (1968)
M. tenella Ortmann. Maldives, Johnston Atoll	Fan branches and plates	0–10. Reef crest, exposed ocean slopes	Medium to strong movement	Maragos and Jokiel (1986), Davies et al. (1971)
M. alcicornis Linnaeus. Caribbean, American seas	Bushy branches, encrusting, lacy flat plates	0–50. Forereef, lagoon patch reef, bank reef, surf zone, reef flat	Intense to light movement	Adey et al. (1977), Cairns (1982), Dunne and Brown (1979), Garrett et al. (1971), Goreau and Goreau (1973), Hoffmeister and Multer (1968), Mergner (1972), Newell et al. (1959), Ramsaroop (1982), Rützler and Macintyre (1982), Squires (1958)
M. exaesa Forskal. Aldabra, Seychelles	Robust branches or rounded masses	0–10. Reef front, reef flats	Turbulent to moderate water movement	Barnes et al. (1971), Mergner (1977), Rosen (1971)
M. squarrosa Lamarck. Caribbean, American seas	Thick plates united in box or honeycomb complex	0–10 (20). Reef crest, reef front, flat, deep water all zones	Turbulent, moderate to heavy wave action, currents in deep water	Dunne and Brown (1979), Kuhlmann (1974), Ott (1975), Roos (1971), Roberts (1972), Stearn and Riding (1973)
M. braziliensis Verrill. Brazil	Robust branches	1–5. Reef front	Moderate to heavy wave action	Laborel (1969a,b), Boschma (1961, 1962)
M. nitida Verrill. Brazil	Rounded clumps of short branches	0–5. Back reef	Moderate wave action	Laborel (1969a,b)

Millepora may occur at all depths and appear to be the first stages of every growth from (Crossland 1928) or cover the surface of dead corals (Scoffin et al. 1980; Shinn 1963; Shinn et al. 1981).

The general view that robust platy forms are found in turbulent water and delicate leafy and branched forms occur in quiet water is supported by contemporary reports (Davies and Montaggioni 1985). The distributions of the most common species are shown in Table 1. *Millepora complanata, M. dichotoma* and *M. platyphylla* are example of bladed or platy species with are found mainly on the reef crest and can withstand heavy wave and surf action. *M. exaesa* and *M. tenella* form robust branches or rounded lumps, and occur on both reef flats and in deeper water as well as on the reef crest, under a range of wave and water movement conditions. *M. alcicornis* forms bushy, lacelike or encrusting branches and has been recorded in the greatest range of depths and growth morphologies. This is due partly to the practice of including *M. complanata* and *M. squarrosa* as varieties of *M. alcicornis* (Adams 1968; Roberts 1971; Fenner 1988). It has also been mistakenly recorded outside the tropical Atlantic (Abe 1937, 1938).

Most attention in the literature has been given to platy species such as *Millepora complanata* because they are the most conspicuous and abundant forms. They are often oriented with their flat sides facing the direction of the prevailing waves or currents (Abe 1937; Mergner 1971; Stearn and Riding 1973; Bak 1975) and are reported to prefer strong light exposure (Storr 1964;

Table 2. Abundance of *Millepora* spp. on coral reefs (percentage of total reef surface)

Species	Depth (m)					Reference
	0–5	5–10	10–15	15–20	20–30	
M. alcicornis	<1 (4 transects, 0.5–12 m)					Goodwin et al. 1976)
M. alcicornis	<1–1.4					Dodge et al. (1982)
M. alcicornis		1–5				Rützler and Macintyre (1982)
M. alcicornis	<1	<1	<1	<1		Dustan and Halas (1987)
M. complanata	>10	1–10				Rützler and Macintyre (1982)
M. complanata	1–48 (mean = 12)					Dustan and Halas (1987)
M. complanata	21.7 (shallow reef), 0.3 (deep reef)					Fenner (1988)
M. dichotoma	10–36	4	<1	<1	<1	Loya and Slobodkin (1971)
M. dichotoma	16 (mean 12 transects over reef flats)					Loya (1976)
M. platyphylla		0–60 (mean = 4)				Maragos (1974b)
M. platyphylla	5 (mean of total reef)					Done (1982)
Millepora spp.	1–25	<1	<1	<1	<1	Bak (1977)
Millepora spp.	2–4 (from 1–6 m)					Stearn et al. (1977)
Millepora spp.	30 (channel walls at 25–30 m)					Veron (1978)
Millepora spp.	7–14 (shallow reef, 0–15 m)					Rogers et al. (1983)

Mergner 1971; Sheppard 1982). Bladed forms may develop into such dense growths that solid ledges, ridges and reef rims are formed (Glynn 1973; Scatterday 1977; Rützler and Macintyre 1982). These structures have been compared to the coralline algal ridges of the Pacific reef crests (Milliman 1973; Morelock et al. 1977) and are resistant to strong wave conditions (Adey and Burke 1977).

