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Abstract

In the last years, mesophotic coral ecosystems (MCEs) received increased attention from the research community. MCEs exist at depths between 30–40 m and until 100 m or deeper. While MCEs were already reported from Japan nearly 50 years ago, mesophotic research in Japan did not progress as in other countries like the USA or Australia. Nonetheless, over the years, several interesting studies were conducted on the MCEs found in southern Japan on various fields from geology to biology, and the momentum of Japanese mesophotic research increased in the recent years. In this chapter, we will summarize the knowledge on MCEs in Japan in different domains such as their distribution, their biodiversity, their occurrence in the fossil record, recent findings on the reproduction of mesophotic corals, their potential ecological role in a global change context, threats menacing these ecosystems, and future directions of MCE research in Japan.

Keywords

Deep coral reefs • Distribution • Biodiversity • Fossil corals • Ecology

10.1 Introduction to Mesophotic Coral Ecosystems

The vast majority of coral reef research has focused on corals found in shallow waters. However, coral ecosystems extend much deeper, where light intensity represents only a few percent of that measured in the first meters under the surface. In this “twilight zone”, light-dependent corals can form rich and complex ecosystems. These ecosystems found from 30–40 m down to over 100 m (165 m in some very transparent waters of the central Pacific) are usually referred to as mesophotic coral ecosystems or MCEs (Hinderstein et al. 2010). In the recent literature, the term MCE is also sometimes used to refer to deep environments not necessarily dominated by zooxanthellate corals but by sponges or algae. Although the strict definition of MCE is still under discussion (and in our

opinion the terms mesophotic algal ecosystems and mesophotic sponges ecosystems should be introduced for situations where these organisms are the main habitat builders), the shared characteristic of these different ecosystems is the presence of light-dependent sessile organisms despite a largely reduced light availability compared to the overlying shallow waters. Therefore, it is not surprising that “shallow” mesophotic communities have recently been found in areas with particularly low light penetration (Muir and Wallace 2015). Likewise, in addition to eurybathic species (species tolerating a wide range of depths) some species can be observed both in the mesophotic zone and in shaded parts of shallow reefs. Despite many gaps remaining in our understanding of mesophotic ecology, parameters other than light likely define MCEs. For example, cave ecosystems, although light limited and potentially sharing some species with MCEs, should be treated independently as they depend on different hydrodynamic, geomorphological, and biological processes. Nevertheless, overlapping species between shallow and mesophotic depths have become of great interest for researchers following the hypothesis that

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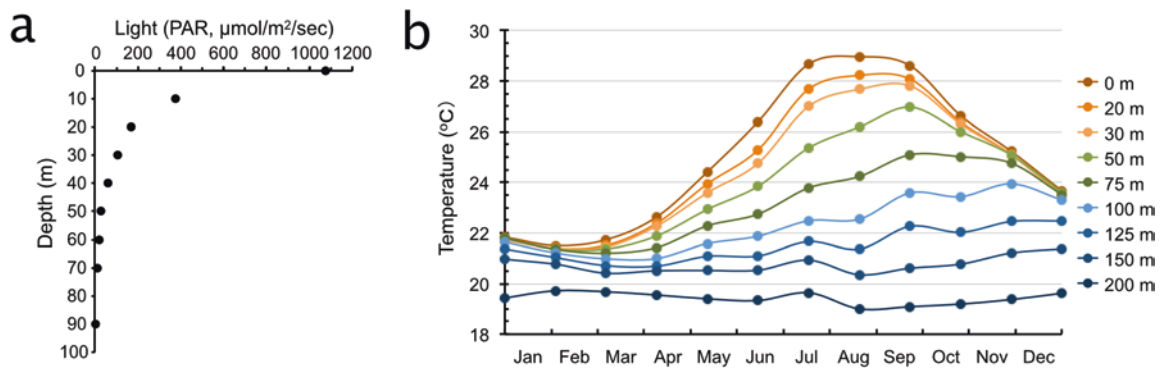


Fig. 10.1 Light and temperature from the surface to mesophotic depths. (a) Light measured on a sunny day offshore of Sesoko Island in March. (b) Monthly average temperatures over multiple years west of

Okinawa Island between 26–27 °N and 127–128 °E (Source: Japan Oceanographic Data Center, <http://www.jodc.go.jp/service.htm>)

“deep reefs could serve as refuge for shallow coral species under thermal stress” Glynn (1996). In addition to the excitement of discovering unknown communities and ecosystems, this hypothesis contributed significantly to the development of mesophotic research by motivating researchers to investigate on the relations between shallow and mesophotic corals and alerting decision makers and funding agencies on the potential importance of MCEs in a global context of climate change. Paradoxically, despite some of the first mesophotic coral ecosystems having been discovered in Japan (Yamazato 1972; Yamazato et al. 1967), Japanese MCEs remain relatively poorly explored (in comparison with the Great Barrier Reef, Hawaii, or the Caribbean Sea). However, this situation is progressively changing with reports of Japanese mesophotic corals increasing in recent years.

10.1.1 Environmental Conditions

In the Ryukyu archipelago, light penetration varies greatly depending on the sites and the seasons. Except in the relatively large islands of Amami, Okinawa, Ishigaki and Iriomote, the small size and limited watershed of most islands of the archipelago limits the potential for river sedimentary inputs. However, the extensively developed agriculture often accompanied by poor measure to prevent soil erosion was shown to affect shallow reefs (Omija 2004; Hongo and Yamano 2013; Yamano et al. 2015) and likely impacts coastal MCEs as well even though such impact remains to be investigated. At one of the most studied site near Sesoko Island offshore of the main island of Okinawa, the light (measured as Photosynthetic Active Radiation, PAR) reaching a diverse upper mesophotic community at 40 m represents 7.7 % of the light reaching the surface in average (Prasetia et al. 2016). Further offshore, only 5.5 % of the surface light was measured¹ near a deeper mesophotic

community at 40 m and 0.3 % at 90 m. At this location, zooxanthellate scleractinian corals are still found at a depth of 70 m, reached by only 0.8 % of the surface irradiance (i.e., $8.6 \mu\text{mol photon m}^{-2} \cdot \text{s}^{-2}$) (Fig. 10.1a).

