



Michel Pichon

Abstract

French Polynesia is composed of 118 high islands and atolls stretching in a vast oceanic expanse in the central Pacific Ocean, from just below the equator to almost 30° S. It is composed of five archipelagos, which all differ in terms of their geological origin and history, environmental conditions, and reef development. The Tuamotu Archipelago is entirely comprised of atolls, whereas fringing or barrier reefs are found in the Society, Gambier, and Austral Islands (only one atoll), and coral reef accretion is almost nonexistent in the Marquesas. Coral reef studies have concentrated mostly on the Society and Tuamotu Archipelagos, and, except for occasional observations, been restricted to a depth of 30–40 m on the reef slopes. Our knowledge of mesophotic coral ecosystems is therefore limited, particularly for the deeper zone, below 80 m depth. The scleractinian mesophotic fauna is highly diverse compared to shallow reefs, with 38 genera and 96 species recorded. This fact is likely to be a consequence of water clarity, allowing the photophilic shallow coral species to extend deeper than usual. In some areas, substratum cover by *Pachyseris speciosa* reaches values of 80% at depths of ≥ 70 m, and a typical “deep” mesophotic assemblage dominated by *Leptoseris* spp. has also been recognized. Quantitative data on other major biotic components of the mesophotic assemblages are either lacking or insufficient to allow their characterization as depth generalists or depth specialists.

Keywords

Mesophotic coral ecosystems · French Polynesia · Atolls · Volcanic islands · Scleractinia

24.1 Introduction

French Polynesia is composed of 118 islands (including 83 atolls) of volcanic origin, covering a surface area (including lagoons) of 16,230 km² stretching over approximately 2,500,000 km² (a surface area larger than that of Europe), with a corresponding exclusive economic zone of 5,500,000 km² (Aubanel et al. 1998). The islands are situated in the central South Pacific Ocean between latitudes 07°50' S (Motu One, in the Marquesas) and 27°55' S (Marotiri, Austral Islands) and longitudes 134°28' W (Temoe, Tuamotu) and 154°42' W (Scilly, Society Islands). The nearest neighbors to French Polynesia are the Cook Islands in the west and the Pitcairn Islands in the southeast (Fig. 24.1).

The islands of French Polynesia are grouped into five archipelagos: the Marquesas Islands (11 high islands, 1 atoll), Society Islands (9 high islands, 5 atolls), Tuamotu Islands (76 atolls), Gambier Islands (9 high islands surrounded by a barrier reef), and the Austral Islands (6 high islands, 1 atoll). Geographically, the Gambiers are often considered as part of the Tuamotu ensemble. However, they represent the southeastern most part of a line of low-lying islands stretching in a southeast-northwest direction over more than 1700 km, up to Hereheretue, parallel to, but separate from, the Tuamotu Islands proper (Salvat and Bacchet 2011).

In each of the archipelagos, the islands are approximately distributed in a southeast-northwest direction. They are hypothesized (Salvat and Bacchet 2011) to have originated from the intermittent activity of volcanic hot spots situated, respectively, near Pitcairn (Gambier-Tuamotu), Macdonald Seamount (Austral), Mehetia (Society), and Fatu Hiva (Marquesas). Their age (within the range 0.3–12.2 million years) increases from southeast to northwest following their drifting (at a rate of 0.12 m year⁻¹), accompanied by a slow subsidence, away from their respective hot spots due to the movement of the Pacific lithospheric plate, thus representing a particularly clear illustration of the Darwin (1842) scheme of atoll formation (Gabri e and Salvat 1985).

M. Pichon (✉)
Biodiversity and Geosciences Program, Museum of Tropical
Queensland, Queensland Museum Network,
Townsville, QLD, Australia



Fig. 24.1 Map of French Polynesia (from Salvat and Bacchet 2011) with inset showing the exclusive economic zone (EEZ). (Inset courtesy of Google Earth; EEZ modified from GML file obtained from Flanders Marine Institute)

Coral reef studies have concentrated mostly on the Society and Tuamotu Archipelagos and, except for occasional observations, have been restricted to a depth of 30–40 m on the reef slopes. Our knowledge of mesophotic coral ecosystems (MCEs; 30–150 m; Hinderstein et al. 2010) is therefore limited, particularly for the deeper zone, below 80 m depth. This chapter summarizes what is known about the MCEs of French Polynesia.

24.1.1 Research History

Among the expeditions of the eighteenth and nineteenth centuries that were commissioned to explore the Pacific Ocean, a number of them sailed through the waters of what is now known as French Polynesia, and called at a number of islands, mostly Tahiti. Even though in most instances a naturalist, botanist, or zoologist accompanied these expeditions (a role sometimes fulfilled by one of the surgeons), there is

little or no record of scleractinian corals being collected even on an ad hoc basis during the voyages of the French explorers. Indeed, proximity of coral reefs was always (and still is) avoided as much as possible, particularly in the Tuamotu Islands, where a succession of low-lying islands scattered in uncharted waters makes navigation particularly hazardous.

At least four (i.e., the *Porcupine*, *Flying Fish*, *Peacock*, and *Vincennes*) out of the squadron of seven vessels which took part in the US Exploring Expedition sailed through the Tuamotu in August and early September 1839, recognizing at least six of the atolls, before reaching Tetiaroa and Tahiti. Thereafter, leaving the westernmost part of the Society Islands on September 30, after a short visit by the *Vincennes* to Motu One, then known as Bellingshausen (Stanton 1975). Dana (1846) reported on the zoophytes collected during the expedition. Dana (1846) recorded 20 species of scleractinian corals including 2 from the Society Islands, 16 from Tahiti, and 2 from the Tuamotu, but as was the case then, no depth data were recorded.

During the second half of the nineteenth century, the British vessel HMS *Challenger* visited Tahiti, where she spent about a fortnight in September 1875 (Linklater 1972). During that time, 42 species of scleractinian corals were obtained, of which 11 were considered new at the time (Quelch 1886). No depth data are given by Quelch (1886), with the notable exception of *Domoseris regularis* (now *Leptoseris scabra*), collected between 30 and 70 fathoms, and considered a common denizen in MCEs. Type material of another two species *Domoseris solida* and *D. porosa* (now lumped under *Leptoseris solida*) from Tahiti are also without depth record, but the species is deemed to be preferentially found in MCEs. Thus, due credit is to be given to Quelch for having provided the first glimpse of Polynesian mesophotic scleractinia.

Studies on coral reefs in general and on scleractinian corals in particular (Chevalier 1979; Chevalier and Kühlmann 1983) intensified considerably during the second half of the twentieth century following the establishment of research facilities, including field stations, by several national institutions such as the Muséum National d'Histoire Naturelle and the École Pratique des Hautes Études at Moorea and the Office pour la Recherche Scientifique et Technique Outre Mer at Tahiti and Tikehau, concomitant with the activities of the Direction du Centre d'Essais Nucléaires (DIRCEN) on the atolls of Mururoa and Fangataufa (Gout et al. 1997). Although a considerable effort has been directed toward coral reefs, their geological history, living components, organismal assemblages, and functioning, most of the research activity on the reef outer slopes was limited to the depth of ca. 30–40 m with only a few exceptions (Tikehau: Faure and Laboute 1984; Takapoto: Kühlmann and Chevalier 1986; Moorea: Mazeas 1993; Vigliola 1993) and to a few scleractinian specimens collected incidentally by dredging

on the fore-reef slopes of Tubuai by the DIRCEN vessel R/V *Marara*. This is due essentially to the logistical and regulatory constraints associated with the use of SCUBA, but even during the last two decades, no attempt was made to use the modern tools that became available for deeper studies, such as manned submersibles, remotely operated vehicles, autonomous underwater vehicles, or technical diving using trimix and closed-circuit rebreathers. As a result and in the absence to date of any coordinated and integrated research program on MCEs, our knowledge on the subject is limited and remains very much in its infancy.

