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Chapter

Ecology, Biology and Genetics of *Millepora* Hydrocorals on Coral Reefs

Caroline E. Dubé, Chloé A.F. Bourmaud, Alexandre Mercière, Serge Planes and Emilie Boissin

Abstract

Coral reefs are one of the most productive and diverse ecosystems on Earth. However, climate warming is occurring at an unprecedented rate and has negatively affected coral reefs worldwide. Evaluating the life history of reef-building species carries important implications for coral reef conservation. This chapter examines the taxonomy, biogeography, ecology, symbiosis, morphology and reproductive biology of *Millepora* hydrocorals, an important but relatively unstudied component of coral reefs. An emphasis is also placed on the influence of variable reef environments on *Millepora* life history traits, providing a fascinating opportunity to study the interplay between ecology and evolution. Special attention is given to ecological and evolutionary benefits of asexual versus sexual reproduction in the maintenance of genetic and phenotypic diversity. Lastly, this chapter discusses whether life-history strategies of *Millepora* hydrocorals and tolerance to different stressors can influence their ability to adapt and survive to future climate change, and other natural and anthropogenic disturbances.

Keywords: *Millepora*, coral reefs, taxonomy, biogeography, symbiosis, morphology, reproduction, population genetics

1. Introduction

1.1 Coral reefs: biodiversity and threats

Coral reefs were formed only 230 million years ago and are largely limited to warm shallow waters [1], yet they are among the most biologically diverse and economically important marine ecosystems. Coral reefs do not only shelter thousands of species; they also provide critical services to humans, including fisheries, coastal protection, medicines and tourism activities [2–4]. The economic value of coral reefs worldwide has been estimated to be around 30 billion US$ of net benefit per year [5]. Often called the rainforest of the sea due to their outstanding biodiversity, coral reefs only cover less than 0.1% of the ocean seafloor [6, 7] or approximately 5% that of rainforest areas [8]. Coral reefs thrive under nutrient-poor and oligotrophic waters [9–11], but yet harbour more than 25% of all known marine species [12, 13]. This ecosystem is sustained through efficient nutrient recycling strategies developed by corals [14] and algae [15], the primary reef producers, and

other key organisms, i.e., microbes [16] and sponges [17]. In coral reef ecosystems, many calcifying benthic organisms contribute to reef accretion and build the complex and massive three-dimensional structure of reefs, including scleractinian corals, the major habitat architects, and hydrocorals [18]. These reef-builders are key components of coral reef health and biodiversity as they offer food, shelter and nurseries for thousands of reef-dwelling organisms and fishes [19].

Reefs are dynamic systems that are frequently punctuated by perturbations [20]. For instance, human activities can alter both global (climate change associated with CO_2 emissions) and local reef health (e.g. coastal habitat loss, pollution, sewage, overfishing and invasive species) [21, 22]. As a consequence, several reports of coral reef declines have been recorded, averaging 30–50% reductions in reef cover globally [4, 23, 24], including recent losses of coral cover following the multiple global bleaching events that occurred between 2014 and 2017 [25–27]. Since coral reefs are integrated ecosystems, declines in reef-building corals are often accompanied with declines of other species, such as many coral reef fishes [28], further hampering their capacity to deliver important ecosystem services to more than 500 million people [23, 29]. Yet, reef corals and the ecosystem they create can recover and a key factor underpinning such recovery is the ability of coral species to grow back, to maintain or renew their populations. Such an ability to respond to acute and chronic stressors in coral species is often linked to morphological traits, reproductive strategies and symbiont partners (among others). As we progress further into the Anthropocene, understanding and predicting these stress responses require prior knowledge on the life history traits of keystone reef corals, and some assessment of the influence that environmental changes may have on those traits.

1.2 *Millepora* hydrocorals

To date, the vast majority of studies on species' life history traits in coral reefs have mainly focused on scleractinian corals due to their key role in providing much of the habitat framework and structural complexity of reefs [30–34]. The extent to which other non-scleractinian reef-building organisms might rescue reef populations in response to environmental change is largely unknown. More information on such organisms is therefore needed. *Millepora* hydrocorals, known as fire corals because of their painful sting via toxic nematocysts [35, 36], are important components of reef communities where they, similar to scleractinian corals, contribute to reef accretion and community dynamics [37, 38]. *Millepora* species are Hydrozoans (Medusozoans), and together with hermatypic corals (Anthozoans), belong to the phylum Cnidaria [39]. *Millepora* spp. are members of the monogeneric family Milleporidae, the sub-order Capitata and the order Anthomedusae [40–42]. Milleporidae and Stylasteridae are the only two Hydrozoan families producing skeletons of calcium carbonate. The first scientific report of *Millepora* spp. was from Linnaeus in 1758 [43], with subsequent species reports and descriptions by several authors (e.g. [44, 45]), and the seminal work of Boschma [46, 47]. There has been a surge of interest in fire corals over the last two decades (**Figure 1**), and especially in the last 7 years. These recent studies focused on genetics and coincided with the development of new molecular markers [48–50]. While there is much known now about fire corals (reviewed in [51]), the literature is scattered, particularly that of biogeography and population genetic research, and needs to be summarized. In this chapter, we will document what is known about taxonomy, biogeography, ecology, symbiosis, morphology and reproductive biology of *Millepora* hydrocorals, using both published and unpublished information, and will highlight areas where knowledge is especially lacking.
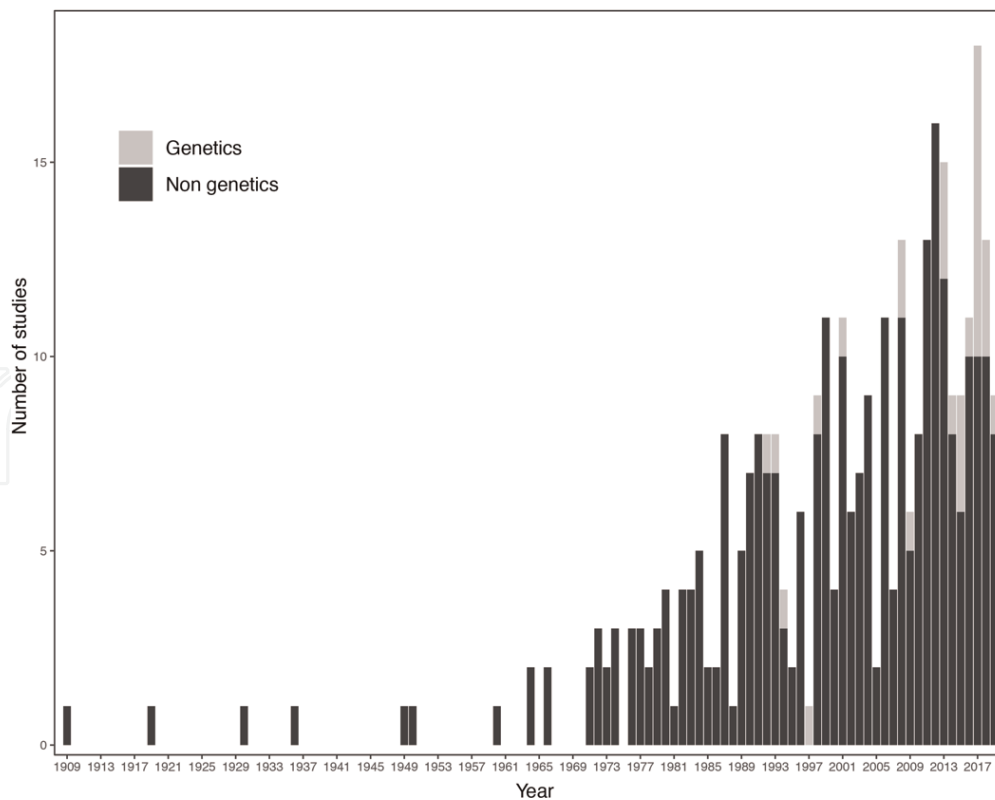
Figure 1.
The literature search in web of science identified 326 publications referring to Millepora *hydrocorals, wherein only 29 were using genetic approaches.*

2. Biodiversity and biogeography

2.1 Fossil records

Hydrocorals have a relatively long evolutionary history since many fossils from Tertiary deposits have been assigned to *Millepora*. However, Boschma [52] recognized only two species, *Millepora tornquisti* from Eocene rocks (56–33 mA) of Madagascar and *M. alcicornis* in Pleistocene deposits (2.58 mA–11,700 ya) from the Panama Canal zone [53]. Other branching milleporids were also reported from the Upper Cretaceous (100–66 mA) in northern Spain [54]. Recently, fossils of *M. alcicornis* have been recorded in deposits from the Early Miocene (~23 mA) [55]. *M. exaesa* fossils were also recorded in more recent deposits in the Seychelles, dating from the last interglacial sea-level high-stand, ~129,000–116,000 ya [56].