Seawater temperature fluctuates seasonally down to 150 m depth. In winter, the water column is relatively homogenized with average temperatures² between 21.4 and 20.4 °C from the surface to 150 m depth. However in summer, while temperature below 150 m remains relatively constant around 19 °C, average temperatures in the first 100 m water depth range from 29 to 22.5 °C (Fig. 10.1b). Probably, the most peculiar environmental phenomenon in the region is the temperature inversion occasionally observed in winter, when mesophotic water is warmer than the surface water. Despite such events being limited in time and sporadic, they are recurrent enough for the monthly average temperatures in both December and January over several years showing slightly higher values at 50 and 75 m depth compared to 20 and 30 m (between 0.02 and 0.1 °C). Such events were also reported in punctual measurements recently made in the area (Prasetia et al. 2016). While leading to an unstable situation, this pattern of warmer deeper water can be easily understood when considering the geographical setting of the region. The Ryukyu archipelago receives warm water from Kuroshio, and this inflow of tropical water allows the high diversity of coral species to develop at this rather high latitude (24–29° latitude) and even at higher latitudes along the coasts of Kyushu, Shikoku, and Honshu islands in “mainland” Japan. In winter, however, cold North wind blowing over the archipelago leads to extreme heat flux between the warm water (around 18–20 °C) and the atmosphere (down to 8 °C or less). Heat fluxes were measured in winter as low as $231 \text{ cal} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$ in warm periods up to $1,584 \text{ cal} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$ in cold (North wind)

¹Data measured in March 2016.

²Monthly average temperatures over multiple years west of Okinawa Island between 26–27 °N and 127–128 °E (source: Japan Oceanographic Data Center, <http://www.jodc.go.jp/service.htm>).

periods (Agee and Howley 1977). In this context, MCEs can be relatively isolated from the rapid cooling of the surface layer of the ocean. Whether this situation is unique to specific locations and topographic configuration, as well as the influence of the deeper waters of the Kuroshio on MCEs remain to be investigated.

10.2 Distribution of Mesophotic Coral Ecosystems in Japan

Currently, in Japan, MCEs have been reported only from the Ryukyu archipelago (Fig. 10.2). In addition to the lack of dedicated studies on mesophotic communities at higher latitudes in Japan, light and temperature conditions may limit the maximum depth for zooxanthellate coral communities to develop (Muir et al. 2015). Indeed, even though isolated coral colonies (unless indicated otherwise, here and in the following sections, the term “coral” refers to zooxanthellate corals) can be found deeper, the bottom of the reef slope has been shown to be shifting from 80 m depth in Hateruma Island, the most southern island in Japan, to only 30 m depth at Yaku Island (Yakushima) on the northern edge of the

Ryukyu archipelago (Hori 1990) suggesting a shallowing trend from South to North.

MCEs can be found in three main types of bottom topography: (a) nearshore vertical walls, (b) nearshore deep terraces and gentle slopes, and (c) topographic heights such as banks and pinnacles (Fig. 10.3). The walls limit light availability while providing hard substrates suitable for corals and other photosynthetic benthic cnidarians to prosper. Along these drop-offs (Fig. 10.3a), sciaphilic communities, such as gorgonians and antipatharians, more frequent in deeper environments offshore can develop at relatively shallower depths (Fig. 10.4a). Sponges and other benthic organisms follow the same patterns, for example, the foraminifer *Cycloclypeus carpenteri*, most frequently found between 60 and 70 m depth off Motobu Peninsula (Hohenegger 1994; Hohenegger and Yordanova 2001), is relatively abundant already at 45 m at the bottom of vertical drop-offs along the main part of Okinawa Island (Fig. 10.4b).

Deep terraces, banks, and pinnacles (possibly including submerged fossil reefs) represent the other types of bottom topography suitable for MCE development (Fig. 10.3b, c). While most of these environments remain to be explored, they cover a vast area along the Ryukyu archipelago and

Fig. 10.2 Map of the area. The numbers correspond to the different reports of MCEs. (1) Kikai Island, Humblet et al. (2014) (*fossil*); (2) Okinawa, Kume, Miyako, Ishigaki Islands, Yamazato et al. (1967); (3) Off Sesoko Island, Sinniger et al. (2013); (4) Off Okinawa Island, Ohara et al. 2013; (5) Kume Island, Kimura et al. (2011); (6) Off Miyako Island, Arai et al. (2016); (7) Sekisei lagoon, Humblet et al. (2009a); (8) Amitori Bay, Iriomote Island, Nishihira and Veron (1995), Sinniger (2016)

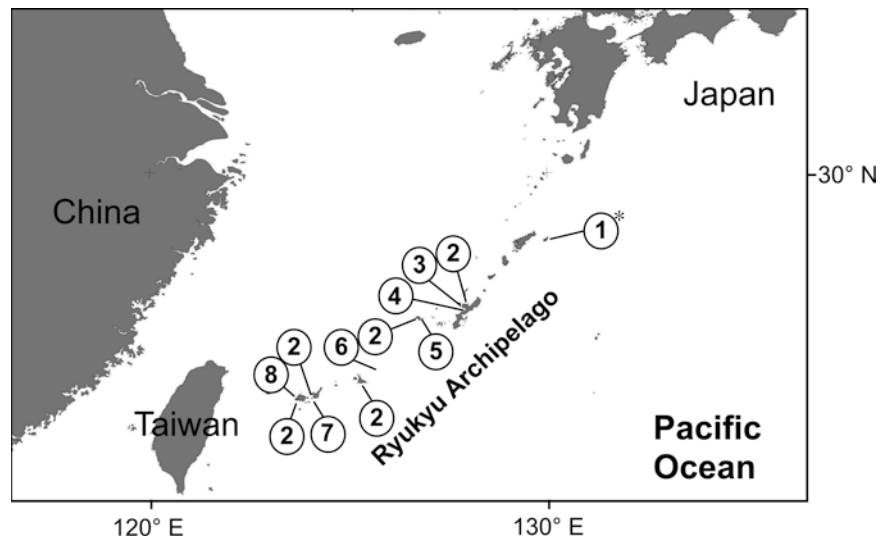


Fig. 10.3 Different topographies of MCEs in Japan. (a) Nearshore vertical walls, (b) nearshore deep terraces and gentle slopes, and (c) topographic heights. The orange and red lines represent 30 m and 100–150 m depth respectively