24.2 Environmental Setting

The major environmental factors controlling the composition and structures of organismal assemblages at mesophotic depths are light penetration, bathymetric profile, nature of the substratum, and temperature. To a lesser extent, bottom current may also play a role in shaping fore-reef slope communities, but too little is known about them to ascertain their actual role.

Light No depth profile for light penetration is available, but a few Secchi disc measurements have indicated that in oceanic waters, outside the reef front, maximum Secchi disc visibility was 40–45 m during the dry season (May to September) and up to 30 m during the wet season, i.e., November to April (Gabrié and Salvat 1985). This suggests that, as a crude approximation, the compensation depth (1% surface irradiance) varies approximately between 75 and 115 m. Furthermore, water transparency outside the reefs is expected to be higher for atolls than high islands, particularly during the dry season, due to the decreased input of sedimentary particles of terrigenous origin.

Bathymetric Profile and Substratum Type Bathymetric profile and substratum type play a major role in shaping MCE composition. The fore-reef slope inclination and its geographic orientation have a direct effect on light availability, and the substratum type influences the ability of benthic organisms' larvae to settle on the bottom.

Off atolls, there is a relative uniformity in the principal characteristics of the outer slope profiles, although there are almost always some differences between windward and leeward sides. Basically, the upper slope shows with increasing depth a succession of a spur and groove structure followed by a gently sloping terrace starting at variable depth and extending horizontally to a variable degree (Fig. 24.2). The lower slope, which is more steeply inclined (generally >50%), can begin at depths as shallow as ca. 20 m, but often deeper. In some instances (e.g., Mururoa), the fore-reef slope starts at a depth of around 50 m and is preceded in shallower

Fig. 24.2 Outer slope bathymetric profiles in three atolls in the Tuamotu Archipelago (modified from Montaggioni et al. 1987). Measure of horizontal distances can be derived from the scale: Distance (m) provided in the lower left

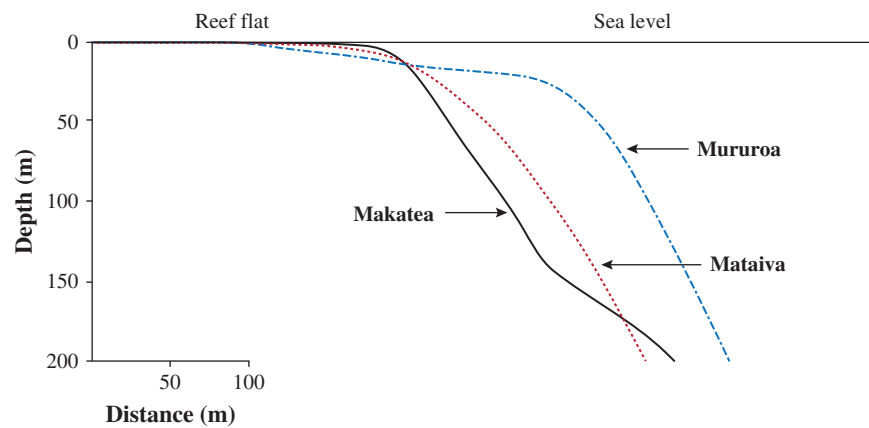
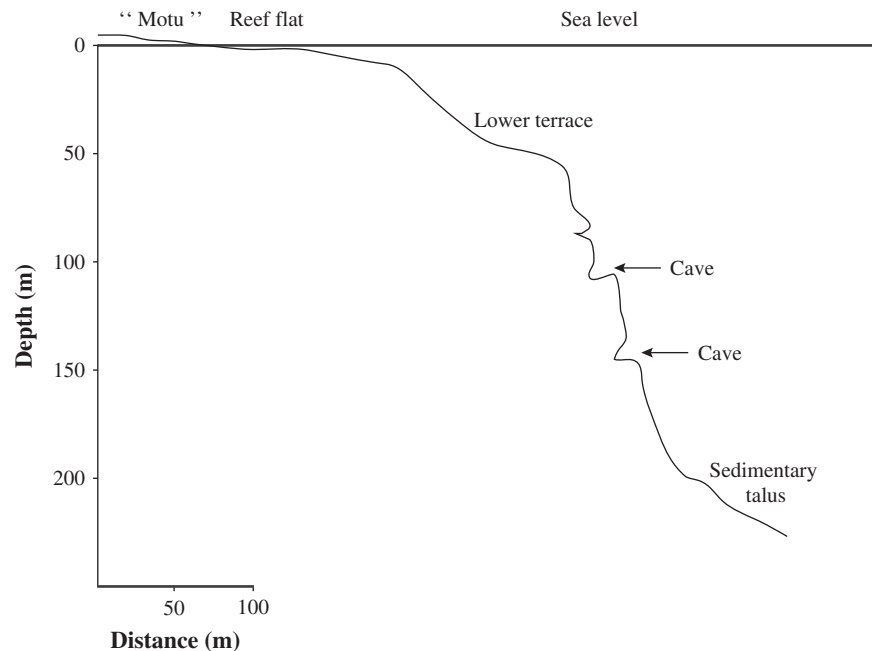


Fig. 24.3 Outer slope bathymetric profile, Mururoa Atoll, Tuamotu (modified from Montaggioni 2011). Measure of horizontal distances can be derived from the scale: Distance (m) provided in the lower left



water by a well-defined lower terrace. Submarine caves have also been observed on the drop-off at depths of 100–110 and 140 m (Fig. 24.3). The caves are interpreted as erosion features in the limestone framework formed at times of standstills in the sea level, which occurred during the last deglacial episode.

Fore-reef slope profile may be more variable on the high islands, as the sublittoral morphology is directly influenced by the presence of more recent volcanic formations on the shoreline and in shallow water. In some instances (e.g., Vairao, in southwest Tahiti), the upper reef slope is followed, below approximately 10 m depth by a near vertical wall or drop-off down to at least 70 m, with an average slope inclination of 90% or more (Fig. 24.4a). More frequently, the upper slope shows a succession of (1) moderately sloping spurs and grooves, (2) a subhorizontal sedimentary terrace, and (3)

more steeply inclined buttresses and valleys terminating at a depth of around 30 m (Salvat et al. 1972; Battistini et al. 1975; Jaubert et al. 1975). Below ca. 30 m and down to 70 m depth, the substratum is less inclined and of variable nature. It can be a predominantly hard bottom, with significant coral cover or, as is the case around most of the island of Moorea, a sedimentary slope (inclination between 15% and 30%). This sedimentary slope is known locally as the “sandy plain” (Mazeas 1993; Vigliola 1993) and is virtually devoid of any sessile benthos (Fig. 24.4b). The thickness of the sediment layer can reach 80 cm. The upper part of the sedimentary slope is strewn with dead coral blocks, sand, smaller coral debris, and larger coral rocks partly buried in the sediment are frequent in the lower part. Beyond 70 m depth, sedimentary deposits are absent and replaced by a steep slope or drop-off, with an inclination of 60% or more.