2.2 Species delimitation

As in many corals, the morphological species concept was traditionally applied to the species delimitation of *Millepora*, which is based on colony growth forms. *Millepora* species have a great diversity of growth forms and can be encrusting, branching, plate-like, massive or even columnar (**Figure 2**). Interestingly, the typical growth forms of *Millepora* species are broadly the same in the Red Sea and the Indo-Pacific. Arrigoni and colleagues [57] hypothesized a morphological convergence for these species. Similarly, in the Atlantic, there is also one plate-like and one branching species, as well as other massive/encrusting forms. As these growth forms do not form monophyletic groups on the phylogenetic reconstructions [57],
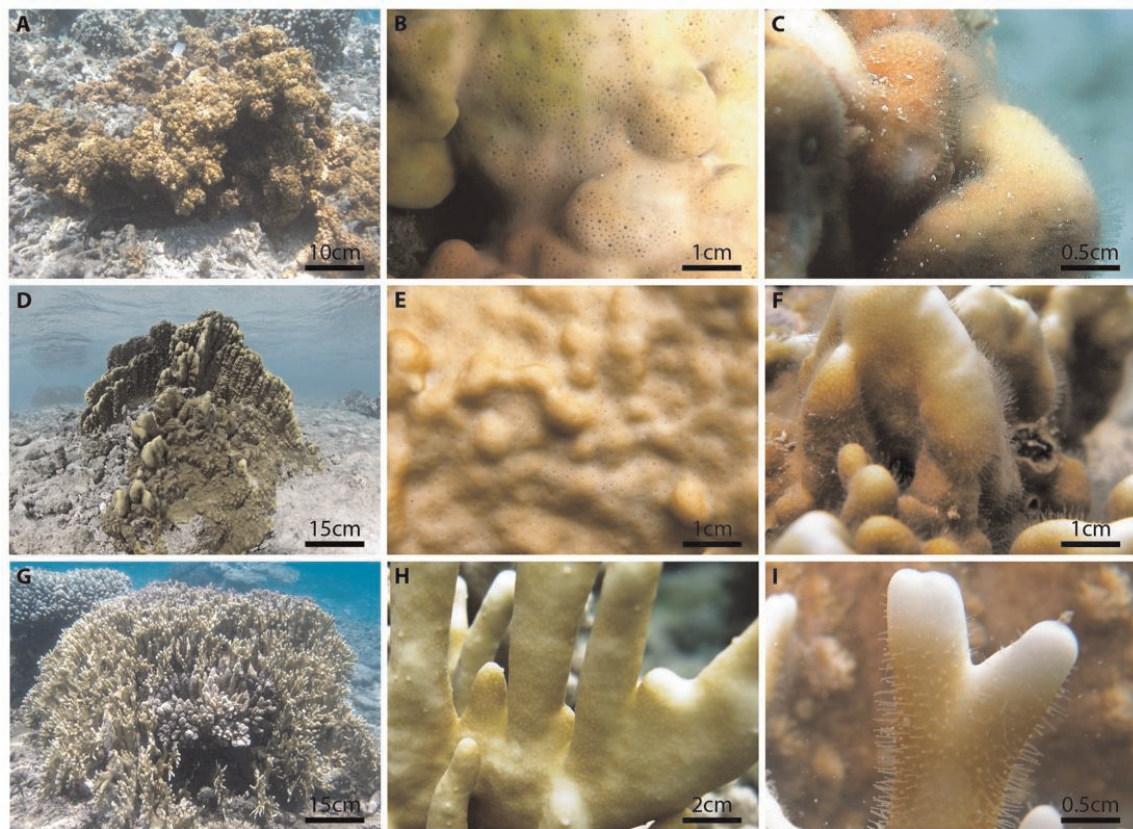
Figure 2.
Growth forms, pores and polyps of three Millepora *species. (A–C) M. cf. exaesa encrusting growth form, pores and polyps, respectively; (D–F) for the massive M. cf.* platyphylla *and (G–I) for the branching M. cf. tenera. D photograph is courtesy of Gilles Siu.*

they seem to have appeared independently and likely evolved in relation to the hydrodynamic conditions of their environment.

This group is also known for its great phenotypic plasticity [46], and environmental factors are known to greatly influence the morphology of *Millepora* colonies. Recently, Dubé and colleagues [58] demonstrated phenotypic plasticity among clonal colonies distributed in habitats with different hydrodynamic characteristics (see Section 4). To further complicate the matter, fire corals have been shown to overgrow stony corals, hydrocorals and gorgonians, which gives them additional peculiar growth forms (**Figure 3**) [59, 60]. Consequently, about 100 nominal species were described [61]. While Duchassaing and Michelotti [44, 62] identified 24 *Millepora* species based on trivial morphological differences, Hickson [45, 63] reckoned that there was only one *Millepora* species, *M. alcicornis*, and that all other morphological growth forms were only ecological variations. There is a true 'species boundary problem' within *Millepora* and it has been subject to much debate for over 150 years [45–47, 64, 65].

Apart from colony growth forms, pore traits are the most widely used characters in *Millepora* species delimitation. The pores in *Millepora* are like the corallites for the scleractinian corals, accommodating the polyps. There are two types of polyps in *Millepora* species: feeding polyps (gastrozoids) which are provided with a gastrovascular cavity opening by a mouth, and defensive polyps (dactylozoids) without a mouth. The gastropores and the dactylopores, from which the gastrozoids and the dactylozoids are able to extend outside to catch food, are organized in cyclosystems formed by a circle of dactylopores surrounding a single gastropore (**Figure 2**). While Boschma [46] concluded that the colony growth form was the most important character for the distinction of species, and that the other characters were not sufficient delimiting criteria, subsequent studies have used pore
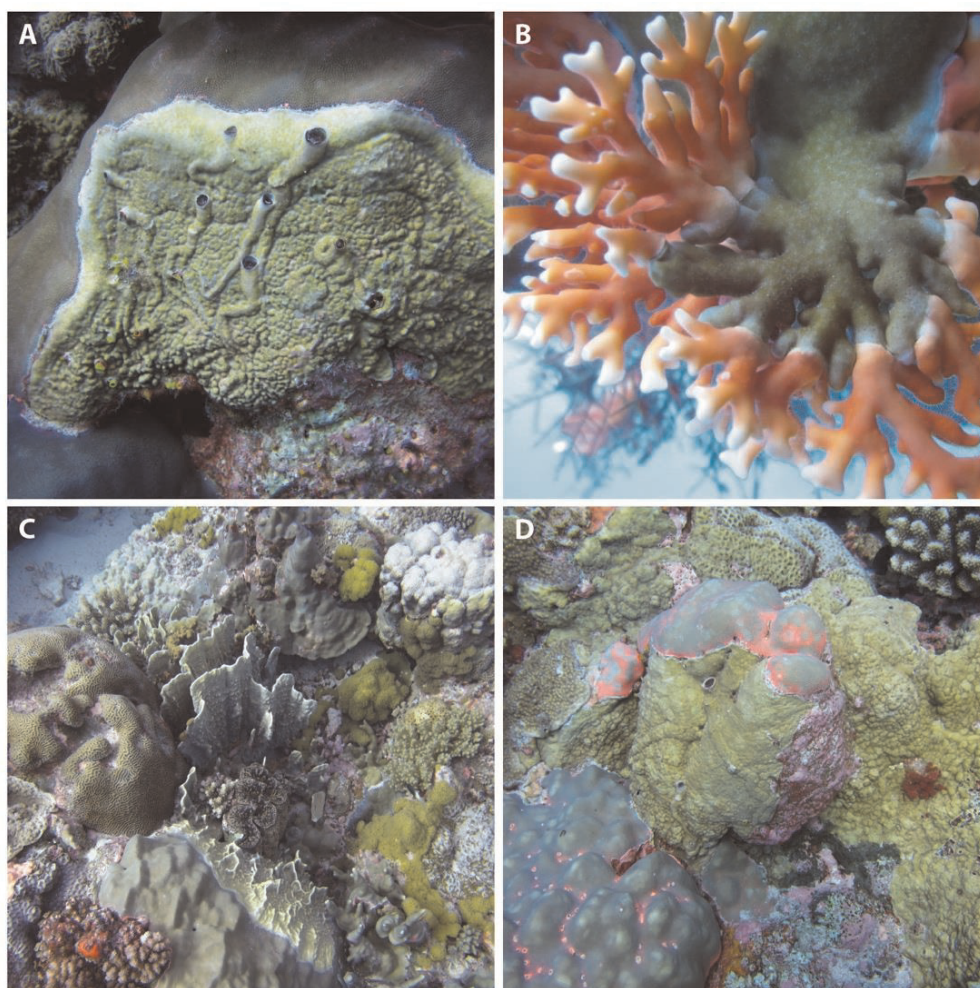
Figure 3.
Millepora *hydrocorals overgrowing living reef corals at Europa Island (Indian Ocean), including massive Porites (A, C and D), Distichopora sp. (B) and Astrea sp. (D). M. cf.* platyphylla *can overgrow giant clam shells (C).*

characters. Using a more elaborate quantitative approach on pore characters, Moschenko [66] considered 11 traits (e.g. numbers and diameters of gastropores and dactylopores, distances between dactylopores and gastropores, number of dactylopores per gastropore) in one plate-like (*M. platyphylla* Hemprich and Ehrenberg 1834) and five branching *Millepora* species (*M. cruzi* Nemenzo 1975, *M. dichotoma* Forskal 1775, *M. intricata* Milne Edwards 1860, *M. murrayi* Quelch 1884 and *M. tenera* Boschma 1949). His results distinguished only *M. platyphylla*, while all branching species shared important overlap in trait values with gradual transition from one species to another [66]. However, *M. cruzi* and *M. murrayi* have been subsequently synonymized (with *M. tenera* and *M. intricata*, respectively) and this could explain some of the trait overlaps between species. More recently, Razak and Hoeksema [65], based on colony growth forms and pore characters, revised the Indonesian *Millepora* species and synonymized 6 of the 13 recognized Indo-Pacific species. In particular, the gastropore and dactylopore diameters were shown to be discriminant among many *Millepora* species [57, 67, 68]. Boissin and colleagues (submitted) analyzed 13 pore characters and could distinguish the three species present in Reunion Island. This latest study showed that gastropore and dactylopore numbers, as well as diameters, were informative and should be used as standard traits in future *Millepora* studies. This study also showed that polyp features were discriminant, such as the presence or absence of capitate tentacles or capitations, and the presence, absence or abundance of Symbiodiniaceae. Additional biological traits seem to be helpful to delineate milleporid species, such as reproductive periods, medusoid features and nematocyst morphology [36, 57, 69, 70].

The advent of DNA barcoding greatly helped delimiting species of many marine invertebrates [71–74]. Consequently, the more recent works on *Millepora* spp. used a combination of morpho and molecular characterization. Mitochondrial sequence data were successfully used to delineate milleporid species from the Caribbean, revealing two genetic entities: *M. squarrosa* Lamarck 1816 and a species complex composed of *M. alcicornis* Linnaeus 1758–*M. complanata* Lamarck 1816 [67]. Similarly, the four *Millepora* species from the Brazilian province were discriminated using the 16S mitochondrial gene coupled with morphological characters [68]. Recently, a study on milleporids from the Red Sea successfully distinguished three species *M. platyphylla*, *M. dichotoma* and *M. exaesa* Forskal 1775, using both morphological and molecular characterization [57]. Similarly, Boissin and colleagues (submitted) successfully used 16S sequences to delineate the three *Millepora* species from Reunion Island.