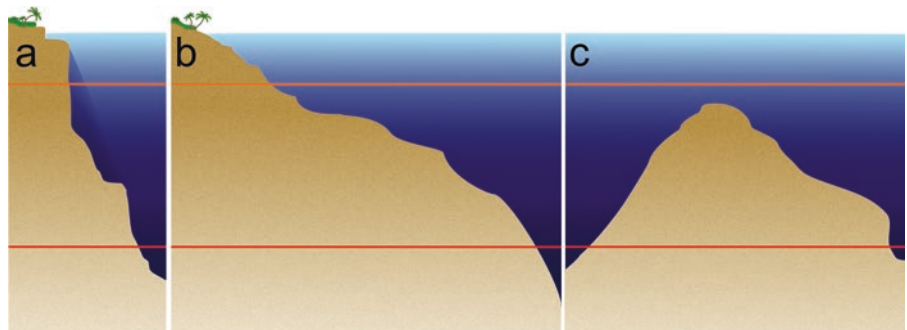
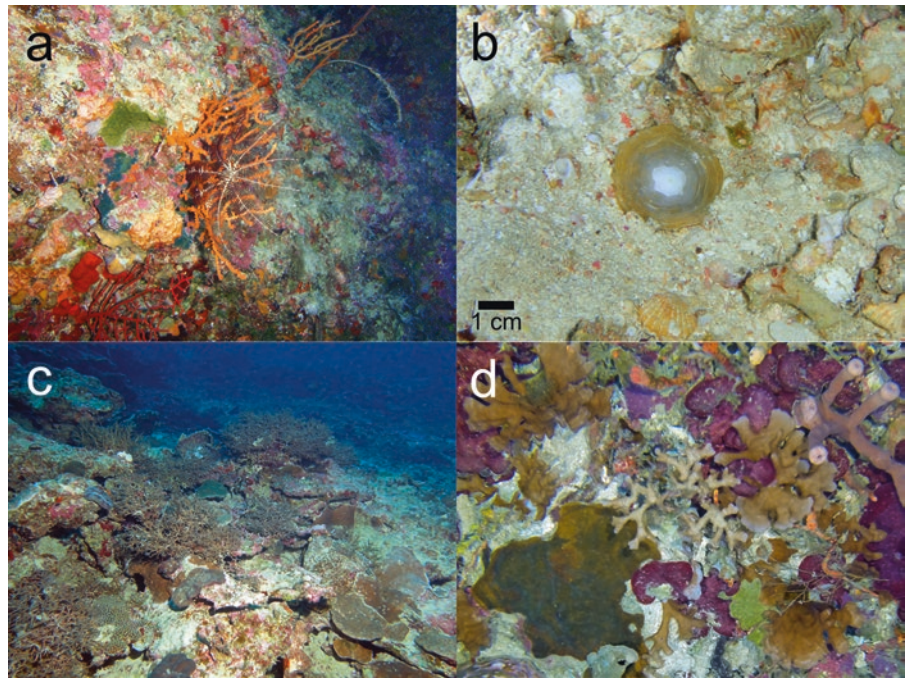


Fig. 10.4 (a) Gorgonians, sponges, algae, and a coral colony on a nearshore vertical wall on the east coast of Okinawa Island, 45 m; (b) *Cycloclypeus carpenteri* at the bottom of a vertical wall, east coast of Okinawa Island, 50 m; (c) *Seriatopora*, other corals and coralline algae on a gentle slope offshore of Sesoko Island, 40 m; (d) *Leptoseris*, sponges, algae and an antipatharian on the top of a “Sone” offshore of Okinawa Island, 75 m



potentially provide a much larger habitat than current shallow coral reef habitats. Often located further out of the shade from the islands, the higher light availability compared to this found on the vertical walls of the islands may explain the diversity of scleractinian corals found in some of these MCEs (Fig. 10.4c, d). The main distinction between the nearshore features (gentle slopes and deep terraces, Fig. 10.3b) compared to topographic heights (Fig. 10.3c) is the source of corals inhabiting these MCEs. In nearshore MCEs, in addition to larval recruitment, fragments of coral colonies can tumble down the slope following strong storms or other destructive actions on shallow reefs and eventually adapt to the new environment. On the other hand, topographic heights rely exclusively on larval recruitment, a constraint that likely affects the biodiversity encountered in these MCEs.

Preliminary observations of the diversity both at species and community levels suggest that the Ryukyu archipelago may figure among the high mesophotic coral biodiversity regions in the world. While drop-offs promote the development of deep species in shallower areas, some shallow species can be found in the deep MCEs located offshore where light availability is not reduced by terrestrial sedimentary input or shade from the islands. Despite data missing for most of the Ryukyu archipelago, already a few of such MCEs have been reported.

10.2.1 Central Ryukyu Islands

10.2.1.1 Okinawa Island

In 1967, during the submersible survey from the government of the Ryukyus, corals were observed during two dives along

50 Years Ago: Pioneer Observations of MCEs in the Ryukyu Archipelago

The first observation of Japanese MCEs was made by the Government of the Ryukyus (1967). Between September and November 1967, a manned submersible “Yomiuri Gou” survey was organized by the Government of the Ryukyu Islands (now a part of Japan) to assess marine resources in the deeper coastal areas around the Ryukyu archipelago. This survey explored five islands (and a total of 21 sites) in the archipelago at depths from 16 to 290 m. The main objective was to investigate fisheries resources (e.g., fishes, crustaceans, precious corals); therefore, numerous sites investigated did not cover suitable environments for mesophotic corals (i.e., too deep or sandy substrates). Nevertheless, mesophotic corals were observed at nine sites during the ascent phase of several dives (Yamazato et al. 1967). These pioneering observations are among the earliest in situ sightings of mesophotic corals in the world and overall three reef zones were defined. In zone 1 (30–50 m), corals were dominant with little amount of coralline algae found between them. Coral coverage on reefs reduced to 20–50 % in zone 2 (50–70 m) while algal presence increased. In this zone, the bottom topography is often composed of topographic features resembling shallow spurs and grooves perpendicular to the coastline. On the shelf of Miyako Island, a similar type of feature strongly influenced by tidal currents was described by Tsuji (1993) and referred to as