Fig. 24.4 (a) Outer slope bathymetric profile at Vairao, Tahiti. (b) Bathymetric profile of the outer reef slope, Tiahura, Moorea. (Redrawn from Jaubert et al. (1975) and Vigliola (1993))

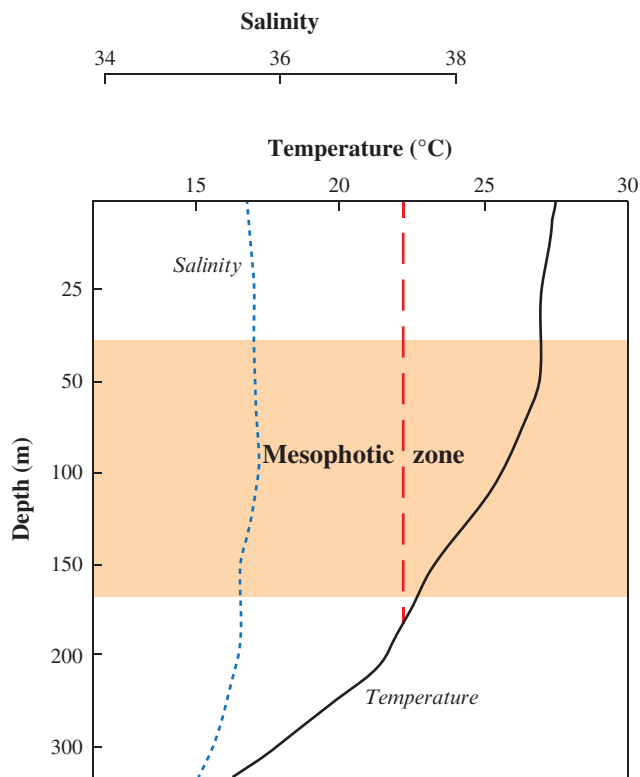
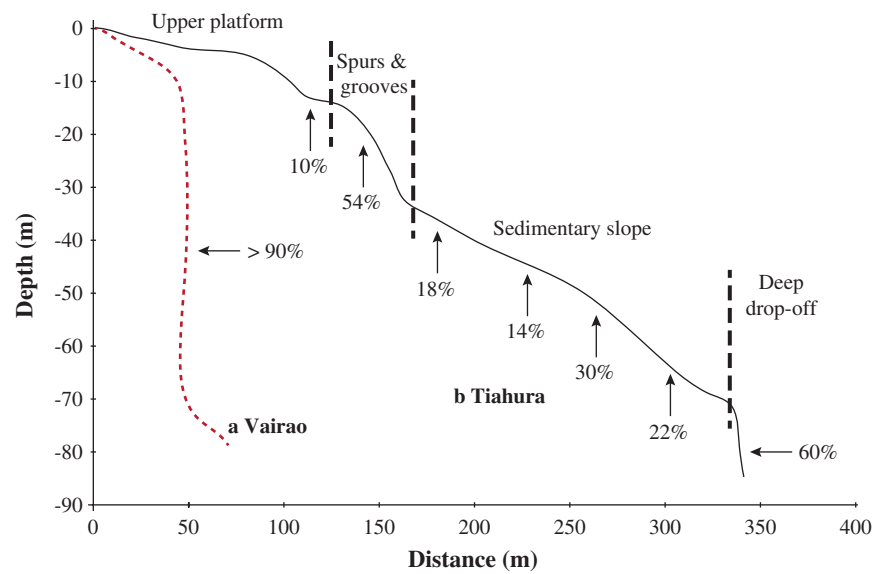


Fig. 24.5 Temperature and salinity profiles, offshore Tahiti, 21 September 1992 (modified from Wolanski and Delesalle 1995a). Broken line indicates temperature value of approximately 22 °C

Temperature On a broad geographic scale, average sea surface temperatures for offshore waters show a gradual decrease toward higher latitudes (down to 20–22 °C in the southern Austral Islands) and also eastward. The yearly amplitude of variation is higher in the high latitudes than

for instance in the Society and Tuamotu Archipelagos, where surface temperatures remain around 26–28 °C. A depth profile of temperature from 21 September 1992 offshore of Tahiti (Wolanski and Delesalle 1995a) shows only a minor decrease in temperature down to ca. 70 m and a slightly more rapid decrease to approximately 200 m, where the temperature remains above 22 °C (Fig. 24.5). It can be therefore inferred that the temperature in the whole mesophotic zone remains well within the range compatible with normal scleractinian requirements. However, very short-term (intervals of only a few hours) temperature fluctuations of significant amplitude can occur in the waters near the fore-reef slopes at mesophotic depths: even though temperature remains stable through the same time period at shallower depths (30 m), fluctuations of 2.5 °C have been observed at 85 m depth and nearly 4 °C at 125 m, off the slope of the barrier reef of Papeete, Tahiti (Wolanski and Delesalle 1995b; Fig. 24.6). Over a period of 6 months, such large fluctuations have been shown to be common, with at least one and occasionally two occurring in a 24 h period every third day. They are the result of the occurrence of large amplitude internal waves, which can lift the deeper nutrient-rich waters by up to 100 m. Such internal waves and associated short-term temperature fluctuations have also been observed in Palau (Wolanski et al. 2004; Colin 2009). In French Polynesia, they have been evidenced not only in Tahiti but in the atolls (Mururoa) as well (Wolanski and Delesalle 1995b). Although the lowest temperature values recorded during these events are only on the order of 21 °C, the effects of such rapid, frequent variations in temperature (and increased nutrient levels) on the mesophotic and even on the shallower reef benthos remain unknown.

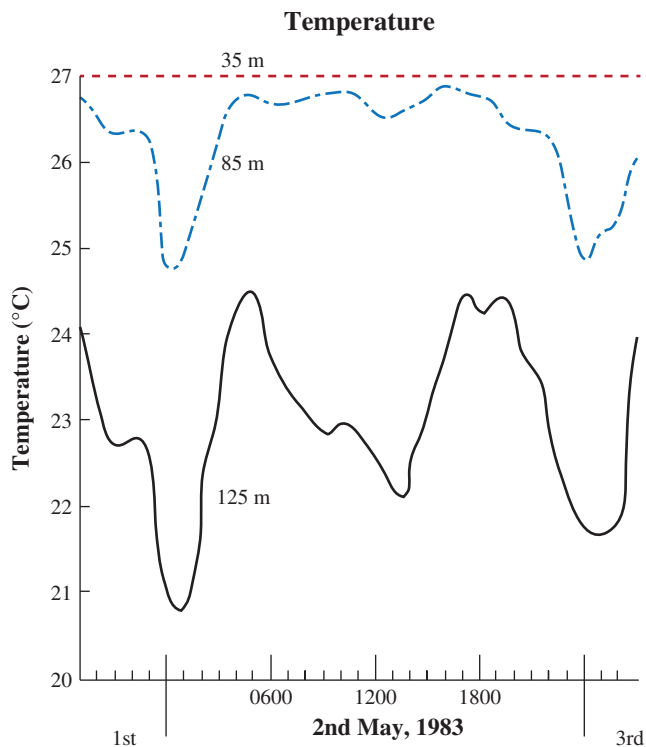


Fig. 24.6 Short-term variations of temperature at 35, 85, and 125 m depth, off Papeete barrier reef, 2 May 1993. (Redrawn from Wolanski and Delesalle 1995b)

24.3 Habitat Description

Coral reefs are associated with most of the islands of French Polynesia, but they display considerable variations in terms of their morphological features. Coral reefs can be broadly classified in two major types. The first type is distinguished by coral-dominated communities without framework accretion. This type can be only found in the Marquesas, which have a very depauperate scleractinian coral fauna, with only 26 zooxanthellate species (Benzoni and Pichon 2016) compared to the rest of French Polynesia. The second type includes fringing reefs and barrier reefs encircling high islands with lagoon of variable width, and atolls that range from submerged atolls to a raised or uplifted atoll (on Makatea only). Furthermore, the general shape of the atolls may vary considerably, with consequences on the degree of exposure to wind and swell of the upper outer slopes, and also their size (from 1720 km² for Rangiroa to only 3.1 km² for South Tepoto) and depth of the lagoon (from only a few decimeters at Nukutepipi to nearly 70 m at Hao and Rangiroa).