2.3 Biogeography

Fire corals are found in tropical/subtropical regions around the globe, nearly ubiquitous on reefs in the Atlantic, Indian and Pacific Oceans (**Figure 4**). Currently, 10 species are considered valid in the Indo-Pacific and 6 in the Atlantic Ocean [57, 61, 65, 68, 75]. The species status of two other Indo-Pacific species, *M. nodulosa* Nemenzo 1984 and *M. latifolia* Boschma 1948, are still unclear [65]. Several Indo-Pacific species show an extensive geographic distribution from west of the Indian Ocean to west (*M. dichotoma*, *M. tenera*), centre (*M. platyphylla*) or east of the Pacific Ocean (*M. exaesa, M. intricata*), while *M. foveolata* Crossland 1952 and *M. boschmai* de Weerdt and Glynn 1991 have restricted distributions (Philippines and Indonesia, respectively, **Figure 4**). In the Atlantic, two species are endemic to the Caribbean province (*M. complanata*, *M. squarrosa*) and three species are endemic to the Brazilian province (*M. braziliensis* Verrill 1868, *M. nitida* Verrill 1868, *M. laboreli* Amaral 2008), while *M. alcicornis* is present in both provinces as well as in the Canary Islands, Cape Verde and Ascension Island (**Figure 4**) [46, 76].

However, with recent morpho-molecular re-evaluations of species boundaries in this group, our understanding of the biogeographic patterns is still evolving. The recent highlight of cryptic species between the Red Sea and the rest of the Indo-Pacific provinces [57] pointed out that *M. platyphylla*, *M. dichotoma* and *M. exaesa* in the Indo-Pacific need taxonomic re-description. The number of Indo-Pacific species was thus raised from 7 to 10 in the last few months. This number is likely to grow in future years, as *M.* cf. *exaesa* for instance includes several lineages over its Indo-Pacific range and likely represents another case of species complex (Boissin et al., unpublished).

Additionally, the range of *M. platyphylla* (now *M.* cf. *platyphylla*) was recently extended back to the eastern Pacific [77] from where it was documented as extirpated decades ago [78]. In the Atlantic, *M. alcicornis* has recently established in the Canary Islands (Macaronesia), far north of its tropical distribution [79], possibly by means of drifting material from the Caribbean Sea or transportation through ballast waters of large vessels and fouling of hulls [79–81]. Long-distance dispersals in milleporids have also been demonstrated in the Pacific, with *Millepora* colonies recorded on drifting pumice [80]. This alternative mode of dispersal can explain such a wide geographic distribution for a species with a short pelagic stage (see Section 5.3). However, as noticed by Lewis [51], it is surely remarkable that a family of worldwide distribution, with a long geological history and apparent ecological success, is represented by less than 20 species.
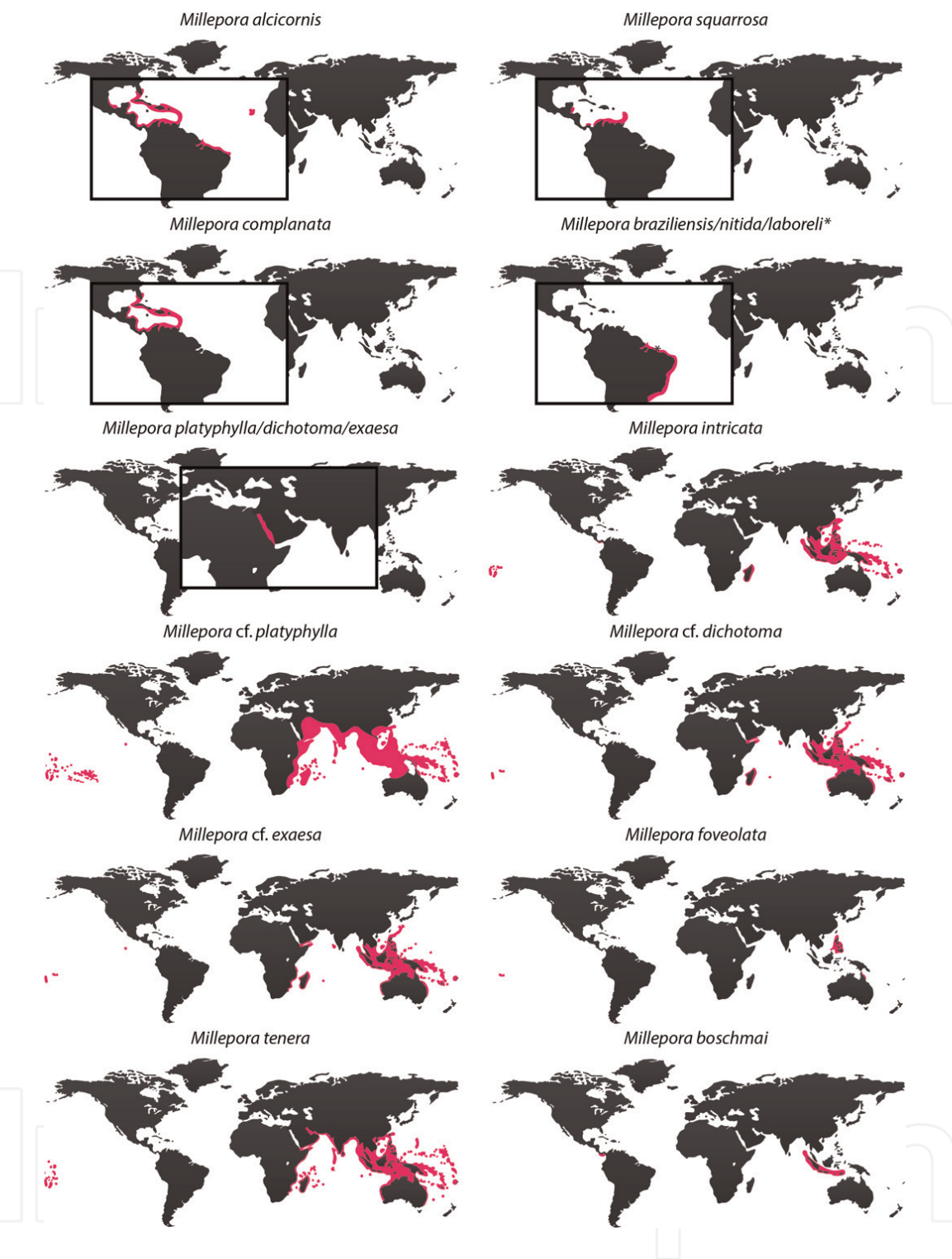
Figure 4.
Geographic distribution of the 16 recognized species of Millepora *in the Atlantic and Indo-Pacific Oceans.*

3. Ecology and symbiosis

3.1 Distribution, abundance and ecological roles

Fire corals occur worldwide in tropical seas and are limited in distribution from the intertidal zone to depths of approximately 50 m [51, 82, 83]. Although fire corals can be abundant locally [84–86] and dominate shallow water communities in some coral reef ecosystems [87–90], they usually cover less than 10% of the overall reef

substratum [51, 91]. *Millepora* spp. are also found in many environments and waves, water movement, light intensity and habitat depth were identified as key factors influencing their distribution and growth forms [51, 82, 91–93]. On barrier reefs, the amount of wave energy is highest on the reef crest, where wave breaking first occurs and subsequently attenuates towards fore reef and lagoonal environments (**Figure 5**) [94, 95]. This gradient in wave energy, combined with *Millepora*'s sensitivity to wave-induced breakage, were showed to strongly influence colony and size distributions of *M.* cf. *platyphylla* at Moorea (French Polynesia), with highest densities recorded on the fore reef and larger colonies on nearshore reefs [91]. *M.* cf. *platyphylla* colonies occurred in a contagious pattern of distribution (i.e. colonies close to one another), as described for other Caribbean species [96], and colony breakage and subsequent fragment re-attachment were suggested as explanations for such colony aggregations [58]. Three *Millepora* species were also identified on the reefs of Reunion Island [97], where each species is distributed according to their proximity with the shore and reef crest, mostly related to the wave energy dispersal. *M.* cf. *exaes*a is the first species encountered close to shore on the shallow reef flat (2 m depth), replaced by *M. tenera* when approaching the reef crest, and *M.* cf. *platyphylla* colonies live from the crest to 35 m depth on the outer slope.