“ridges and furrows.” In this text, we will use the term “deep spurs and grooves” to refer to these structures occurring at mesophotic depths and reported by Yamazato et al. (1967). Corals are distributed mainly on the top of the ridges, while coralline algae cover the sides, and the bottom of the grooves is covered by either sand or gravels (that can be encrusted by various benthic fauna or algae). Finally in zone 3 (70–100 m), corals were rare with less than 20 % coverage and lower species richness while large foraminifers were commonly encountered. This zone shows similarities to the deep sea observed on the shelf margin (below the mesophotic zone) with the occurrence of gorgonians and antipatharians (black corals). However, these three zones are not always present or equally developed at the different sites. The deepest coral was reported from a depth of 102 m and constitutes the deepest observation of a zooxanthellate scleractinian in Japan so far (Yamazato 1972); unfortunately no details were provided on this sighting. However, the deepest corals identified in the report are some *Pachyseris* and *Leptoseris* reported from 98 to 100 m depth off Ishigaki Island. This maximum depth distribution of corals is shallower than other North Pacific Ocean islands such as Hawaii, the Mariana Islands, or Johnston Atoll but comparable to the deepest corals found in American Samoa and deeper than most records of Atlantic mesophotic corals (summarized in Baker et al. 2016). Yamazato et al. (1967) also discussed more specifically the bathymetric distribution of hermatypic corals. In his discussion, they compared maximum depth of coral distribution between the Ryukyu archipelago and observations from Bikini Atoll (Wells 1954). Despite the limited data available on the subject, they suggest that the difference in the depth of the deepest corals (100 m in Japan vs 144 m in Bikini Atoll) could be due to bathymetric distribution of temperatures and limited light availability at higher latitudes.

the Kouri Sone (a “Sone” is a Japanese fisherman term to define bathymetric height similar to a shoal or a knoll in English). This location, originally referred to as “Kei reef,” was unique in comparison of other coral sites explored as macroalgae represented the dominant benthic organisms (Yamazato et al. 1967). Between 20 and 30 m, *Sargassum* sp. covered most of the substrate and was progressively replaced by *Spatoglossum stipitatum* (referred to as *Zonaria stipitata*) between 30 and 50 m. Plate *Acropora*, *Pocillopora*, and *DipsastraealFavites*-like corals (referred as “faviid-like”) along with some massive corals were found in the shallowest

part of the surveyed area (around 20 m depth). At 40 m, only *Acropora*-like and *Dipsastraea speciosa*-like corals were reported, and at 50 m *Leptoseris*-like corals were observed. Coral occurrence increased until 50 m depths, reaching coverage of about 10 % corresponding to a ratio of 1:1 between corals and macroalgae. Between 50 and 70 m coverage of both coral and macroalgae decreased and the deepest corals were observed around 70 m depth. Sponges and hydrozoans were sampled on rocks at 70 m, and below 90 m, octocorals (*Anthogorgia*, *Callogorgia*, *Dendronephthya*, *Siphonogorgia*), the black coral *Cirrhopathes spiralis*, and stylasterid corals were observed. At this location, no deep spurs and grooves were observed.

During the same submersible survey, a second site offshore of the west coast of the central part of Okinawa Island showed very high densities of corals (branching *Acropora* sp., *Millepora* sp., and *Turbinaria* sp. or *Montipora*-like plate corals) from 40 to 55 m depth with 100 % coral coverage (Yamazato et al. 1967). Between 55 and 65 m, the coverage decreased with smaller coral colonies (10–20 cm diameter). Below coverage continued to decrease with rare colonies of *Leptoseris* at 87 m being the deepest corals reported at this site. Among other organisms, *Siphonogorgia* and other gorgonians occurred below 65 m. From 90 to 110 m, the topography was rather flat and sandy with rocky outcrops covered in sponges, gorgonians, and other octocorals such as *Telesto* and *Ellisella*, attracting swarms of small fishes (*Apogon*).

More recently, a diverse mesophotic coral community was reported from 40 to 50 m depth between Sesoko Island and Motobu Peninsula (Sinniger et al. 2013). At 40 m, this community dominated by *Pachyseris speciosa*, *Seriatopora hystrix*, and the rare *Acropora tenella* is developing in a nearly flat area characterized by low-elevation rocky outcrops (the main substrate for most corals, including *Pachyseris*) separated by patches of sand or rubbles (the main habitat for unattached *Acropora tenella* colonies) (Fig. 10.4c). *Seriatopora hystrix* can be found on both rubbles and hard substrates. The seaward margin of this area gently slopes down to 50–55 m where a progressive transition to sand occurs, with a different species assemblage found in this sandy rubble area. In addition to widely distributed corals such as *Seriatopora* or *Pachyseris*, species more specifically encountered in this environment include *Euphyllia paradivisa* (Eyal et al. 2016), *Madracis kirbyi*, as well as several *Alveopora* and *Leptoseris* species. On the shallower side of this MCE, the topography progressively slopes up and connects with the typical Okinawan shallow-reef communities.