24.4 Biodiversity

Shallow species diversity for algae and several invertebrate groups in French Polynesia is reasonably well known (Richard 1985), although there is much disparity in the level of knowl-

edge of the various phyla and classes. By and large, the lagoon, reef flat, and shallow-water reef environments have been more studied from both a faunistic/floristic biodiversity and community ecology aspects than the outer reef slopes. However, even for the better-known groups, data on depth distribution is either completely absent or lacking the resolution that would be necessary to identify the species or suite of species that could indicate some degree of characterization and be distinctive of the mesophotic coral environment.

In the absence of any coordinated and integrated program for MCE research in French Polynesia, only little information, obtained mostly incidentally, is available, and the little existing is scattered in the literature. The following is an attempt at synthesizing information and data obtained through various unrelated projects and without uniformity of approach, sampling protocol, and sampling effort.

24.4.1 Macroalgae and Sea Grasses

The algal flora is diverse (Payri et al. 2000), but depth data are lacking for many species. The vast majority of them seem to be limited to shallow reefs and are not found below 20 or 30 m. *Caulerpa serrulata* and *Halimeda incrassata* are present in sedimentary areas, the latter being locally very abundant, with its broken down calcified particles representing up to 80% of the sediment particles. Both species do not extend on the fore-reef slope beyond 40–45 m depth.

Except for the occasional presence of *Caulerpa seuratii* (rare to uncommon), the slope below 30–40 m is essentially the domain of the rhodophytes, which are represented by *Cryptonemia umbraticola* and *Peyssonnelia inamoena*, both reaching ca. 40 m depth, to which one can occasionally add *Titanophora weberae*, the gelatinous *Predaea laciniosa*, *Platoma abbottiana*, and the even less common *Gibsmithia hawaiiensis*. The obvious exception to the above is the chlorophyte *Caulerpa bikinensis*, which is present on the outer slope of some atolls of the Tuamotu (e.g., Takapoto) where it forms dense, continuous carpets with a substratum cover of more than 70% at a depth of 35 m and can still form dense monospecific stands well beyond 70 m depth (Meinesz et al. 1982).

The only seagrass species present on the fore-reef slope at mesophotic depths is *Halophila decipiens*. It is limited to gently sloping areas where sediment of appropriate characteristics can be found. This is the case, in particular of the “sandy plain” on the outer slope of Moorea, where it usually forms isolated patches which can be observed down to 45–47 m deep (Mazeas 1993).

24.4.2 Anthozoans

24.4.2.1 Scleractinian Corals

Inventories of scleractinian coral species occurring in French Polynesia by Chevalier (1979) and Pichon (1985) were based

on collections and observations made on shallow reefs and did not provide any information on the fauna of the deeper reef slope. A list of zooxanthellate scleractinian species present in the various archipelagos and islands at depths of more than 30 m is presented in Table 24.1 and is a first compilation for the mesophotic reef environment of data available in the literature, to which only a handful of recent records from visual observations or in situ photographs have been added. Scleractinian nomenclature has been updated as far as practical to conform to the recent taxonomic revisions, but only obvious cases of synonymy have been taken into account. Whenever data were available, presence is given for bathymetric zones of increasing depths, but there is no consistency between them for the various locations.

Overall, for French Polynesia, a total of 96 zooxanthellate species have been recorded to date below 30 m and to a depth of 150 m, representing 49% of the total zooxanthellate scleractinian fauna of French Polynesia, which includes 195 species (excluding subfossil and undescribed species referred to by Chevalier (1976, 1978, 1980)). The known species are distributed in the five archipelagos as follows: Society, 126 species; Tuamotu, 108; Gambier, 54; Austral, 134; and Marquesas, 26.

24.4.2.2 Non-scleractinian Cnidarians

There is a paucity of data concerning diversity and abundance of non-scleractinian cnidarians in the MCEs of French Polynesia. Among the calcified hydrocorals, *Millepora* sp. has been observed in the “upper mesophotic” zone (ca. 30–45 m depth) but is uncommon. *Distichopora violacea* is also occasionally present in small cavities or crevices at mesophotic depths, but this species can also be found in a few decimeters of water, including on the reef flat. *Stylaster sanguineus* has been observed, particularly on vertical or even overhanging walls on the slopes of Tikehau, where it can develop into dense aggregations of up to 25 colonies per m² (Faure and Laboute 1984). The most frequent non-calcified hydroid, the tall *Macrorhynchia philippina* is mostly present when the slope of the substratum is moderately steep. Alcyonaceans (particularly the Nephtheidae) and gorgonians are significant components of the mesophotic assemblages and reefscape, but no inventory or abundance data is available at the species level. Likewise, several antipatharians belonging to the genera *Antipathes*, *Myriopathes*, and *Cirripathes* can generally be observed in the mesophotic zone (including the deeper zone, below ca. 90 m, for the first two genera), but they have not been identified to species level.

24.4.3 Sponges

Although a significant amount of information on the sponges of French Polynesia is available (Petek and Debitus 2017), no data are provided on their depth range. In the associated

database maintained by the Queensland Museum, Brisbane, Australia, 88 species out of a total of 308 entries are recorded at or below 30 m depth and nine at or below 60 m, from collections made by SCUBA diving to a maximum of 68 m (Merrick Ekins, pers. comm.).

24.4.4 Fishes

A considerable amount of research has been carried out on the fishes of French Polynesia, resulting in a large number of publications. As far as the ichthyofauna of coral reefs is concerned, virtually all published studies on the outer reef slopes have been limited to the 0–30 m depth range (hence excluding the mesophotic coral environment). The major exception is that of Vigliola (1993) and Vigliola et al. (1996), which targeted the ichthyofauna of the lower reef slope (ca. 30–70 m) at Tiahura on the north coast of Moorea. The substratum in this area consists of a moderately inclined sedimentary slope, with numerous, sometimes large-sized dead coral blocks present in both the shallower and deeper parts of the sedimentary slope. The fish fauna includes 75 species belonging to 24 families. The most diverse families are the Labridae (ten species), Acanthuridae (ten species), Pomacentridae (seven species), Balistidae (six species), Serranidae (five species), and Mullidae (five species). Most species are found in the areas where hard substrates are important, toward the top and bottom of the slope. Conversely in the central sandy part of the slope, fish diversity and abundances decrease markedly, with only eight species recorded. This zone, though, has two species of garden eels (Heterocongrinae), *Heteroconger lentiginosus* (very rare) and *Gorgasia galzini*, the latter of which has an average density of six individuals per m² (Vigliola et al. 1996). Other common species in the Heterocongrinae zone are the Balistidae *Odonus niger* and *Sufflamen fraenatus* and the Mugiloididae *Parapercis schauinslandi*. The occurrence of Heterocongrinae in reef environment is uncommon, albeit known from other reefs in several parts of the Indo-Pacific (Fricke 1973; Randall et al. 1990). In French Polynesia, *Gorgasia galzini* has been recorded only on the outer slope of Moorea; *Heteroconger lentiginosus* has also been observed in the Marquesas (Vigliola et al. 1996).