Millepores are important reef framework builders, second only after scleractinian hard corals [51, 82]. Their complex structure is a habitat for other species adapted to stinging cells, including scavenger crustaceans (e.g. crabs, shrimps and barnacles, [51, 98–100]), as well as fish [38, 101–103], serpulids [104, 105], spionid polychaetes [51] and scleractinian corals [106]. Interestingly, high fire coral cover on Caribbean reefs was associated with increased fish richness species [86]. Many studies have described hydrocorals as opportunistic species that show rapid growth rates with high fecundity [51] and the ability for clonal propagation through fragmentation [58]. Fire corals are capable of colonizing both natural and artificial substrates, including dead gorgonians, rocks and ships [107, 108], as well as living seagrass stems, hydrocorals, gorgonians, scleractinian corals and other reef invertebrates (e.g. giant clams) through pursuit, contact and overgrowth
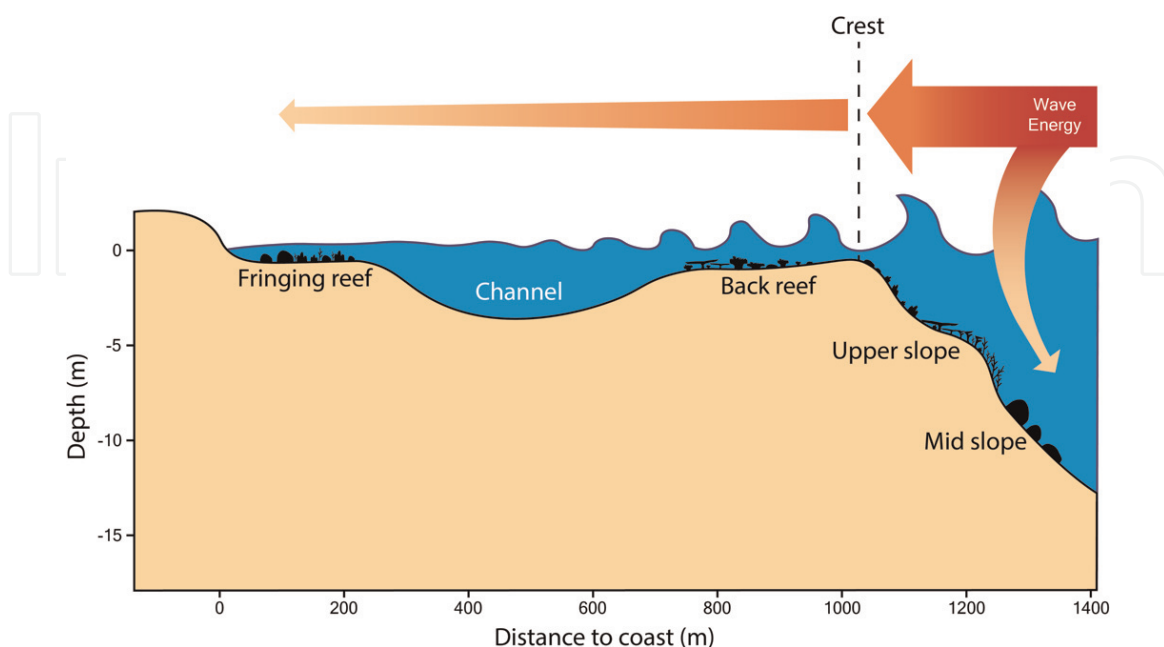

Figure 5.
Wave energy dispersal on a barrier reef (modified from [94, 95]). The fore reef experiences strong wave action from incoming waves that break on the reef crest, near the upper slope, with a significant decrease in swell exposure towards deeper waters. The reef crest dissipates ~70% of the incident swell wave energy with gradual wave attenuation from the back reef to nearshore fringing reefs.

(**Figure 3**) [59, 60]. This ability to inhabit different substrates and its rapid colonization rates [79] provide a competitive advantage for potential habitat expansions. Although fire corals compete with other corals, they also contribute to coral survival during *Acanthaster* outbreaks [106], highlighting their key ecological role in reef resilience. In fact, the corallivorous predator *Acanthaster planci* tends to avoid *Millepora* species [109], thus providing predator-free sanctuaries to nearby scleractinian corals.

3.2 Endosymbiosis with photosynthetic dinoflagellates (Symbiodiniaceae)

Many members of the phylum Cnidaria, including corals, octocorals, sea anemones and hydrocorals, host unicellular dinoflagellate endosymbionts (i.e. zooxanthellae) belonging to the family Symbiodiniaceae [110]. These associations are often obligatory and of fundamental importance to coral reef ecosystems as they enhance the growth of calcifying corals that form the reef. For instance, the zooxanthellae contribute to host nutrition (up to 95% of the energy requirements in scleractinian corals [111]) and skeletogenesis by providing photosynthetically fixed carbon, while the cnidarian host provides inorganic nutrients and refuge from herbivory to its symbionts [112–114]. Previous studies have demonstrated that the association of Cnidaria–Symbiodiniaceae is not stochastic, but mostly determined by host phylogeny and geography [115, 116]. Like scleractinian corals, hydrocorals feed heterotrophically on a variety of resources (mostly planktonic feeders [51, 117]) and rely on a mutualistic symbiosis with Symbiodiniaceae algae for autotrophic nutrition and calcification [118, 119]. While coral-Symbiodiniaceae associations have been extensively studied over the last decades (reviewed in [120]), only two studies have recently investigated hydrocoral-Symbiodiniaceae associations on Caribbean reefs [121, 122]. Rodriguez and colleagues [122] showed that Symbiodiniaceae species that associate with *M. alcicornis* vary as a function of its geography, with *Symbiodinium* sp. (formerly clade A) found in samples from Mexico and *Breviolum* sp. (formerly clade B) in the eastern Atlantic, with the exception of samples from the Canary Island and Cape Verde Islands that comprised *Cladocopium* sp. (formerly clade C). Unpublished data collected across *M.* cf. *platyphylla* Indo-Pacific range showed that this species can associate with the genera *Symbiodinium* (dominant symbiont), *Cladocopium* and more rarely with *Brevolium* in French Polynesia, Papua New Guinea and the south-western Indian Ocean (Dubé et al. in prep.; Boissin et al. in prep.). The other Indo-Pacific species (*M.* cf. *dichotoma* and *M.* cf. *exaesa*) investigated so far show the same Symbiodiniaceae associations (Boissin et al. in prep.).

3.3 Bleaching susceptibility

One of the most devastating consequences of global warming is coral bleaching. Bleaching occurs when scleractinian corals, hydrocorals and octocorals lose their photosynthetic symbiotic algae or pigments [21, 111, 123–125], which leads to the white calcium carbonate skeleton being visible through the transparent host tissue. The frequency and severity with which coral bleaching occurs have increased in recent years [126]. Numerous investigations have demonstrated that coral bleaching events are a serious threat to coral reefs worldwide, where they have caused a severe deterioration in reef health (e.g. increase in coral disease, decrease in reef calcification and loss of habitat for related reef organisms [25, 123, 127–129]. The severity of coral bleaching depends on several factors, including specific coral species impacted [130], symbiotic algae assemblages [131] and thermal history [132].

Zooxanthellate hydrocorals are thought to be extremely sensitive to bleaching [130, 133] and can be threatened by future climate change. *Millepora* spp. have been reported to be among the first cnidarians to lose their zooxanthellae symbionts during widespread bleaching events [134] and they have suffered local or regional extinctions from bleaching in the Pacific [78, 85, 135]. Numerous investigations of bleaching events on Caribbean and Florida Keys reefs have reported bleaching of *Millepora* colonies [133, 136–139], with *M. alcicornis*, a finely branched species, being the most severely affected reef corals. Such coral morphology has been described to be more susceptible to bleaching than encrusting and massive species [140]. Yet, bleached colonies of *M. alcicornis* remained alive during a bleaching event affecting a north-eastern Brazilian reef [133], which is in accordance with previous reports that *Millepora* species are also the first to recover from short-term bleaching [136, 137]. In the Maldives Archipelago (Indian Ocean), *Millepora* was reported to be the major reef-building coral in shallow reefs (7 m depth), producing some '*Millepora* zones' [141]. Three species were well documented, the massive species *M.* cf. *platyphylla* [46, 142] and two branching ones, *M. tenera* [51, 143, 144] and *M. latifolia* [143]. However, many recent surveys of the Maldivian reefs have identified another pattern of distribution, where none to low abundances of *Millepora* species were recorded (1–2 depending on the species) [145–148]. Gravier-Bonnet and Bourmaud [148] suggested that milleporids were extirpated from several Maldives atolls, following the 1997–1998 El-Nino Southern Oscillation event (ENSO). ENSO has induced a strong bleaching and massive coral mortality (of up to 90%) in the tropical Indian Ocean, including the Maldives [145, 149]. On the Great Barrier Reef, *Millepora* spp. were also the most susceptible taxa to the mass bleaching event of 1998, with 85% of mortality [130], while they showed no evidence of bleaching at Moorea, although scleractinian corals were severely bleached at this location [150]. During 2014–2017, the worst documented bleaching event observed [26, 27], *M.* cf. *platyphylla* showed no sign of bleaching at Moorea, although about 60% of scleractinian corals were bleached on the fore reefs (**Figure 6A**). Since February 2019, Moorea's reefs are suffering from another mass bleaching event, with colonies of *M.* cf. *platyphylla* showing sign of bleaching and mortality (**Figure 6B**). Differential susceptibilities to this bleaching event were also observed between *M.* cf. *platyphylla* colonies (**Figure 6C**). Ongoing surveys will help quantifying bleaching susceptibility and mortality among coral taxa and locations, as well as between fire coral growth forms and genotypes (Dubé et al. in prep). Nevertheless, a previous study has shown that temperature is the primary factor related to bleaching in *M. alcicornis*, but that synergism with exposure to solar radiation may play a key role in hydrocoral bleaching [151]. Also, multifocal bleaching in hydrocorals, consisting of numerous scattered bleached spots, has been first described as a syndrome caused by an infectious disease affecting several colonies of *M. dichotoma* in the Red Sea [152]. 16S rRNA gene sequencing showed that affected tissues match sequences of bacteria belonging to *Alphaproteobacteria* and *Bacteroidetes* members previously associated with various diseases in scleractinian corals [153]. Yet the mechanisms of multifocal bleaching, its aetiology and mode of transmission remain unknown. Nevertheless, many studies have addressed the aetiology and effects of bleaching in Anthozoan species, wherein changes in the expression of genes and proteins were observed, and particularly heat shock proteins and transcription factors [154–159]. A recent study demonstrated that bleached specimens of *M. alcicornis* in Mexican Caribbean undergo a moderate decrease in symbiont's density and photosynthetic pigments, in addition to differential expression of 17 key proteins, such as calmodulin, actin and collagen
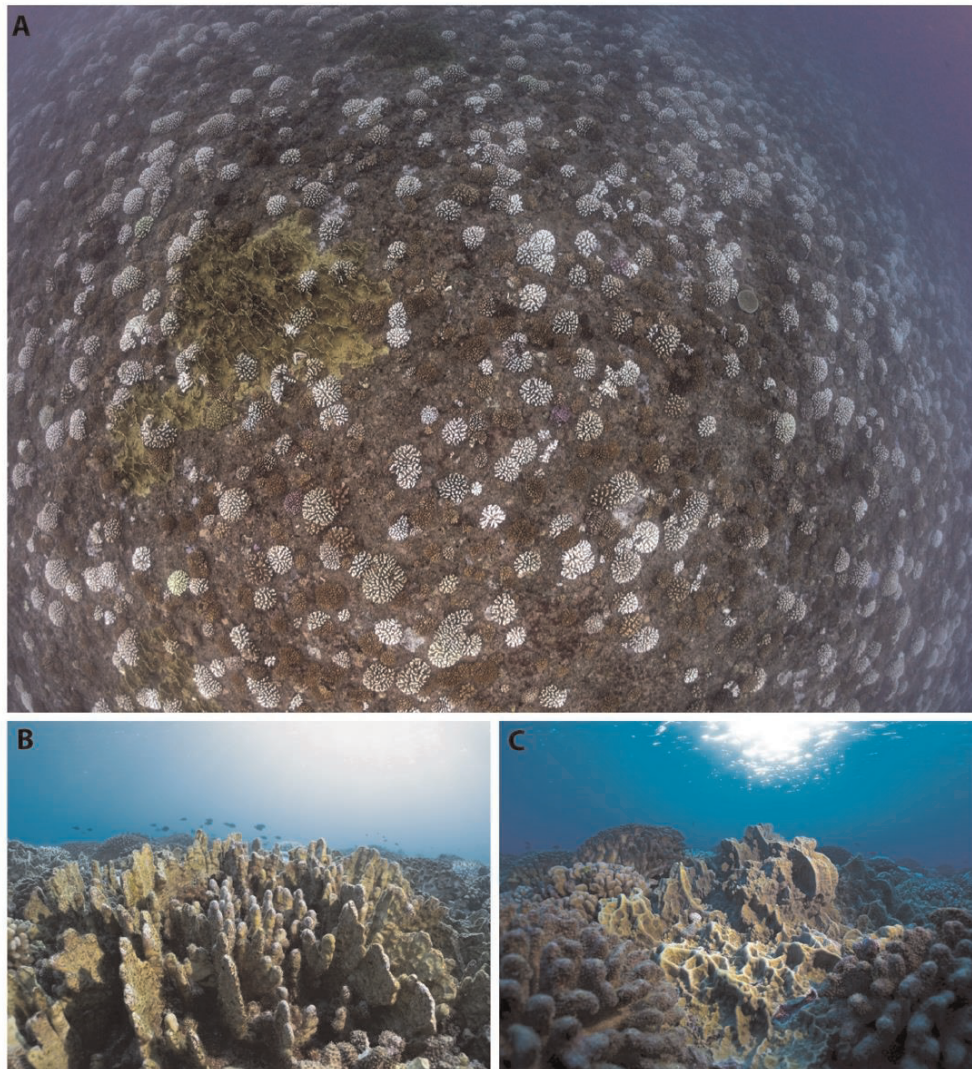
Figure 6.
Bleaching susceptibility of M. cf. platyphylla *during massive bleaching events occurring on the fore reefs at Moorea Island (French Polynesia). (A) View of the fore reef at Moorea during the bleaching event of 2016, showing healthy colonies of M. cf.* platyphylla *and bleached colonies of scleractinian corals, mostly of the* Pocillopora *genus. M. cf.* platyphylla *was sensitive to the recent bleaching event of 2019 at Moorea, where colonies bleached and died (B) from the rise in temperature, while other colonies showed sign of resistance to bleaching on the same reef (C). Photographs are courtesy of Yannick Chancerelle (A) and Yann Lacube (B and C).*