Although millepores are reported as abundant or even dominant on reefs, there are very few quantitative data on abundance. *Millepora* abundances expressed as percent cover of the whole reef surface, are shown in Table 2. *Millepora* spp may be abundant locally but, over a whole reef, generally cover less than 10% of the surface. *M. dichotoma* in the Red Sea and *M. complanata* in Florida are examples of species which are more abundant (up to 36% and 48% respectively) in shallow water between 0 and 5 m but cover less than 1% of the reef surface between 10 and 30 m. *M. alcicornis* in Florida and *M. platyphylla* in Australia are examples of species with low abundances (<1 and 5% respectively) over whole reefs.

Abundances of *Millepora* have also been expressed as relative percentages of coral cover on reefs. Liddell and Ohlhorst (1981) reported *M. alcicornis* in Jamaica comprised only 1%–2% of total coral cover. Salvat and Richard (1985) reported 1.6% to 17% of total coral cover at Takapoto Atoll in the Pacific was composed of *Millepora*. Relative percentages are less useful than absolute values for estimating millepore abundances unless total coral cover is known.

Percent cover of corals on reefs is usually calculated from a plan view, i.e. from the projected length of colonies underlying a transect line or measured within a unit quadrat (Loya 1978). Such measurements are biased towards flat surfaces and should not be applied to colonies of millepores with erect branches. Dahl (1973) recommended a correction factor of 5.6 X to be applied to plan view estimates of *Millepora* cover. Figure 1 shows the relation between plan view colony diameter and colony surface transect length of *M. complanata* on several reefs in Barbados, West Indies. Colony diameters were measured as projected lengths in plan view. Colony transect lengths include blade heights, measured with a flexible tape laid along the diameters. The equation of the regression line is $y = 6.88\ x - 28$ where y is the colony transect length and x is the plan view diameter (both in cm). The regression coefficient (6.88) is slightly greater than the correction factor determined by Dahl (1973). It is evident that measured blade heights are required for accurate estimates of surface cover and that previous mesurements of *Millepora* living surface cover on reefs may have been seriously underestimated.

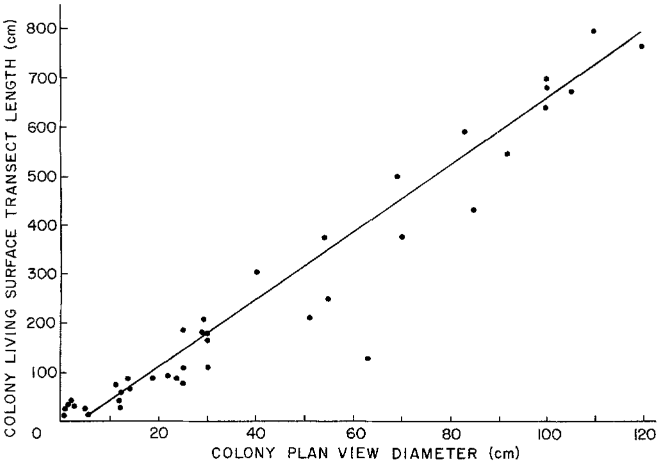

Fig. 1. Regression of living surface transect length on colony plan view of *Millepora complanata*. The positive slope indicates the correction necessary for estimating living surface cover abundance of *Millepora* on reefs (see text)