24.4.5 Other Biotic Components

24.4.5.1 Mollusks

The malacological fauna of the deep fore-reef slope is hardly known. Information available suggests that in contrast to what is observed on the reef flat and in lagoons, both species diversity and biomass are low. Two species of gastropods live in the sedimentary areas: *Lambis lentiginosus*, found mostly between 30 and 40 m depth, and *Cerithium clava*, between 40 and 60 m (Mazeas 1993).

Table 24.1 (continued)

Species	Society Islands			Tuamotu Islands			Gambiers			Austral Islands		
	Tahiti (1)	Moorea (2)	Takapoto (3)	Tikehau (4)	Mururoa Fangataufa (5)	Gambiers (6)	Tubuai (7)	Rapa (8)	Tubuai (7)	90–100	40–90	30–40
	30–60	30–35	30–40	35–70	30–38	>30	30–40	30–40	30–40	90–100	40–90	30–40
Family	30–60	30–35	30–40	35–70	30–38	>30	30–40	30–40	30–40	90–100	40–90	30–40
<i>Echinopora gemmacea</i>	MER						X					
<i>Echinopora lamellosa</i>	MER								X			
<i>Goniastrea pectinata</i>	MER											X
<i>Goniastrea stelligera</i>	MER	X			X							
<i>Leptoria phrygia</i>	MER											
<i>Paragoniastrea australiensis</i>	MER											X
<i>Paragoniastrea russelli</i>	MER											X
<i>Platygyra daedalea</i>	MER		X									X
<i>Coscinaraea columna</i>	COS											X
<i>Coscinaraea fossata</i>	COS								X			
<i>Madracis</i> sp.	POC										X	
<i>Pocillopora damicornis</i>	POC					X						X
<i>Pocillopora elegans</i>	POC											
<i>Pocillopora solida</i>	POC											
<i>Pocillopora verrucosa</i>	POC		X									X
<i>Stylocoeniella guentheri</i>	POC		X									X
<i>Psammocora hainiana</i>	PSA											X
<i>Psammocora profundacella</i>	PSA		X									
<i>Leptastrea cf. bottae</i>	INC											
<i>Leptastrea purpurea</i>	INC		X								X	
<i>Leptastrea transversa</i>	INC											

(1) Pichon (unpublished data), (2) Chevalier and Kühlmann (1983), (3) Bouchon (1983), Kühlmann and Chevalier (1986), (4) Faure and Laboute (1984), (5) Faure (1997), Gout et al. (1997), (6) Chevalier (1974), (7) Chevalier (1980), (8) Faure (1986), Adjeroud et al. (2012)
 ACR Acroporidae, AGA Agariciidae, EUP Euphylliidae, FUN Fungiidae, INC Incertae sedis, LOB Lobophylliidae, MER Merulinidae, POC Pocilloporidae, POR Poritidae, PSA Psammocoridae

24.4.5.2 Echinoderms

Except for the infrequent sea star *Culcita novaeguineae* rarely found much below 30 m depth, echinoderms are represented in the parts of the fore-reef slope with sediment deposits (Tiahura, Moorea) by the holothurians *Thelenota ananas*, *T. anax*, *Holothuria fuscogilva*, and *Bohadschia argus*, which, except for the former, limited to 30 m, can extend to a depth of ca. 60 m (Mazeas 1993). On the deep outer slope of the atolls (Takapoto, Tiahura), *Linckia multi-fera* (Asteroid), *Holothuria turricelsa* and *Microthele nobilis* (Holothuroids), *Echinothrix calamaris* and *Paraselenia gratioiosa* (Echinoids), and *Ophiolepis superba* (Ophiuroid) have been reported between 40 and 80 m depth (Laboute 1985). None of the above species, however, are restricted to MCEs in French Polynesia.

24.4.5.3 Crustaceans

Comprehensive lists of crustaceans (decapods and stomatopods) mostly compiled from bibliographic records for all types of environments in French Polynesia have been published by Poupin (1996, 1998), who notes that the crustacean fauna is, like for most other biotic components, less diverse than that of the Indo-Malayan region. Whenever available depth data are given as “littoral” (to a depth of a few meters only), “sublittoral” (10–100 m depth), and “deep” (>100 m depth). Hence, species found in the mesophotic zone could be referred to from a bathymetric standpoint as “sublittoral” or as “deep,” noting that “sublittoral to deep” is also used occasionally. It is likely that few species, if any, are limited to MCEs. The database by Legall and Poupin (2017) indicates the presence of 89 species of decapods between 10 and 190 m depth for French Polynesia, with 28 species in the Society Archipelago, 23 in the Tuamotu, 72 in the Austral, 5 in the Gambier, and 54 in the Marquesas.

24.5 Ecology

24.5.1 Scleractinian Coral Diversity and Depth Distribution

The proportion of species living below 30 m depth is high compared to the total zooxanthellate scleractinian fauna (Table 24.2) reaching up to 44% in the Austral Islands. This may be in part a consequence of the overall water clarity of oceanic waters. There is, however, a sharp decrease between the number of species present below 30 m and below 60 m. This could indicate that a high proportion of the shallow-water species (depth generalists) extend into the upper mesophotic zone (ca. 30–60 m), but not to the lower mesophotic zone (below 60 m). Hence, the suggestion that the scleractinian assemblages in the upper mesophotic zone are simply an impoverished aspect of the shallow-water community could be put forward. Alternatively, a case could be made to con-

Table 24.2 Number of zooxanthellate scleractinian species recorded for each archipelago and number of species and corresponding proportion of the total scleractinian fauna present below 30 and 60 m

Archipelago	Total number of zooxanthellate species ^a	Number of species present below 30 m ^b	Number of species present below 60 m ^b
Society	129	36 (28%)	6 (4.5%)
Tuamotu	106	42 (40%)	5 (4.7%)
Gambier	55	6 (11%)	No data
Austral	149	65 (44%)	6 (4.0%)
Marquesas	26	1 (4%)	0 (0%)

^aPichon (unpublished data)

^bSee Table 24.1

sider that the upper mesophotic zone actually starts at a depth lower than the largely arbitrary value of 30 m, but there are presently insufficient data to confirm that this is true.

When considering separately each archipelago, both Tuamotu and Austral show a percentage of mesophotic species (below 30 m depth) of the same order as the overall average. The lower figure for the Society Island (28%, Table 24.2) may be the combined result of under sampling, particularly in the lower mesophotic zone, and the fact that in the most studied island (Moorea) much of the zone between 30 and 70 m depth approximately is a gently sloping platform, covered with sedimentary deposits of various sizes (the “sandy plain”), a substratum which is not conducive to the presence of significant scleractinian assemblages. Mesophotic depths in the Gambier have also been under sampled.

The Marquesas represent a different situation, although they are situated at much lower latitudes than the other archipelagos; the zooxanthellate fauna is very depauperate, with only 26 species recorded (Benzoni and Pichon 2016). Several reasons to explain such low species diversity have been suggested, including the isolation and the recent geological age of the archipelago, the lack of habitat diversity, unfavorable hydrodynamic conditions for larval fixation, competition with macroalgae, occasional phytoplanktonic blooms, and/or influxes of terrigenous sediments (Ranson 1952; Sournia 1976, 1977; Chevalier 1978). Although the mesophotic depths there have probably been under sampled, fossil reef terraces are known to occur at depths of around 80 and 120 m, but so far the only living species observed below 30 m is *Leptoseria hawaiiensis* between 53 and 61 m (pers. obs.).