In addition, in the same region, Hohenegger et al. (1999) compared large light-dependent symbiotic foraminifer communities between two transects at nearby sites with distinct topographies and environmental conditions. The northern

transect lies north of Sesoko Island at depths ranging from 3 to 100 m. The proportion of living corals at 40 m was reported at slightly over 40 % before decreasing to nearly 0 % at 50 m. The southern transect on the other hand is located west of Sesoko Island along the slope of a well-formed reef crest at depths of 5–100 m. Coral cover along this transect was significantly lower at all depths except near the surface, and no living corals were found at 40 m or below. Following the observation that the water was less transparent (higher light attenuation coefficient) at the northern transect despite the highest coral coverage, Hohenegger et al. (1999) suggested that the high abundance of corals at mesophotic depths is related to higher nutrient inputs. While the role of nutrients remains to be investigated in Japanese mesophotic corals, different hydrological conditions and high rates of sedimentation also likely affect the abundance of corals in the south transect. The topography of the sites may also influence the coral community structure. While water was slightly more turbid in the northern transect, this transect receives light throughout the day as it is never shaded by Sesoko Island. The slope is also less steep, especially between 30 and 40 m. The southern transect being located on the west side of Sesoko Island this area is more shaded during the morning hours (as the measurements of light intensity in Hohenegger et al. (1999) were made at noon, this effect is impossible to detect based on their data). The southern transect is also more exposed to strong storms and typhoons which may destroy corals both through direct intense water motion and through the fall of debris from the shallow reef down the slope. In this context, a steeper slope will negatively affect the presence of corals. Based on the data presented in Hohenegger et al. (1999), the high proportion of sand at all depths, but especially below 30 m, provides the simplest explanation for the lower abundance of corals. However, despite providing the simplest explanation, substrate characteristics may not always be the most determinant parameter affecting coral distribution. Indeed, hard substrate does not necessarily involve high coral cover and that factors other than substrate type must play a role in controlling coral distribution.

On the west coast of Okinawa Island, another upper mesophotic community was reported (Ohara et al. 2013). This MCE, named Ryugu Reef, consists in the lower part of a larger coral community extending from shallower depths (White et al. 2013). Between 30 and 42 m, *Pachyseris* largely dominates the community, while below 42 m the sandy substrate is not suitable for extensive development of corals.

10.2.1.2 Kume Island

During the 1967 submersible survey, further west of the main Okinawa Island, a site on the southern side of Kume Island was investigated at depths ranging between 30 and 290 m (Yamazato et al. 1967). At mesophotic depths, the

seafloor can be divided into three geomorphological zones: an irregular steep forereef slope (30–50 m), deep spurs and grooves (50–70 m), and a gentle slope consisting of sandy gravels (70–100 m). The mesophotic coral community in the upper zone was dominated by table *Acropora* along with *Millepora* sp. and coralline algae. The rough rocky surface was mostly covered by corals (about 90 % coverage) at 35 m and plate corals reached up to 70–80 cm diameter. Coral cover and colonies diameter decreased with increasing depth. No abrupt shift in coral diversity was observed with the transition to the spurs and groove zone, and the decreasing trend in coral abundance and size with increasing depth continues. Several *Dipsastraea speciosa* and one *Mycedium elephantotus* (referred to as *M. tenuicostatum*) were sampled at 68 m where the coral cover was estimated to be about 20 %. Other corals, possibly *Acropora* and *Porites*, were observed at this depth along with hydrozoans, sponges, and macroalgae such as *Zonaria*. Below this second zone, on the gentle slope down to 100 m, some patches of rubbles composed of 20–30 cm diameter limestone gravel host some corals, especially “*Dipsastraea*-like” colonies along with gorgonians, hydrozoans, sponges, and macroalgae such as *Padina* and *Peyssonnelia*. Large *Cycloclipeus* foraminifers were observed around 90 m depth. The bottom of this zone, at 102 m depth, consists of rubbles with *Peyssonnelia* and coralline algae, and it is at this depth that the deepest coral was observed. Although no details are available on this observation, it still constitutes the record depth for a zooxanthellate scleractinian in Japan nowadays. The high transparency of the water (50 m horizontal visibility was measured at 130 m depth) at this site may explain this deep finding.

Near the site explored by Yamazato et al. (1967), in the southeastern part of Kume Island, a dense coral community dominated by branching *Acropora horrida* was discovered in 2010 (Kimura et al. 2011). This upper mesophotic community extends from 15 m down to 40 m and covers a small mound rising out of a sandy slope, with a live coral coverage up to 90 % between 25 and 30 m (Fujita et al. 2012). In addition to the dominant *A. horrida*, several other species such as *A. latistella* or *Favites* were observed (Kimura et al. 2011).

10.2.2 Sakishima Islands (South Ryukyu Islands)

10.2.2.1 Miyako Island

In the 1967 submersible survey, two of the three explored sites covered mesophotic depths (Yamazato et al. 1967). At the first site, off Tomori, the mesophotic slope appears to exhibit a similar zonation as observed in Kume Island, with a steep reef slope and rough hard substrate above 50 m giving way to a deep spurs and grooves topography between

50 and 70 m and finishing by a gentle sedimentary slope covered by sand and gravels until 100 m. However, as the study started at the depth of 50 m, detailed comparison of corals in the upper mesophotic zone cannot be made. Between 50 and 70 m, corals cover about 30 % of the substrate with table *Acropora*, *Dipsastraea speciosa*-like corals, *Leptoseris*, and *Millepora*. The remaining substrate is colonized by black corals (*Cirrhopathes*), large gorgonians, sponges, and coralline algae. At 60 m *Leptoseris scabra* was observed, and at 70 m algae such as *Halimeda* or *Codium minus* (referred to as *Codium mamillosum* var. *minus*) and coralline algae are mainly reported. Below this zone, no corals were observed on the gravels and small rocks, yet some black corals (*Cirrhopathes*) and octocorals such as fan-shaped gorgonians or *Ellisella* sea-whip were found among macroalgae (e.g., *Aneurianna*, *Halimeda* sp., *Ulva* sp., *Padina* sp.).

In the second site, off Kurima Island, beside Miyako Island, the coral slope extends until 110 m contrary to the previous site off Tomori where a gentle sandy slope occurred between 100 and 120 m (Yamazato et al. 1967). While the survey extended down to a depth of 280 m, corals occurred only in the upper part of the zone surveyed. As observed in Kume Island and off Tomori, the bottom of the reef slope is forming deep spurs and grooves until 70 m before giving way to a sand and gravel slope. Only a very narrow band of corals was observed as the lower limit of coral distribution was established at 70 m. At this depth, scattered colonies of several corals were observed and some specimens collected, such as *Dipsastraea speciosa*, *Goniastrea* sp., *Porites* (referred to as *Porites (Synaraea) hawaiiensis*), and *Pachyseris speciosa*. Below the sand and gravel, only small gorgonians, sponges, and other benthic organisms along with coralline algae were found.