often coupled with calcium homeostasis, exocytosis and cytoskeleton organization in Anthozoan species [139].

Coral reefs are also threatened by ocean acidification associated with the increasing CO_2 partial pressure, which depresses net calcification of corals and hydrocorals [160, 161]. Physiological responses of reef organisms to ocean acidification are relatively well known [162, 163]. Examples include changes in gene expression consistent with metabolic suppression, increased oxidative stress, antioxidant system, apoptosis and symbiont loss [164, 165]. Yet little information on the effects of ocean acidification on the physiology of fire corals is available in the current literature. Luz and colleagues [166] demonstrated that the antioxidant defense system of *M. alcicornis* is capable of coping with acidic conditions for a short period of time, while long-term exposure induces oxidative stress with consequent oxidative damage to lipids and proteins, which could compromise hydrocoral health and influence negatively the zooxanthellae-coral symbiosis and ultimately lead to bleaching [167].

4. Morphology and phenotypic plasticity

In coral reefs, some calcifying species, such as corals and hydrocorals, are known to have a high degree of morphological plasticity in response to hydrodynamic changes and light availability, which strongly influences their performance, including resource acquisition and light capture, thereby benefiting colony growth, reproduction and survival [168]. Branching and plating growth forms grow quickly into large arborescent colonies in shallow reef environments, where irradiance is high and water flow is low, which makes them effective competitors for space [169, 170], light and food [171]. However, this growth strategy renders them extremely vulnerable to breakage when large waves and storm events occur, often resulting in fragmentation or coral mortality [172, 173]. Intraspecific morphological variation has been reported in many colonial reef organisms in response to environmental gradients, which ultimately affect their survival and growth [174–177]. Such plastic developmental responses are often induced during ontogeny of modular organisms with persistent effect on adult phenotypes [178]. These phenotypic responses can also change independently from the genetic background of reef corals (acclimatization), but they often rely on a genetic basis (adaptation) [179, 180].

Fire coral species are also known for their extensive morphological variability and vulnerability to fragmentation varies greatly among their morphologies [51, 58, 91, 181]. Examples include variations in growth forms of *M.* cf. *platyphylla* colonies that were found in distinct reef environments at Moorea; the fore reef at 15 and 6 m depth (mid and upper slope, respectively), the back and fringing reefs [58, 91]. Colonies on the mid slope and back reef were mostly encrusting, while the massive morphology was dominant in the fringing and patch reefs (**Figure 7A, B**). The sheet tree morphology of *M.* cf. *platyphylla* [182], the most vulnerable to wave-induced breakage, was nearly exclusive to colonies encountered in the upper slope (**Figure 7C**), where waves can break the blades, while the encrusting bases remain intact [181].

To date, the flexibility for a single genotype to produce a range of phenotypic responses to distinct environmental conditions (i.e. phenotypic plasticity) has rarely been documented in natural marine populations, mostly because of the difficulty in identifying naturally occurring clonal genotypes across variable environments. Dubé and colleagues [58] have described the first example of phenotypic plasticity among fire coral clones, where clones of the same genotype display different morphologies across distinct reef habitats (**Figure 8**). The fire coral *M.* cf. *platyphylla* seems to invest in a vulnerable morphology that increases the contribution of asexual reproduction through fragmentation in high-energy reef habitats. This is a unique example of phenotypic plasticity as corals typically have wave-tolerant growth forms in such dynamic reefs. Such phenotypic responses suggest

Figure 7.
Morphologies of M. cf. platyphylla *colonies in habitats experiencing contrasting hydrodynamic regimes. (A) Massive wave-tolerant morphology in the patch reef, a lagoonal habitat (photograph is courtesy of Gilles Siu); (B) encrusting wave-tolerant morphology in the back reef, a lagoonal habitat at <1 m depth and (C) sheet tree morphology vulnerable to wave-induced breakage in the upper slope, a fore reef habitat at 6 m.*
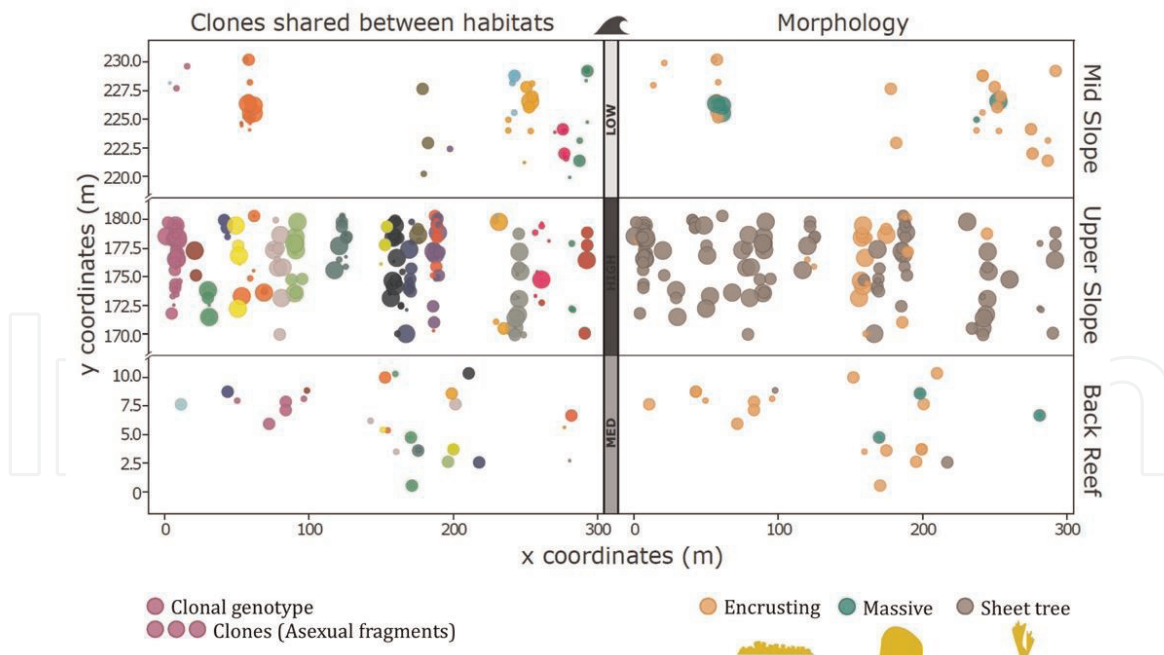
Figure 8.
Graphical abstract showing the occurrence of phenotypic plasticity among fire coral clones, where clones of the same genotype display different morphologies across distinct reef habitats [58]. Geographic coordinates of each georeferenced colony collected in the three reef habitats are shown in meters on the x and y axes. On the left side: each genotype is represented by a unique color; on the right side: colonies with encrusting morphology are shown in orange, massive in green and the vulnerable sheet tree morphology in grey.

that fire corals being susceptible to wave-induced breakage have benefits in terms of reproduction outweighing the costs of getting injured.