Parasites and predators

A number of parasites and predators of the Scleractinia also attack *Millepora*. The best known of these are barnacles of the subfamily Pyrgomatinae (Hiro 1938; Mergner 1971; Newmann et al. 1976) which at high densities may distort colony growth (Boschma 1948). The polychaete worm *Phylochaetopterus* sp. may have a similar effect (Crossland 1931). Brander et al. (1971) examined the fauna living on and in *Millepora platyphylla* at Aldabra. In addition to the commonly occurring barnacle *Pyrgoma* sp. there were 11 species of polychaetes, 7 crustaceans and 3 species of echinoderms. There was a strong commonality between the polychaete fauna of *M. platyphylla* and the corals *Pocillopora eydouxi* and *Stylophora mordax* but very little overlap in the crustacean fauna of corals and hydrozoans. Associations between the caridean shrimp genera *Thor* and *Hamodactyloides* and *Millepora* were reported by Bruce (1976) and Kropp (1987) reported burrowing by the snapping shrimp *Alpheus obesomanus* in *M. platyphylla* at Guam and Palau.

The polychaete *Hermodice carunculata* which feeds on a variety of corals (Marsden 1962; Glynn 1973) was also reported as a predator on *Millepora complanata* (Ott and Lewis 1972). *H. carunculata* caused permanent damage to colonies of *Millepora* by inhibiting hydrocoral growth and forming lesions which were rapidly colonized by algae (Witman 1988). A number of fish feeding on *Millepora* have been reported. The remains of *M. alcicornis* were found in the stomachs of two file fish. *Alutera scripta* and *Cantherines macrocerus* (Randall 1967). Glynn (1973) noted a pomancentrid fish feeding on *Millepora* and Stoddart (1969) suggested that a number of scarids damaged colony surfaces when seeking food associated with *Millepora*. The nudibranch *Phyllida bourgini* feeds on *Millepora* (Vincente 1966) and gastropods of the genus *Pedicularia* are reported as associates of Stylasterine hydrocorals (Hadfield 1976). Two species of brittle stars of the genus *Ophiocoma* have been noted in the folds of *Millepora* plates in the Red Sea (Clark 1976). There are several accounts of overgrowth of *Millepora* by algae (e.g. Witman 1988). *Millepora* is apparently avoided by the starfish *Acanthaster planci* (Endean 1973; Glynn 1963).

Growth and production

Millepores are slow growers with rates of reef accretion of 3–6 m/1000 years (Adey 1978). Witman (1988) reported branch tip vertical growth of *Millepora complanata* of 8.0 mm per year. Branch length increments of *M. complanata* were measured in Jamaica by Strömgren (1976) and at Curacao by de Weerdt (1981). Strömgren obtained mean values of 15 and 55 μm per day (0.45 and 1.65 mm per month) by a laser diffraction method from specimens held in aquaria. The growing edge area increments measured by de Weerdt from photographs of transplanted specimens, ranged between 3 and 13 mm^2 per month (recalculated as a mean length of 1.4 mm per month from original data). While the growth rates from these reports are comparable, growth of undisturbed colonies in the field might be expected to be somewhat higher.

Calcification rates were measured in two species (*Millepora alcicornis*, 480–696 μg Ca mg N d^{-1} and *M. complanata*, 960–1176 μg Ca mg N d^{-1}) by Goreau and Goreau (1959). Rates of calcification were of similar magnitude to the rates measured in branching corals at the same time but rates were highly variable from day to day and among colonies.

Measurements of production and respiration in *Millepora* are among the rates listed for a variety of reef corals by McCloskey et al. (1978). Because of the variety of units used the measurements of production by various authors are not comparable. However, in all species except *M. alcicornis* (Beyers 1966) P/R ratios are greater than unity. Rates of O_2 uptake and of production were similar in magnitude to coral rates measured at the same time. Thus for both growth and production, hydrozoan rates are similar to hermatypic coral measurements per unit living surface area, length or unit volume. Hoegh-Guldberg et al. (1987) observed that the mitotic index (growth rate) of algal symbionts of *M. dichotoma* from the Red Sea was similar to those of the symbionts of the coral *Stylophora pistillata* and other symbiotic cnidarians.

In addition to their autotrophic mode of nutrition (Goreau 1961, 1963) millepores are also voracious plankton feeders. Capture of live net zooplankton and *Artemia* sp. larvae was reported by Abe (1938) and de Kruijf (1975). Responses to chemical stimuli and feeding behaviour in *Millepora alcicornis* and *M. complanata* were found to be similar to those of other hydroids by de Kruijf (1975). Although Hyman (1940) was of the opinion that millepore polyps, like corals, were only expanded at night, Porter (1974) observed that zooids expanded at night as well as during the day.