More recently, a large submerged reef structure was reported near Miyako Island (Arai et al. 2016). This topographic structure extends up to 1 km in length and about 500 m in width at depths between 56 and 80 m. Between 56 and 66 m, the geological structure exhibits clear spurs and grooves similar to those observable in the shallow reefs around the Ryukyu archipelago. The benthic covers appeared to be dominated by algae, soft corals, and sponges. While no scleractinian corals were reported, a colony of potentially encrusting coral can be seen in one of the illustrations although the resolution of the image is not sufficient for confident identification. Rhodoliths occur on the deeper terraces neighboring this submerged reef at depths from 100 to 130 m.

Despite the apparent low coral cover, the complex topography of this area combined to its isolation from neighboring islands make it an interesting target for further studies of the mesophotic communities inhabiting submerged reef structures.

10.2.2.2 Ishigaki Island

In Ishigaki Island, two sites were explored by the submersible survey of the government of the Ryukyus (Yamazato et al. 1967). One submersible dive, just out of Sekisei Lagoon barely overlapped with the mesophotic zone as the dive begun at a depth of 213 m and ended at 98 m. Yet colonies of *Pachyseris speciosa* and *Leptoseris* together with large foraminifers and sponges were found down to 100 m on rubbles in a sand/gravel flat area. Shallower depths were surveyed in the other site as the dive at the entrance of Nagura Bay, off the Cape Osaki, started at a depth of 90 m and finished at around 40 m, with still some observations on the slope until 32 m on the way up. Compared the other sites explored, the visibility was considerably less, with only 12 m horizontal visibility at 78 m. Nonetheless, dense coral coverage was also observed in the upper part of the survey. Between 32 and 43 m, the reef slope was essentially composed of round table *Acropora* and discoidal *Cyphastrea* sp. colonies. *A. longicyathus* and *C. serailia* were collected at 41 m. At 40 m, the coral coverage was estimated to be around 80 %, and living corals and coralline algae were observed down to 55 m. Below this depth, the bottom presents a different topography with rocky outcrops separated by sandy patches on a gentle slope extending to 90 m. In this environment, sponges, octocorals (*Dendronephthya*, *Siphonogorgia*, *Ellisella*, and *Echinogorgia*), antipatharians (*Cirrhopathes spiralis*, *Antipathes* sp.), bryozoans, and hydrozoans dominated the fauna. Around 85 m, large *Melithaea* colonies were observed.

Two more recent surveys have been conducted around Ishigaki Island. Below 30 m depth north of Ishigaki, off Yonehara, low scleractinian coverage (at most 10 %) was reported (Iryu et al. 1995). At this site, the coral assemblage was dominated by foliaceous species such as *Pachyseris speciosa* or *Leptoseris scabra*. Later, in 2004, a ROV survey of along the southern margin of the Sekisei Lagoon southwest of Ishigaki Island revealed higher scleractinian coverage at mesophotic depths (Humblet et al. 2009a). Table *Acropora* spp. dominated the scleractinian assemblage comprising also encrusting, plate-like, and foliaceous corals between 40 and 55 m. In contrast with the previous study further north, the scleractinian coverage in this area reached up to 35 % at 50 m. Below 55 m, coral coverage drastically decreased and the assemblage was dominated by encrusting and laminar growth forms, including *Pachyseris speciosa*. Other benthic organisms included sponges, octocorals and, below 60 m, the large foraminifer *Cycloclypeus carpenteri*. Below this depth and down to the limit of the study (100 m), scleractinian corals became rare with only a few isolated *Leptoseris* colonies observed between 80 and 85 m. On the other hand, other benthic invertebrates such as sponges and octocorals became abundant.

10.2.2.3 Iriomote Island

The southernmost site explored was near Kanokawa, south of Iriomote Island (Yamazato et al. 1967). This dive explored a portion of the slope between 58 and 90 m. Deep spurs and grooves shaped the bottom down to 68 m. Several disc-shaped corals were found on the top and sides of the spurs, with *Porites*, *Dipsastraea speciosa*, and table *Acropora* identified from visual observations only. Gorgonians and antipatharians were also present. At the bottom of the grooves, rounded rubbles 20–30 cm in diameter were covered with macroalgae and coralline algae. Between 68 and 80 m, only shallow grooves remained with sand or gravel as main substrate. Large foraminifers became abundant at 72 m although their number was reduced on sandy bottom. *Pachyseris speciosa* was the deepest coral found at 75 m (Yamazato 1972; Yamazato et al. 1967). Macroalgae such as *Padina* or *Halimeda* were found on the rubbles down to 85 m, along with gorgonians and other invertebrates.

After a gap of nearly 30 years in Okinawan mesophotic coral research, another dense community of mesophotic corals was found by Dr. H. Yokochi in Amitori Bay around 50 m depth (Nishihira and Veron 1995). This community is dominated by different *Leptoseris* species showing a distinct depth zonation in their distribution (Yokochi unpublished; Sinniger 2016). A dense thicket of *Leptoseris amitoriensis* occupies the deepest part of this community. As suggested by its name, this species was first found in Amitori Bay and described based on specimens from the extensive stands found at a depth of around 50 m. Deeper than about 55 m, the bottom of Amitori Bay consists of a gentle slope composed of fine sediments down to the maximum depth of the bay. Apart from *L. amitoriensis*, another *Leptoseris* species, *L. gardineri*, coexists in the deepest zone of this ecosystem. Above the community of foliose *Leptoseris*, the minute and crispy *L. papyracea* forms a dense population that covers a high proportion of the substrate. Further up, another high coverage population of *Seriatopora* connects upper mesophotic and shallow reef. Despite a rather low diversity in comparison with the high coral coverage, the density of corals and the zonation displayed by the different species make this MCE one of the most spectacular in Japan.