5. Reproduction

5.1 Reproductive strategies

Although only a few species are exclusively reproducing asexually, clonality has evolved repeatedly in many reef organisms (e.g. [183–186]). In coral reef ecosystems, there are many organisms that can reproduce through both sexual and asexual reproduction, including scleractinian corals [187], hydrocorals [58], hydroids [188], coralline algae [189], sea anemones [190], sea cucumbers [191], gorgonians [192] and sponges [193]. Asexual reproduction produces genetically identical offspring, often leading in local populations dominated by few adapted clones [194–196]. In the contrary, sexual reproduction enables genetic recombination and production of genetically diverse propagules, thus generating the genotypic variation required for adaptation [197] and colonization of new habitats [198]. In many colonial reef organisms, asexual reproduction can occur through fragmentation, fission, budding, polyp expulsion or polyp bail-out [187, 199–201], while sexual reproduction often involves a wide range of reproductive strategies, i.e. gonochorism, hermaphroditism, internal (brooders) and external (spawners) fertilization [187, 202].

Despite their ecological importance to the ecosystem functioning of coral reefs, *Millepora* hydrocorals have been relatively understudied and information regarding their reproduction and dispersal patterns remain scarce. Fire corals are gonochoric broadcast spawners that reproduce sexually by producing medusoids and planula larvae (**Figure 9**). They also rely on asexual reproduction through fragmentation [58, 181], but the production of asexual larvae has never been documented within this genus though described for some *Pocillopora* species [203, 204].
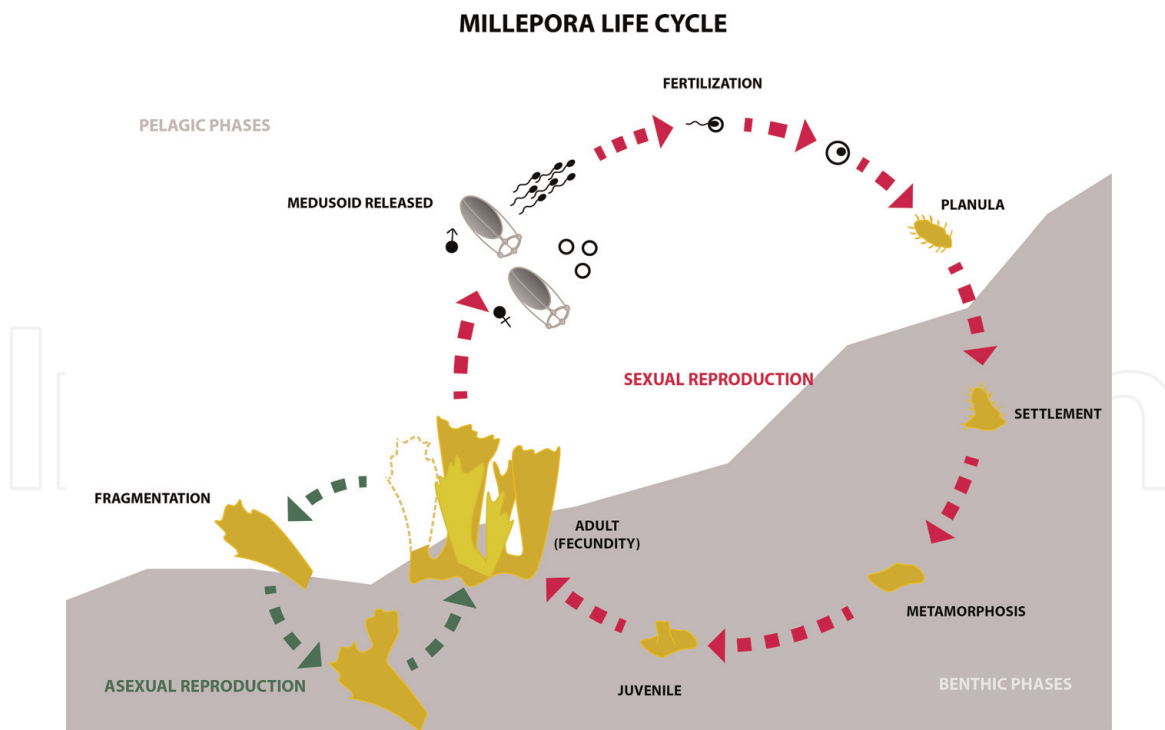
Figure 9.
Millepora *life cycle.* Millepora *hydrocorals are gonochoric broadcast spawners that reproduce sexually by producing medusoids and planula larvae. The medusoids release the gametes in the water column for external fertilization. The ciliate larvae sink and crawl on the reef substratum and metamorphose in a new calcifying polyp, founder of a new colony.* Millepora *also relies on clonal propagation through fragmentation and grow via asexual budding.*

5.2 Spawning, medusoids and larval development

Milleporid sexual reproduction is seasonal [69]. *Millepora* colonies become mature during the spring or summer (or austral summer for the southern hemisphere). Sexual reproduction period is usually correlated with the increase of the sea water temperature [69, 70, 205, 206], but some studies based on ampullae observations suggest a reproduction throughout the year [207–209]. Spawning occurs at different dates according to species, preventing hybridization [69, 70, 206]. The empty ampullae are visible during 1–2 months on the colonies (**Figure 10D**) before the skeleton reconstruction.

The sexual reproduction process begins with the growing of special cavities, called ampullae, developed in tissues and designing densely packed white dots on the coenosteum of the gonochoric colonies. These ampullae were first described by Quelch [210, 211] and further studied by Boschma [46, 207, 208, 212] and Moschencko [66]. Each ampulla contains one developing medusoid, i.e. a 'regressed' short-lived medusa, shed with mature gametes. Male and female medusoids are liberated after the disintegration of the dense network of the trabeculae covering the ampullae (**Figure 10A–C**). They have marginal bulbs but no tentacle, no circular or radial canal, no manubrium, no statocyst or any sense organ (**Figures 10C** and **11A**), and they are not able to feed on zooplankton. On the contrary, as true medusae, they are able to actively swim with their muscle fibres distributed in the bell and display a velum. Gonads are attached to the short spadix and fill entirely the subumbrellar cavity. Female medusoids contain 2–5 zooxanthellate oocytes (**Figure 11A**) and male medusoids contain a spermatic mass (**Figure 10C**). The medusoids detach themselves from the fertile colonies by active bell pulsations in a few minutes and their swimming activity leads to the release of
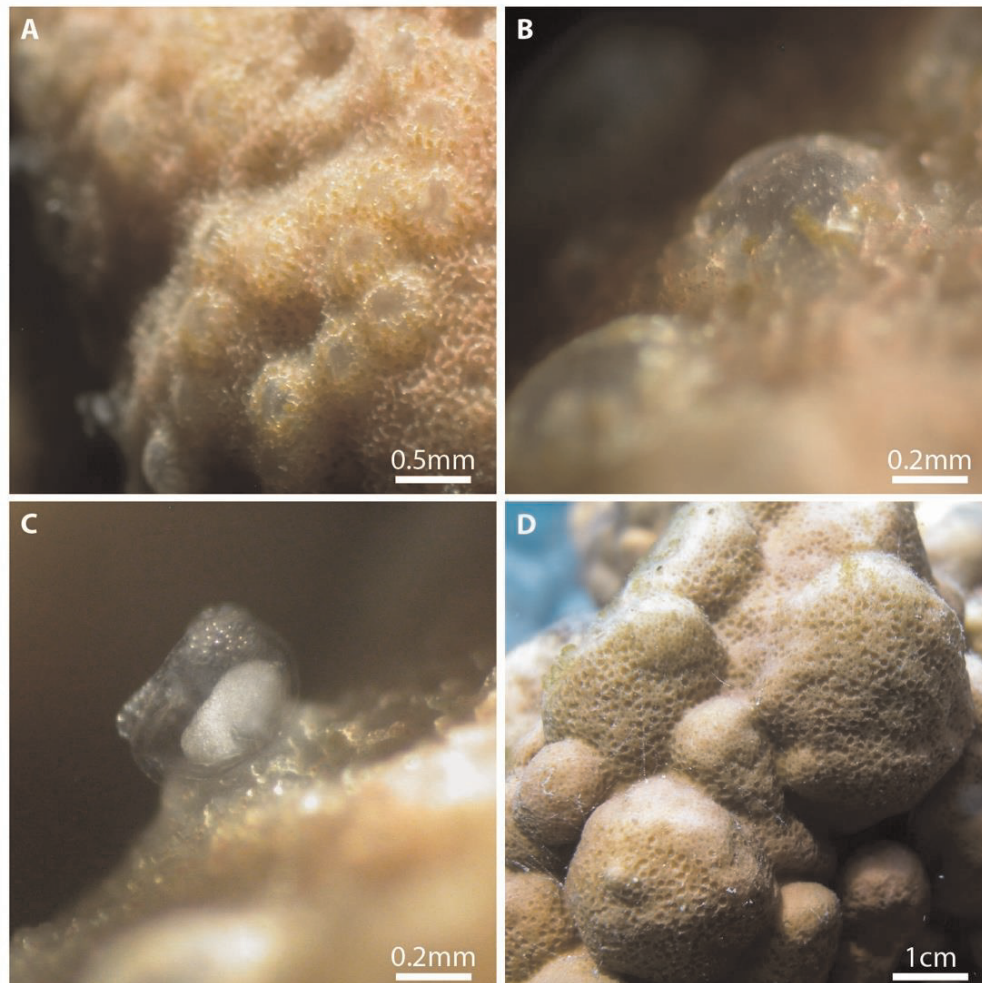
Figure 10.
Before, during and after medusoid release in M. cf. exaesa *in Reunion Island (modified from [69]).*
(A) Ampullae showing a small opening resulting in skeleton dissolution few days before the medusoid release.
Notice that the cyclosystems have disappeared because of the high ampulla density; (B) medusoids protruding
through the open ampullae and (C) male medusoid release with the umbrella opening towards the surface.
Notice the big tentacular bulbs with refrigent nematocyst and the sperm sac filling the subumbrellar cavity;
(D) empty ampullae visible during 1–2 months after the massive medusoid release event. A, B and C
photographs were taken using a stereomicroscope; photograph D was taken underwater.