A relatively high species diversity, when compared to the Tuamotu or the Society Archipelagos, is recorded from the Austral Islands, particularly at the high latitude island of Rapa (27°28' S) (Adjeroud et al. 2009, 2012, 2016), and this is reflected in the high percentage of species recorded from mesophotic depths. The high species diversity in the Austral Islands has been explained by the fact that the general oceanic circulation in this part of the Pacific Ocean brings to the archipelago a flux of larvae originating from the Cook Islands, which has a more diverse coral fauna than French



Fig. 24.7 *Pachyseris speciosa* is a conspicuous component of mesophotic assemblages in the Society and Tuamotu Archipelagos, Tahiti at 65 m. (Photo credit: Gilles Siu)

Table 24.3 Relative importance of each scleractinian coral family in the mesophotic environment as a proportion of the total scleractinian fauna

Family (Genus)	Number of species in French Polynesia ^a	Number of species recorded below 30 m ^b	Percentage of species recorded below 30 m
Acroporidae	89	26	29
(<i>Acropora</i>)	52	13	25
Agariciidae	15	15	100
(<i>Leptoseris</i>)	6	6	100
Euphylliidae	2	1	50
Poritidae	9	6	66
Fungiidae	21	12	57
Lobophylliidae	10	8	80
Merulinidae	26	14	54
Coscinaraeidae	1	1	100
Pocilloporidae	13	6	46
Psammocoridae	6	2	33

^aPichon (unpublished data)

^bSee Table 24.1

Polynesia (Chevalier 1980, 1981). However, a common and widespread genus such as *Pachyseris* with its keystone mesophotic species *P. speciosa* (Fig. 24.7) is totally absent from the Austral Islands (and also from the Gambier and Marquesas) but is common in the Society and Tuamotu Archipelagos (See Table 24.1 and references therein).

For each of the families represented in French Polynesia, the proportion of species present in the mesophotic environment (Table 24.3) varies from 29% (Acroporidae) to 100% (Agariciidae and Coscinaraeidae, with the latter represented by only one species). Among the Acroporidae, only 25% of the species in the genus *Acropora* are present below 30 m, which is the lowest of all percentages. This value is in agreement with the trend observed throughout the Indo-Pacific, indicating that this genus, the most diverse of all scleractinian genera, has not been particularly successful in colonizing MCEs (Kahng et al. 2010). More recent studies suggest that there may be local exceptions (Muir et al. 2015). Conversely, all genera in the family Agariciidae are found in



Fig. 24.8 Several species of *Leptoseris* sometimes forming large plate-like colonies co-occur and often become dominant below 55 m, Tahiti at 60 m. (Photo credit: Gilles Siu)

the mesophotic zone and all species of the genus *Leptoseris* occur below 30 m (Fig. 24.8). The three other most diverse families (Poritidae, Fungiidae, and Lobophylliidae) are reasonably well represented in the MCEs of French Polynesia, where, respectively, 66, 57, and 80% of the genera have been observed.

At the species level, out of the 96 species occurring below 30 m, 12 are known to occur below 60 m (Table 24.4). In French Polynesia, the deepest recorded species is *Leptoseris hawaiiensis* at 150 m at Tubuai, followed by *L. fragilis*, *Cycloseris wellsii*, and *Echinopora lamellosa* at a depth of ca. 100 m (Chevalier 1980). It should be noted that these species were collected by dredging with R/V *Marara*, and although the team on board had considerable dredge sampling experience, there is always some degree of uncertainty as to the exact depth of dredge sampling. The presence of *L. hawaiiensis* at a depth of ca. 150 m is not completely surprising as the species has also been collected at 165 m at Johnston Atoll (Maragos and Jokiel 1986). Other species of *Leptoseris* are also known to extend to the deepest part of the mesophotic zone, for instance, to 153 m for *Leptoseris* sp. at Hawai'i

(Kahng and Maragos 2006) and 145 m for *Leptoseris* cf. *fragilis* in the Gulf of Eilat, northern Red Sea (Fricke et al. 1987). At Tahiti (Vairao), *Leptoseris fragilis*, *L. mycetoseroides*, *L. scabra*, and *Echinophyllia aspera* (Fig. 24.8) have been recorded at a depth of 85 m. Out of the 12 species listed in Table 24.4, only 2 (*Alveopora allingi* and *Leptoseris fragilis*) have not been recorded in the shallow (<30 m) reef environment. This would suggest that the mesophotic scleractinian fauna of French Polynesia is predominantly composed of depth generalists or eurybathic species and that the depth specialists represent only a small proportion of the total mesophotic coral fauna.

24.5.2 Quantitative Aspects

Although no systematic study of coral abundance and dominance have been carried out at mesophotic depths in French Polynesia, a few incidental, mostly visual records are available in a limited number of instances, and they are generally expressed in terms of percentage substratum cover by the

Table 24.4 List of scleractinian species recorded from the mesophotic environment (>60 m), by archipelago

Species	Society (Tahiti) > 60 m	Tuamotu (Tikehau) > 70 m	Austral (Tubuai) > 90 m	Austral (Rapa) > 60 m
<i>Alveopora allingi</i>	0	0	0	1
<i>Leptoseris fragilis</i>	1	0	1	0
<i>Leptoseris hawaiiensis</i>	0	1	0	0
<i>Leptoseris mycetoseroides</i>	1	0	0	0
<i>Leptoseris scabra</i>	1	0	0	0
<i>Pachyseris speciosa</i>	1	1	0	0
<i>Cycloseris wellsii</i>	0	0	1	0
<i>Porites lobata</i>	0	0	1	0
<i>Acanthastrea echinata</i>	1	0	0	0
<i>Echinophyllia aspera</i>	1	1	0	0
<i>Echinophyllia echinata</i>	0	0	1	1
<i>Echinopora lamellosa</i>	0	0	1	0
Total number of species: 12	6	3	5	2

See Table 24.1



Fig. 24.9 The “coral rose garden” on the fore-reef slope, north coast of Moorea, 45 m. (Photo credit: Yannick Chancerelle)

coral assemblages or by individual, dominant species. The information available can be summarized as follows:

24.5.2.1 Society Islands

Off the northern coast of Moorea, the parts of the fore-reef slope which are not covered by the sedimentary deposits, between ca. 30 and 70 m depth, show an almost continuous monospecific cover of the substratum (up to 70–80%) by *P.*

speciosa, over large areas (pers. obs.). The colonies themselves are often of a large size, composed of stacked irregular twirls of crateriform laminae, giving the reefscape a characteristic appearance, appropriately named locally “coral rose gardens” (Fig. 24.9). At Tahiti, on the outer slope of the barrier reef of Papeete (between Fare Ute and Taunoa), substratum cover by corals is 70–80% at a depth of ca. 40 m, decreasing to approximately 40–50% at depths between 60



Fig. 24.10 *Pachyseris speciosa*, growing on a near vertical drop-off in southwest Tahiti. Coral cover is generally lower on steep slopes than on gently inclined substrata, 80 m. (Photo credit: Gilles Siu)

and 80 m with a relative slight increase of branching forms compared to lamellar forms (Mombet 1987). The “coral rose” formations of *P. speciosa* are present around most of Tahiti but in general are not as spectacular as on the fore-reef slope of the northern coast of Moorea. No data are available for the deeper drop-off. On the near vertical walls of the fore-reef slopes present in parts of the Tahiti-Iti peninsula (Vairao), coral cover decreases dramatically to 10% or even less between 60 and 90 m, with the dominant species being *P. speciosa* (Fig. 24.10) and *Leptoseris* spp. (Fig. 24.11).

24.5.2.2 Tuamotu Islands

Quantitative data on scleractinian coral distribution in the atolls of the Tuamotu are available for Takapoto (Bouchon 1983; Kühlmann and Chevalier 1986), Tikehau (Faure and Laboute 1984), and, to a lesser extent, Fangataufa (Gout et al. 1997). The mesophotic information provided though is not easily extracted.