Tissue biomass of *Millepora* per unit area of the reef was measured by Odum and Odum (1955) who reported less than 100 gm dry wt m^{-2} at Eniwetok Atoll. Values between 10 and 60 gm dry wt m^{-2} were reported by Frost (1977) from lagoons, reef flats and forereefs. Tissue biomass (animal tissue plus associated algae) of *Millepora* exceeded hermatypic coral biomass in a shallow reef flat zone where colonies abounded.

Storms and other disturbances

Within the considerable literature on the effects of disturbances (including pollution) on coral reef communities (reviews: Brown and Howard 1985; Pastorok and Bilyard 1985, Loya 1976; Loya and Rinkevotch 1980; Endean 1976; Tomascik and Sander 1987) there are frequent references to *Millepora*. The information is qualitative but by all accounts, physiological and ecological responses of *Millepora* are similar to those of the Scleractinia. For example in extreme disturbances such as hurricanes, Woodley et al. (1981) reported that in Jamaica, *Millepora* colonies were sheared off at the substratum and encrusting colonies on gorgonids were shattered and destroyed. In French Polynesia two cyclones in 1982 and 1983 devastated atoll reefs and partial destruction of colonies of *M. platyphylla* occurred down to about 20 m (Laboute 1985). On the other hand, Rogers et al. (1983) found no significant effect on the percent cover of *Millepora* by a severe storm in St. Thomas, U.S. Virgin Islands, whereas severe damage occurred at the same time to the coral *Acropora palmata* in St. Croix (Rogers et al. 1982). In Florida, physical disturbance and urban pollution are thought to have contributed to a decrease in mean colony size but increases in colony numbers of *Millepora alcicornis* and *M. complanata* over a period of eight years (Dustan 1985; Dustan and Halas 1987). Mah and Stearn (1986) found that although there was a marked decrease in other coral cover on Barbados reefs after a hurricane, there was no statistically significant difference between pre- and post-hurricane counts for *Millepora*. It appears that wave resistant morphologies of *M. complanata* and *M. squarrosa* are of selective advantage during severe storms (Mah and Stearn 1986). Recovery of damaged colonies may be rapid. Stoddart (1974) noted that extensive new growth of *Millepora* formed in the 2 year post-hurricane period on Belize reefs and that platy forms of *Millepora* were more resilient and better resisted storm damage (Stoddart 1985).

While *Millepora complanata* is reported to be able to withstand exposure to air for several hours (Glynn 1973; Scatterday 1977), low tides and high temperatures may cause bleaching and discoloration in other species (Jaap 1979). Coffroth et al. (1984) reported bleaching and loss of zooxanthellae is a number of species of corals and *Millepora* over several months in Panama. Recovery occurrend in most species, but was most rapid and the condition was of shortest duration in *M. alcicornis*. Bleaching was likely due to unusually high temperature. Rogers (1979) observed expulsion of zooxanthellae in *M. alcicornis* which was kept shaded for 4 weeks. After a catastrophic low tide in the Red Sea, Loya (1976) found that both the number of colonies of *M. dichotoma* and *M. platyphylla* and the size of colonies, decreased drastically. Killed colonies of *M. dichotoma* were able to regenerate quickly and overgrew exposed skeletons of hermatypic corals (Fishelson 1973a). Tilmant and Schami (1981) found that *Millepora* was highly susceptible to damage caused by recreational activities in a marine park in Florida.

Although there is very little precise information, *Millepora* appears to be as adversely affected by diverse forms of pollution as are the Scleractinia. Tomascik and Sander (1987) found that relative percent cover of *M. complanata* and *M. squarrosa* were generally lower on highly eutrophied than on less eutrophied reefs. *M. dichotoma* was less affected by chronic oil pollution than were sclerctinian corals in the Red Sea (Fishelson 1973b). Neff and Anderson (1981) found that effects of crude oil on calcium uptake was the same for *Millepora* as for hermatypic corals. With regard to biological disturbances, Endean (1973) reported that stands of *Millepora* were in the main avoided by the predatory starfish *Acanthaster planci* and increased in cover within 2–3 years of the starfish devastation, presumably in the absence of other space competitors.