10.3 Biodiversity

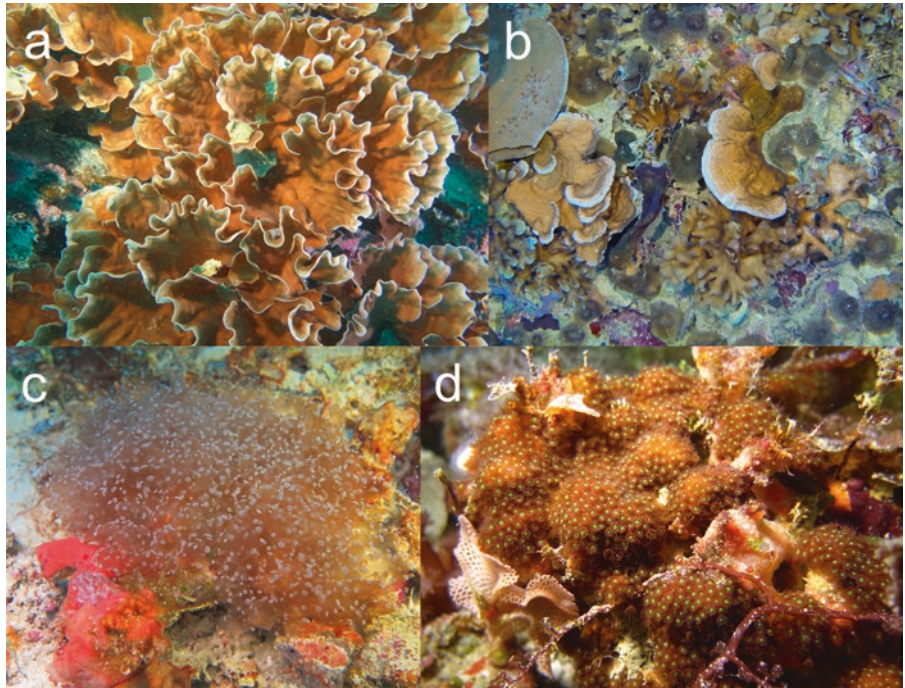
The main difficulties to study MCE biodiversity are the same as for most other studies on remote environments: access and sampling issues. Historically sampling at mesophotic depths has been made by trawling or dredging. However, these methods are very destructive and not ideal for sampling on

hard and irregular substrates due to the risks of losing or destroying the sampling gear. Development of scuba diving allowed more targeted and selective sampling although scuba diving at mesophotic depths requires specific training and equipment (e.g., mixed-gas diving). When examining scleractinian coral diversity, another significant problem arises from the fact that numerous zooxanthellate corals are known to change their morphology in order to adapt to different environmental conditions. Considering that most taxonomic identifications of scleractinian corals are based on morphological characters, such variability is a serious impediment to species identification of coral samples collected in the low light environment of MCEs. Therefore, species identification of mesophotic corals relies heavily on the combination of microstructure observations, molecular biology, and comparisons with shallow samples. Within the Ryukyu archipelago, morphological characteristics of the different corals encountered on MCEs seem relatively conserved within species, and the development of an accurate reference database may be of crucial help for identifying mesophotic corals in the future and should be prioritized. However, until such reference database can be established, considerable taxonomic work must be engaged to solve taxonomic uncertainties one by one.

10.3.1 *Leptoseris*

Leptoseris is the emblematic mesophotic coral genus. The type locality of one species, *L. amitoriensis*, is located in the Ryukyu archipelago. In Japan, *L. amitoriensis* (Fig. 10.5a) was described from Amitori Bay in Iriomote Island and officially reported only from the Yaeyama Islands, in the south of Okinawa Prefecture. However, future surveys in enclosed bays in other islands in the prefecture may reveal a broader distribution of this species. This fragile species forms foliose colonies with more or less divided fronds. While the fronds never get as narrow as in *L. gardineri*, another species found in Amitori Bay (Nishihira and Veron 1995), the largest fronds of older colonies can be confused with *L. foliosa*, and the specific status of *L. amitoriensis* in regard to other *Leptoseris* species is now undergoing a reexamination using both morphological and molecular approaches. Such approach has been successfully applied to clarify relations between agaricids in Hawaii (Luck et al. 2013); however, preliminary results suggest that the situation in the Ryukyu archipelago is more complex, with numerous genotypes and intermediate morphotypes. The whole *Leptoseris* genus deserves a revision, and work on the original type specimens of *L. amitoriensis* and freshly collected samples is still ongoing.

Fig. 10.5 (a) *Leptoseris amitoriensis*, Ishigaki Island, 40 m; (b) Two different morphotypes of *Pachyseris* among *Leptoseris* sp. and unidentified corallimorpharians, “typical” *P. speciosa* on the top left above another morphotype that may be similar to *P. foliosa*, east coast of Okinawa Island, 56 m; (c) *Euphyllia paradivisa*, offshore Sesoko Island, 55 m depth; (d) *Madracis kirbyi*, offshore Sesoko Island, 55 m



10.3.2 *Pachyseris*

Pachyseris corals are commonly encountered in reef slopes, deeper areas of the reef as well as on shallow reefs in shaded places. Only a few species from this genus are currently described and four out of the five existing species were reported from Japan (Nishihira and Veron 1995; Ohara et al. 2013). *Pachyseris foliosa* was reported for the first time in Japan based on samples collected off Okinawa Island (Ohara et al. 2013). However, when comparing figures from Ohara et al. (2013) with the original description of Veron (1990) and *P. foliosa* (all from Papua New Guinea) in Veron (2000), the similarities are inconclusive. Recently, among numerous *Pachyseris* morphotypes present in the region, we found some that could correspond to the same species reported in Ohara et al. (2013) (Fig. 10.5b). While different from the holotype of *P. foliosa*, they are similar to the additional image provided in the original description (see Fig. 77 in Veron 1990). This exemplifies the need for deeper studies to resolve relationships between *Pachyseris* species and morphotypes.