For Takapoto (14°40' S), Kühlmann and Chevalier (1986), for instance, refer to a depth range of either 20–50 m or

20–70 m for the steep lower slope or as part of the outer slope below 30 m. Substratum cover by scleractinians is particularly high between 20 and 30 m, as underlined by Bouchon (1983): “On the outer reef slope... the coral assemblages display[s] an extraordinary vitality, translated by a remarkably high level of substratum cover,” with figures of 75% at 20 m depth and 64% at 30 m, decreasing rapidly between 30 and 50 m (Fig. 24.12). Substratum cover may be spatially variable and influenced by exposure to the dominant swell, which controls the slope topography and amount of sedimentation. On the northwest side of the atoll, coral cover is approximately 40% at 40 m depth, whereas on the southeast side, which is directly exposed to the trade winds, coral cover (which is 10–15% at 30 m) falls to 5% at 40 m and to 1–2% at ≥ 60 m (Kühlmann and Chevalier 1986). Dominant species below 30 m depth are *Porites australiensis*, *Leptoseris incrustans*, *Pachyseris speciosa*, and *Echinophyllia aspera*, and the deeper slope assemblage is characterized by *Leptoseris hawaiiensis*, *L. incrustans*, *L. scabra*, and *Stylocoeniella guentheri* accompanied by the hydrocoral *Stylaster* sp.

At Tikehau (15° S) the fore-reef slope has been studied to a depth of approximately 75 m by Faure and Laboute (1984). They consider that the coral assemblages between 25 and 35 m represent a transition between the typically shallow-water reef communities and the more shade-related assemblages found on the drop-off below, with a progressive replacement of typical surface reef species by *P. speciosa*, with the substratum cover remaining above 50%. Between 35 and 60–75 m, *P. speciosa* remains the dominant species, accompanied by *Porites lobata*, *Gardineroseris planulata*, *Pavona varians*, *Leptoseris incrustans*, and *Echinophyllia aspera*. Below 60–70 m, *Porites* and *Pavona* disappear, and the relative abundance of the species accompanying *P. speciosa* (*L. hawaiiensis*, *L. sabra*, *Echinophyllia aspera*, and *E. echinata*) increases, with a substratum cover with values of 65–75% down to at least 90 m. Locally, when the substratum becomes almost vertical or even overhanging, the *Pachyseris-Leptoseris* assemblage is partly replaced by *Stylaster sanguineus*.

At Fangataufa (22°15' S), scleractinian coral communities on the outer slopes were examined in 1966 (Gout et al. 1997) and surveyed again more thoroughly in 1987 (Faure 1997). Both the windward and leeward sides of the atoll have been investigated, but observations are limited to a depth of 38 m and quantitative data to 30 m. In 1966, the dominant species on the leeward side, between 30 and 38 m, were *Goniastrea stelligera* (already found at depths as shallow as 5 m), *Acropora nasuta*, *Montipora aequituberculata*, and *Pavona maldivensis*. With the exception of *G. stelligera*, the same species are dominant in the communities of the windward slope, with the addition of *Leptastrea transversa*, *Porites lobata*, and *Astreopora myriophthalma* (Gout et al. 1997).

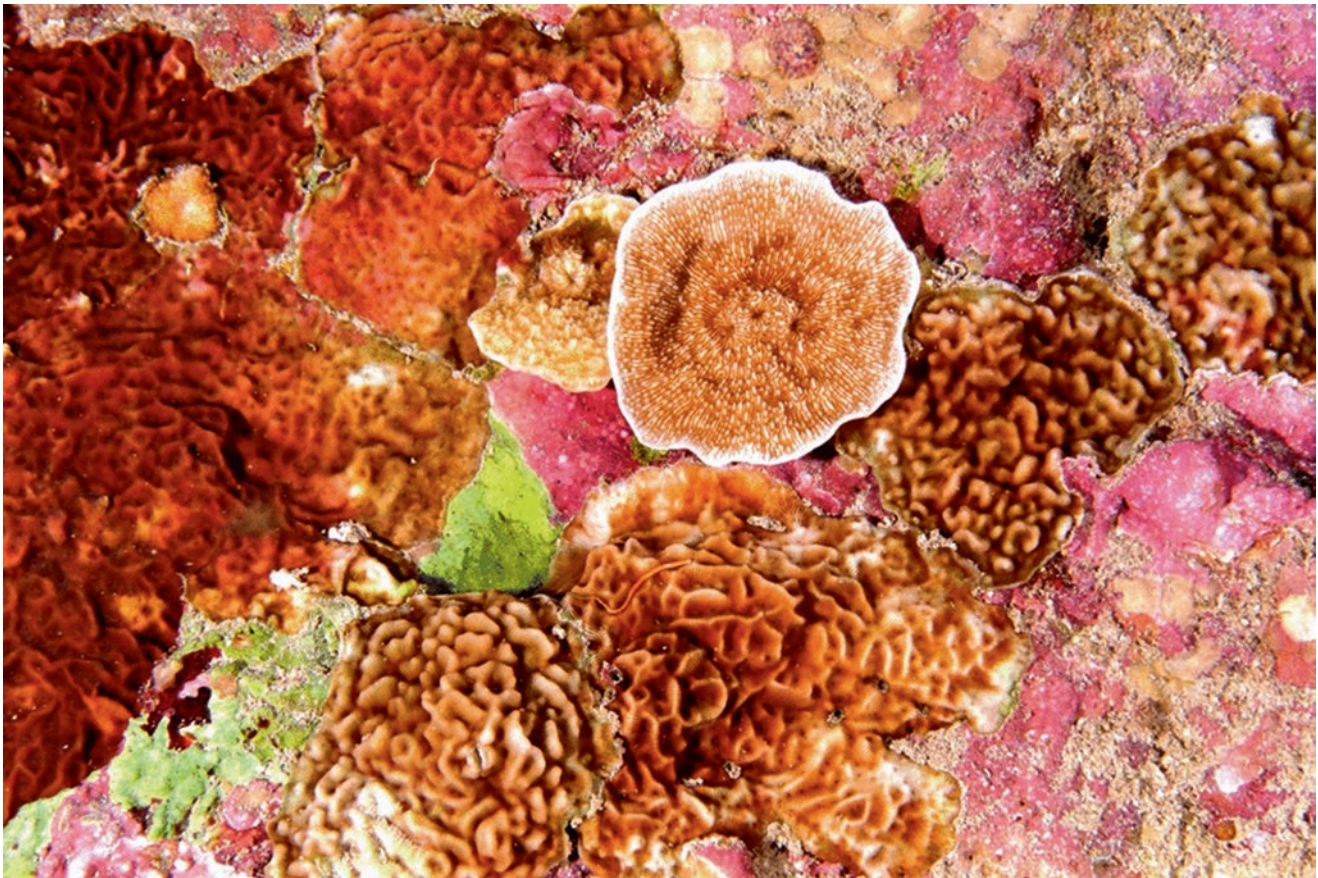


Fig. 24.11 Unusual high substratum cover by *Leptoseris* spp. on a steeply inclined slope, Vairao, Tahiti, at 70 m. (Photo credit: Gilles Siu)