Discussion

The corallum morphology of most species of *Millepora* appears to be extraordinarily plastic and highly variable phenotypic forms of each species can be found over a wide range of depths and conditions (Yonge 1963). The extreme view of Hickson (1898) that all described species *Millepora* were various growth forms of *M. alcicornis* was rejected by Boschma (1948) who emphasized that each species has typical growth forms that may be modified by local conditions but reflects the colony position on the reef. Boschma concluded that each species can make adjustments to suboptimal conditions, resulting in a limited change of form of the colony. He recognized 13 species of *Millepora* worldwide on the basis of growth forms (Boschma 1962). De Weerdt (1981) demonstrated that transplantation to different dephts caused conspicuous changes in growth forms of three species of *Millepora* during a period of six months. Longer term experiments are needed to determine the permanent results of environmental changes on coralla forms.

There are numerous morphological and ecological similarities between the millepores and hermatypic reef corals. The similarities suggest convergent evolution, although many of the morphological characteristics of *Millepora* are those of the hydrozoan class as a whole. However, the ability to secrete a calcareous skeleton, which distinguishes *Millepora* from other hydrozoans, provided new structural possibilities for colonial development (Verwoort 1966) and novel ecological opportunities. The chief morphological similarities are the calcareous skeletons, phenotypic variability of coralla and presence of symbiotic zooxanthellae. Ecological similarities include nutritional modes, plankton feeding strategies, competition for space and susceptibility to attack by parasites and commensals.

The small number of species of the genus *Millepora* is notable, in comparison with the scleractinian corals. Both groups have achieved worldwide distribution in the tropics and were well established in the Late Cretaceous (Boschma 1956). Although there has been no recent comprehensive taxonomic revision of the millepores, Boschma (1956) recorded less than 15 recent species in the genus *Millepora* and only a few valid fossil species of millepores. In contrast, the common coral genera *Acropora* and *Porites* contain more than 250 and 50 species respectively. The allied stylasterinids, with at least 7 genera, are also species diverse. If we assume the same environmental constraints which led to morphological convergence, then the poverty of hydrozoan species suggests that there are response differences to the ecological processes (recruitment, growth, mortality, competition, succession and life history strategies) affecting, the two groups.

One of the reasons for the small number of species of millepores may lie in their reproductive strategies. As far as is known, *Millepora* spp are infrequent breeders and are dioecious (Boschma 1948, 1956). Short-lived medusae bearing gametes are shed into the water (Hickson 1891). Corals, on the other hand, have a wide range of strategies with potential for heavy recruitment under a variety of conditions. However, the reproductive biology of *Millepora* has not been actively investigated for nearly 90 years and alternative strategies such as fragmentation may exist.

There is very little information on growth, recruitment or mortality of millepores, comparable to that for corals. Millepores show some competitive advantage over corals under disturbance conditions (Wahle 1980; Muller et al. 1983) but are just as susceptible to fouling and overgrowth by anthozoans and algae. Recruitment rate appears to be low as juveniles of *Millepora* accounted for only a small proportion (1.5%–3.4%) of all corals recruiting on reefs in Curacao and Bonaire (Bak and Engels 1979). The apparent immunity of *Millepora* to predation by *Acanthaster* (Endean 1973), and to coral diseases (Antonius 1981) and the relative tolerance to severe physical disturbance suggests that millepores could become more prominent on reefs if corals were to decline. Loya (1976) regarded millepores in the Red Sea as strong colonizing species, able to monopolize disturbed habitats.

There is very little information on life-history strategies of *Millepora*. Within a range of responses to r- and K-selection predicted for clonal organisms (Sackville Hamilton et al. 1987) from r-selected, weedy, opportunistic species to K-selected stress-tolerant species, the sparse data for millepores appear to correlate conservative reproductive effort with medium size. Hughes (1983) noted the same combination of attributes in massive corals such as *Goniastrea spp*. However, *Millepora* flourishes in disturbed habitats which are also colonized by small, fast growing corals with a large investment in reproduction. Furthermore, reproduction by fragmentation is more likely in less heavily skeletonized millepores than in the massive corals. Millepore do not fit neatly into either selection category and the need for further information on growth and reproductive schedules is evident, if millepores are to be effectively compared with scleractinians. The comparison of life-history strategies in two such different taxa with convergent morphological properties may provide insights into the relative adaptive values of these strategies as was suggested for coralline algae by Steneck (1986).

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