the ripe gametes in the water column. The spawning of gametes is therefore almost synchronous with the release of medusoids. Spawning always begins before dark, but is not correlated with the lunar or tidal cycles [69, 70, 206]. In shallow water of Reunion Island, Indian Ocean (reef flat), a unique massive spawning event was observed *in situ* for *M.* cf. *exaesa* and *M.* cf. *platyphylla* during the reproductive period, in December for the former species and in January for the later one [69]. Conversely, *M. tenera* seems to spawn regularly but not massively during 2 months of the austral summer, resulting in the observation of both closed and open ampullae on fertile colonies during the reproduction season. Likewise, Nomura [205] and Soong and Cho [206] described several medusoid batches in different *Millepora* species in controlled conditions during the reproductive season in Japan and Taiwan, respectively. Recently, Shlesinger and Loya [70] described massive spawning events in the Red Sea (Gulf of Eilat/Aqaba) for three species, *M. dichotoma*, *M. exaesa* and *M. platyphylla*. Their field observations during the reproductive period (from June to September 2016–2018) also showed one or two spawning events per year for *M. exaesa* and *M. platyphylla*, while *M. dichotoma* colonies released their medusae massively, 4–6 times during the reproductive season. The higher reproductive output of *M. dichotoma* might be in relation with its
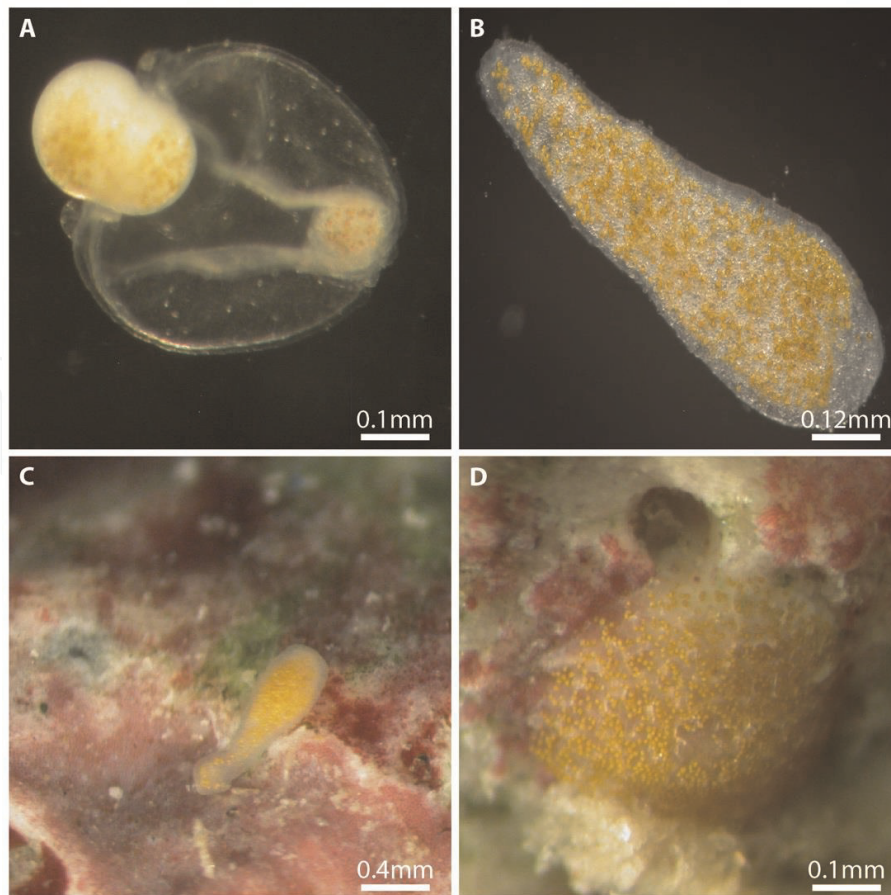
Figure 11.
Gamete spawning, planula larva formation and settlement in Millepora *spp. in Reunion Island (modified from [69]). (A) M. cf.* platyphylla *female medusoid releasing an oocyte through the velum while swimming. Notice the numerous zooxanthellae in the oocyte and spadix tissues; (B) M. cf.* exaesa *zooxanthellate (orange dots in endoderm) planula larva; (C) M. cf.* exaesa *larva finding a sustainable substrate to fix by the tapered pole before metamorphosis; (D) M. cf.* exaesa *recruit with the first pore. All photographs were taken using a stereomicroscope.*

higher abundance in the Gulf of Eilat/Aqaba (i.e. *M. dichotoma* is the most abundant milleporid in the Gulf [70]).

The empty medusoids continue to swim for 1–3 h and die quickly while sinking and shrinking. Male and female medusoids are released synchronously (for a giving species), the spawning of the oocytes and spermatozoids is also simultaneous, and fertilization occurs rapidly. Embryogenesis and planula larvae formation occur in less than 12 h in aquarium [69]. Because of the presence of algal symbionts in oocytes, the planula larvae are zooxanthellate and have the potential to live for several weeks before settlement (more than 1 month in controlled conditions for *M. cf. exaesa* from Reunion Island). This feature is certainly a character to keep in mind to explain the large distribution of *Millepora* species in all oceans. *M. cf. exaesa* planula has been described as a bipolar ciliated larva with a wide anterior and tapered posterior, without a mouth and gastrovascular cavity (**Figure 11B**) [69]. The larva endoderm is full of lipid droplets and zooxanthellae. The larva sinks and crawls until it finds a sustainable substrate to fix and metamorphose (**Figure 11C**). This process leads to the formation of a calcareous structure surrounding the primary polyp, founder of a new colony by asexual budding (**Figure 11D**).

The reproductive output (ampulla density) is variable according to species and within species. Amaral and colleagues [75] found an average of 10 ampullae/cm^2 for *Millepora* species occurring on Brazilian reefs, while the highest density was observed by Soong and Cho [206] in Taiwan with 84–120 ampullae/cm^2.

In Hydrozoans, the reproductive output can vary between and within species, and can often depend on the colony size and environmental conditions [213, 214]. In Reunion Island, the ampulla density of *M.* cf. *exaesa* is positively correlated with the size of colonies, indicating that the reproductive output varies with the colony size. Global change also seems to influence the reproductive output of milleporids as the rate of fertile colonies have decreased considerably in the last 10 years at two contrasting reef sites in Reunion Island (Bourmaud et al. in prep).

5.3 Dispersal and recruitment

For most colonial reef species whose adults are sessile, their early life history includes a pelagic stage. These propagules represent the first step for successful recruitment and have profound implications for population dynamics and renewal, which ultimately affect their evolutionary history [215, 216]. Dispersal in colonial organisms is mostly mediated by the release of gametes and/or larvae during sexual reproduction events, together with the continuous supply in asexual propagules. In many reef species, the extent of dispersal is largely governed by the reproductive biology and early life history ecology. Molecular studies and oceanographic models have uncovered a wide range of dispersal patterns (i.e. dispersal kernels) in coral reefs, from populations primarily sustained by self-recruitment due to limited dispersal potential or retention, to ecologically significant gene flow and connectivity among adult populations [217]. In corals for instance, brooded larvae settle and metamorphose rapidly after being released, which is most likely to enhance local dispersal patterns, while broadcast larvae require a planktonic development phase and settle further away from the parental source [187]. On the other hand, clonal propagation can allow populations to expand locally under unfavorable conditions. Such conditions include fragmented [218], marginal [196] and highly disturbed habitats [186], where clonal reproduction reinforce local adaptation processes and population genetic heterogeneity due to restricted dispersal potential of asexual offspring [58, 219, 220].

Although local demography and self-recruitment have been shown to have major consequences on the genetic diversity and adaptive ability of reef organisms, empirical data of dispersal patterns in reef-building species remain scarce. Dubé and colleagues [221] documented the first genetic estimates of local dispersal and self-recruitment in a marine broadcasting species, the hydrocoral *M.* cf. *platyphylla*. They performed a parentage analysis that revealed a significant contribution from self-recruitment in addition to limited dispersal of sexual propagules on Moorea's reefs. Sexual propagules often settled at less than 10 m from their parents and dispersal events decreased with increasing geographic distances. Sibship analysis showed that full siblings recruit together on the reef, resulting in sibling aggregations. Such limited dispersal abilities in fire corals can be related to their early life history traits. Dispersion during the medusoid stage may not be as effective due to the short pre-competency period time of the hydromedusae in the water column [51, 181]. Other means of dispersal can occur through the propagation of asexual offspring, e.g. fragments that have broken and re-attached to the reef framework. Asexual reproduction through fragmentation in branching hydrocoral can be substantial during disturbances [51, 181] and may therefore contribute to dispersal. However, clonal fragments of the plate-like *M.* cf. *platyphylla* were found to be dispersed close to one another on a barrier reef (mean = 18 m), with clone distribution being perfectly aligned with wave energy dispersal [58]. The maximal distance between fragments of the same genotype in this plate-like species at Moorea Island was about 450 m.

6. Modularity and growth

Modularity is a well-established life history strategy among colonial reef invertebrates, i.e. corals, gorgonians, sea anemones, hydroids, hydrocorals, bryozoans and sponges [222]. Modular organisms grow in size via the repeated, vegetative formation of genetically identical modules, referred to as asexual budding, whereby all modules are derived from the same initial zygote to form a colony [223, 224]. Colony size often correlates with many fitness advantages in response to both physical and biological stressors. For instance, larger colonies can survive better towards predation [225] and competition [226], and their fecundity is often increased due to the large number of polyps that contributes to sexual reproduction [227]. Modules usually remain physiologically interconnected, but may also separate from the colony through fission or fragmentation and persist as discrete units [228], thereafter reducing colony size. There are only few reports of growth rates in *Millepora* species [79, 92, 229–232] that are within the range reported in Acroporidae corals from western Atlantic region [233].