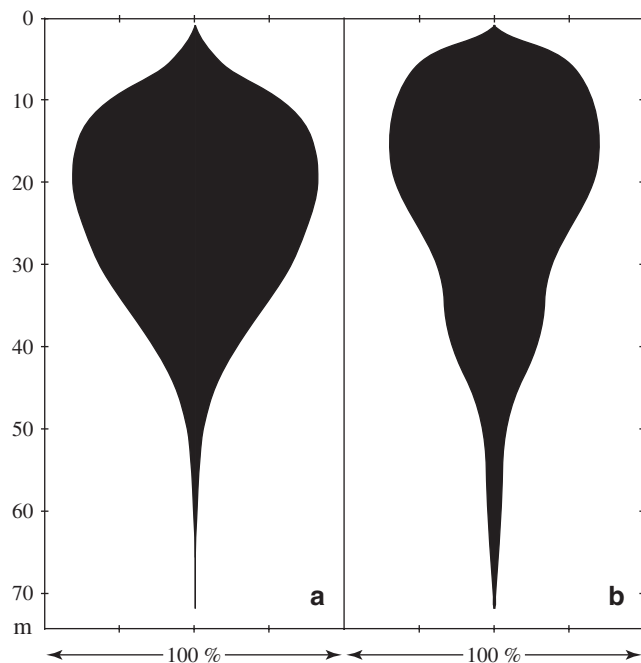


Fig. 24.12 Substratum cover by scleractinian corals as a function of depth at Takapoto: (a) outer windward slope, (b) outer leeward slope. (Adapted from Kühlmann and Chevalier 1986)

In 1987, substratum cover by corals on the windward side was as low as 20% at 30 m, with the two dominant species *Pocillopora elegans* and *Astreopora myriophthalma* making 88% of the coral cover and *Leptastrea transversa* coming in third. At 38 m depth, they were replaced by *Montipora aequituberculata* and *Pavona maldivensis*. On the leeward side, substratum cover at 30 m depth was 60–65%, with the dominant species being *Pavona maldivensis*, *Montipora tuberculata*, *Acropora nasuta*, and *Pocillopora elegans*, with the first two species making up to 90% of the coral cover at one station. At 38 m depth, the substratum cover is estimated to be on the order of 70% and the composition of the coral assemblages remaining basically the same as at 30 m depth, with the addition, at a low level of abundance, of *Leptoseris incrustans* and *L. hawaiiensis*. The significant differences in terms of substratum cover by the coral assemblages between the windward and leeward slopes can be explained by the limiting effects of very strong swell and heavy sedimentation on the windward side (Faure 1997).

In some atolls of the Tuamotu, such as Rangiroa and Hao, the depth of the lagoon is close to 70 m and based on depth alone could harbor MCEs. The presence of such communities is known to exist in the lagoon of Palau at 30–36 m

(Colin et al. 2014) and New Caledonia at 35–45 m (Joannot et al. 2016).

24.5.2.3 Austral Islands

Tubuai (23°22' S) is situated midway in the Austral Islands chain. It is a volcanic high island surrounded by a barrier reef with a total length of 36 km encircling a lagoon with a surface area of 85 km². Data on scleractinian coral distribution on the reefs of Tubuai are given by Chevalier (1980). The upper part of the outer reef slope is moderately inclined down to a depth of ca. 25 m. Beyond 25 m, the slope becomes abruptly steeper and remains more inclined down to depths of 45 to 50 m. Substratum cover by scleractinian corals is approximately 75% but decreases after 40 m. Dominant species are *Goniastrea pectinata*, *Lobactis scutaria*, and *Galaxea fascicularis* in the northern part of the barrier reef and *Porites lobata*, *Lobactis scutaria*, and *Gardineroseris* sp. in the southern part. Beyond 45–50 m, the slope is less steep. The dominant species are at first *Pavona maldivensis* and *Leptoseris incrustans* but are progressively replaced by *L. hawaiiensis* and *L. cf. fragilis*, and then the substratum coral cover decreases sharply, leaving only a few sparsely distributed colonies of *L. hawaiiensis* down to 150 m.

24.6 Threats and Conservation Issues

Except for Tahiti, and in particular the urban center of Papeete, French Polynesia is sparsely populated. Anthropogenic impacts such as pollutants from land-based sources (e.g., sewage outfalls, freshwater runoff, and chemical pollution) and disturbances including some tourist and recreational activities, collecting and fishing, coral sand dredging, and coral rock mining (once widespread but prohibited several decades ago) are more likely to affect fringing reefs and lagoons, where most of the human activity takes place, and to impact the environment close to more populated locations such as Tahiti, Moorea, or Bora Bora. Concern has been expressed in particular as to the possible immediate and long-term effects of agricultural development, particularly pineapple cultivation on Moorea, which releases toxic chemicals into the marine environment such as chloroacetamide derivatives and chlordecone (Roche et al. 2011). Although their presence has been detected in all reef organisms tested, the impact, particularly on MCEs, remains unknown.

The major impacts on MCEs are the consequences of the passage of cyclones. Cyclonic disturbances are not high-frequency events in French Polynesia and occur at irregular intervals. Cyclonic periods have been recorded in particular at the beginning of the twentieth century (1903–1906) and more recently in 1982–1983, 1997–1998, and 2010. Destruction of coral-dominated communities has been extensive, including on the outer slopes. It has been estimated that

at Tikehau, live corals had disappeared, having been smashed or removed, on 80% of the outer slope surface area (to 90 m deep) and on 36% of the outer slope surface area at Takapoto (Laboute 1985). The amount of destruction is greater on the steeply inclined slope than on the gentler slope, due to differential action of the mechanisms involved: between the surface and 15 or even 20 m depth, corals, predominantly branching, are dislodged or smashed by the direct action of cyclonic swell, and the debris pile up on the reef flat. The predominantly massive and often large-sized species living around 15–20 m depth are also smashed (in larger fragments or dislodged), and they roll down the slope, creating an “avalanche” effect, which crushes the more fragile, lamellar colonies dominant on the fore-reef slope (e.g., *P. speciosa* and *Leptoseris* spp.). The avalanche effect is stronger on steep slopes (which are a common occurrence in the atolls of the Tuamotu), and its consequences are felt deeper, eventually leading to the total destruction and disappearance of mesophotic assemblages, down to at least 80 m. Recovery time very much depends on the severity of the destruction, and it is estimated that it varies from 2 to 10 years in cases of limited damage but could be ~50 or more years in cases of total destruction (Harmelin-Vivien and Laboute 1986).

24.7 Conclusions and Perspectives

Isolated in the central part of the Pacific Ocean, exposed to a wide range of environmental conditions, sparsely populated, with 118 islands, most of which have well-developed coral reefs, French Polynesia offers a number of natural advantages and an immense field of research for studies on MCEs. Although proportionally a very small number of its reefs have been studied below the depth of 30–40 m, data available indicate that mesophotic coral assemblages are present in at least three of the five archipelagos (Society, Tuamotu, and Austral) and at times, flourishing to depths of at least 80 m. Beyond that depth, however, it remains *locum ignotum*. The field of investigations, therefore, is huge and much is still to be done to obtain an accurate picture and in-depth knowledge of the deep fore-reef slope assemblages. If some inroads have been made with respect to species diversity for the major components of the mesophotic assemblages, important gaps remain to be filled with respect to their life cycles, community ecology, trophic structures, or metabolism to name but a few. There is light at the end of the tunnel, though: funding has been granted by the French National Research Agency for a major integrated research program (“Deephope”) specifically targeting MCEs in French Polynesia, to be conducted within the framework and with the support of the “Under The Pole” Expeditions. Starting mid-2018, MCEs between 40 and 140 m depth will be investigated at over 40 sites in the 5 archipelagos. It is therefore expected that a major leap for-

ward in our knowledge of deep fore-reef slopes will be forthcoming in the not too distant future.

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