Some marine modular organisms, e.g. corals and ascidians, can also grow larger and quicker via the fusion of distinct colonies [178], which results in genetically heterogeneous colony, also referred to chimera. In addition to chimerism, somatic mutations may arise within a colony, which also results in intracolonial genotypic variability. Both chimerism (fusion) and mosaicism (somatic mutation) were identified in fire corals [234, 235]. At Moorea, for instance, fusion between siblings is likely to occur as fire corals have limited dispersal abilities and are often aggregated due to the co-settlement of their larvae [221]. Puill-Stephan and colleagues [236] demonstrated that high levels of relatedness between juvenile corals correlated with late maturation of allorecognition. The fusion of siblings could thus be related to a low conspecific acceptance threshold and/or a delay in allorecognition maturation for *Millepora* hydrocorals, as described in some hermatypic corals [237, 238]. Considering the common occurrence of somatic mutations in fire coral species, modularity might be a promising strategy to increase genotypic variability in populations that are predominantly sustained through asexual reproduction [235].

7. Population genetics: a case study of *Millepora cf. platyphylla* at Moorea, French Polynesia

Recent genetic studies have uncovered that geographically isolated populations, such as those of Moorea, appear to be more dependent on self-recruitment for local replenishment and sustainability [239, 240], highlighting the importance of studying local patterns of life history traits in keystone species. Moorea is a high volcanic island surrounded by a barrier reef with extensive fringing reefs and lagoon systems [241]. Lagoons and deep interrupted channels separate the fore reefs from the island, and the lagoon is connected to the oceanic waters via deep passes through the barrier reef. Furthermore, coral reefs surrounding Moorea Island have undergone a massive decline in coral cover from a recent outbreak of *Acanthaster planci* and cyclone *Oli* [242, 243], which provides a unique perspective from which to comprehend how fire corals can survive and recover from such disturbances.

By gathering genotypic and phenotypic data, Dubé and colleagues [58, 221, 235] were able to produce a complete picture of ecological and evolutionary strategies involved in the population persistence of *Millepora* hydrocorals. On Moorea's reefs, *M.* cf. *platyphylla* displays a wide range of strategies that ensure its survival by maximizing the acquisition of local resources. Self-recruitment and mosaicism successfully established diverse genotypes within *M.* cf. *platyphylla* population, while

colony fragmentation contributed effectively to population growth (**Figure 12**), where a high number of clonal genotypes have the potential for phenotypic plasticity in response to environmental changes. Genetic data indicated that fragmentation is the dominant reproductive process generating the high abundance of fire corals at Moorea (80% of colonies were clones). Even small recruits were having multilocus genotypes identical to adults and were often positioned below the reef substratum, i.e. frequently on branches of dead coral colonies or side of crevices. These observations suggest that the successful recruitment of clones may be the result of clonal reproduction processes other than fragmentation, such as asexual planula larvae, because asexual fragments are less likely to re-attach on such inclined substrate. The release of ameiotic planula larvae was reported in a number of coral species [187], where larval behaviour allows the settlement of a new individual characterized by its mother genotype (clone mates). However, such clonal reproductive strategy has never been described for the *Millepora* genus, and requires further investigations. In Moorea, fire corals are sustained by a moderate degree of self-recruitment [221] suggesting that despite low gene flow, genetically diverse and locally adapted recruits can successfully establish high local population abundance via their subsequent growth, survival and fragmentation (as described in [244]). However, such populations are predicted to be vulnerable to severe disturbances owing to their isolation from potential source reefs and are often associated with increased extinction risks [245, 246]. A high potential for gene flow and connectivity has been revealed among islands of the Society Archipelago in French Polynesia for some scleractinian species (i.e. Moorea, Raiatea, Taha'a and Tahiti) [218]. Preliminary results from samples of *M.* cf. *platyphylla* collected in several islands from French Polynesia revealed significant genetic differentiation among archipelagos (Marquesas, Austral, Gambier, Society and Tuamotu, Boissin et al. unpublished), highlighting the importance of self-recruitment processes in population sustainability.
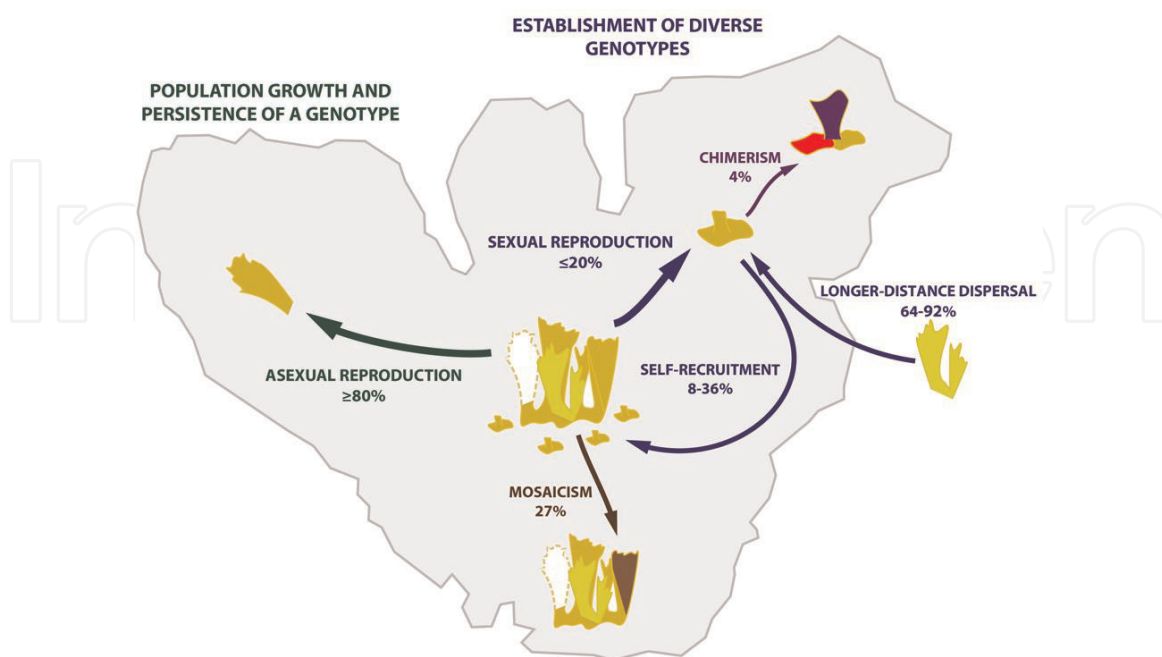

Figure 12.
Summary of life history strategies in M. cf. platyphylla *at Moorea, French Polynesia. M. cf.* platyphylla *heavily relies on asexual reproduction through fragmentation for local replenishment (80% of the colonies are clones), allowing population growth and the persistence of a genotype over time. M. cf.* platyphylla *population is sustained via a significant contribution from self-recruitment (8–36% of juveniles are self-recruits). Mosaicism and chimerism also contribute in creating novel genotypic diversity at the population and individual levels.*

Overall, the evaluation of the life history of *M.* cf. *platyphylla* suggests a competitive strategy, based on few locally produced sexual recruits and their ability of reaching large sizes (fusion [235] and stolonal spreading [59]), which allows them to pre-empt space on coral reefs, but also brought evidence of high susceptibility to fragmentation. This life strategy is well suited for population persistence in the absence of sexual recruitment, but can be risky in unstable environments [247]. Yet *M.* cf. *platyphylla* populations in Moorea have withstood severe disturbances, e.g. *Acanthaster* outbreaks, cyclones and mass bleaching events. Their recovery is foremost sustained by the rapid growth of remnant colonies, mostly those encrusting, and the subsequent local recruitment via both sexual and asexual reproduction. There is evidence that under pressure from environmental changes fire corals might be among the reef coral 'winners', joining some scleractinian species that have already been described as such [32, 85, 140]. Yet more information on how they respond to bleaching events is needed, as *Millepora* species have been reported to be highly vulnerable to thermal stress in other reefs [4, 130, 133]. Nevertheless, the life history of *M.* cf. *platyphylla* is most likely contributing to its colonization success in various reef environments in French Polynesia. Although *M.* cf. *platyphylla* is the only fire coral species reported in this geographic region [50], this species is also characterized by one of the widest ranges of distribution in the entire Indo-Pacific region within the *Millepora* genus [248], but similar to the branching species *M. intricata*. Evaluating the life history of other *Millepora* species with different growth forms will enable to determine whether these strategies are unique to *M.* cf. *platyphylla* or spread within the *Millepora* genus.

8. Conclusions

In recent decades, declines in scleractinian coral cover have challenged their role as key ecosystem engineers of coral reefs [25–27, 249–251]. Assuming rising sea temperatures and increased ocean acidification, climate change can interfere with a range of key processes in the life history of reef corals, including growth, calcification, development, reproduction and behavior [162, 252]. Despite the acclimatization and genetic adaptation of reef corals [2], such persistent physical and chemical conditions can lead to shifts in reef community composition. This phenomenon has already been reported in many reefs, where alternative organisms are dominating reef assemblages (reviewed in [253]). Only few studies have considered hydrocorals in ecological monitoring of coral reefs [130, 254, 255]. For instance, *M.* cf. *platyphylla* can dominate some reefs in the Indo-Pacific region [89] and also contribute to the survival of corals during *Acanthaster* outbreaks [106]. Therefore, it is crucial to gain insights into how populations of this keystone species can adapt and survive in the face of climate change, and other natural or anthropogenic disturbances. In this chapter, we established that fire corals possess a great variety of life history strategies that favor a high degree of genetic diversity and plasticity enabling these organisms to persist throughout environmental variations. Consequently, these *Millepora* species may become one of the major components in some modern reefs and requires more consideration in ecological monitoring.

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Conflict of interest

The authors declare no conflict of interest.

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