In addition, with increasing attention paid to mesophotic corals, the number of species seeing their distribution range expanding and new species discovery will increase without doubts. One additional example of such expansion is the recent finding of *Euphyllia paradivisa* in Okinawa Island (Fig. 10.5c). This species was previously known only from a limited part of the coral triangle and now is known from MCEs in both Okinawa and the Red Sea (Eyal et al. 2016). Likewise, *Madracis kirbyi*, a presumably rare species, not

recorded from Japan, was recently found at mesophotic depths offshore of Motobu Peninsula (Fig. 10.5d). These findings confirm the need for further biodiversity surveys of the mesophotic coral fauna in Okinawa. Beside the discovery of new species and the reassessment/revision of the geographic range of known species, such surveys might also provide useful information on the ecology and abundance of various known coral species. For example, *Lobophyllia* (formerly *Australomussa*) *rowleyensis* is a supposedly rare coral according to Nishihira and Veron (1995). However, in both Okinawa and Kume Islands, this species is regularly encountered around 40 m depth. This suggests that instead of being a rare species, this species simply preferentially inhabits environments that were rarely investigated.

10.4 Fossil Mesophotic Corals

Quaternary fossil reef deposits are extensively distributed in the Central and South Ryukyu Islands, and the age of coral reef initiation in this region is estimated to be 1.45–1.65 Ma (Iryu et al. 2006). The rate of tectonic subsidence/uplift, the amplitude and frequency of sea level changes and the timing of coral reef development are key factors controlling the nature and distribution of fossil reef deposits in the Ryukyu Islands (Iryu et al. 2006; Yamamoto et al. 2006). The resulting successions of Pleistocene strata (Ryukyu Group) contain a diverse and abundant coral fauna associated with a wide range of reef environments, including MCEs (Humblet and Iryu 2014; Humblet et al. 2009b).

Kumejima Expedition 2009

Beside scleractinian corals, MCEs host a large diversity of benthic organisms, and the difficulties in accessing MCEs resulted in a similar lack of knowledge on the taxonomy and distribution of other benthic organisms at mesophotic depths, perhaps compounded by the lesser interest in so-called lower taxa (e.g., polychaetes, bryozoans, ascidians, etc.). All over the world, MCE diversity research focus mainly on corals, sponges, fishes, and algae. In the Ryukyu archipelago, one international expedition was organized in 2009 by Dr. T. Naruse from the University of the Ryukyus to explore the biodiversity of Kume Island, with a primary focus on other groups than those cited above.

Crustacean specialists largely dominated the scientific team, although several other taxonomic groups were also included in this survey. Mesophotic depths were not specifically targeted; however, trawlings and dredgings were performed over the whole mesophotic depth range (Naruse 2012). Because of the destructive nature of the sampling gear and the targeted organisms, mainly coral rubble slopes were sampled using trawling or dredging. Diving explorations focused on shallower depths with only a few rare incursions to the upper mesophotic zone and a few samples collected down to 55 m. Although numerous samples remain to be studied, over 50 new species were discovered (Naruse et al. 2012), and numerous new distribution records were published for crustaceans, echinoderms, or fishes associated with coral rubble environments at mesophotic depths around the island (e.g., Chan and Hayashi 2012; Chen et al. 2012; Osawa 2012; Ota 2012). Probably as a result of the sampling gear used, no mesophotic scleractinian corals were collected during the expedition. However, several new plumulariid octocorals were found and are in the process of being formally described (Nonaka and Sinniger, unpublished). In addition to their value in improving the understanding of marine biodiversity, these findings highlight the lack of knowledge on the diversity of organisms inhabiting mesophotic depths.

Fossil mesophotic coral assemblages are identified based on the analogy with the taxonomic composition of modern mesophotic communities, as well as their association with other key indicators of deep coral reef habitats such as deep coralline algal species (often forming rhodoliths below 50 m in the Ryukyu Islands) or the large foraminifer *Cycloclypeus carpenteri*, commonly found below 65 m (Iryu et al. 1995).

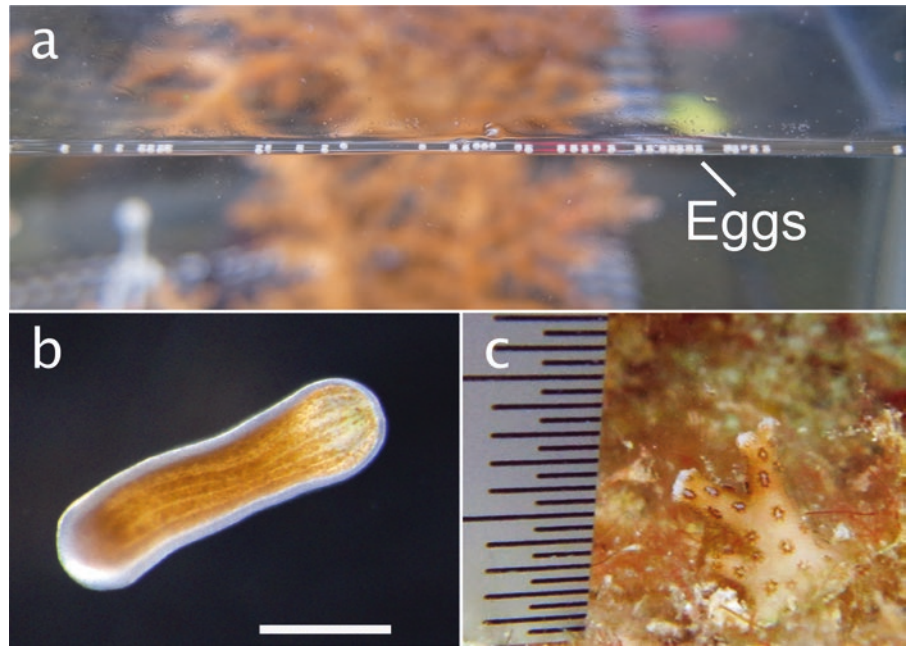
Pleistocene coral assemblages that can be interpreted as fossil MCEs have been reported from Kikai Island in the northern Central Ryukyus, Okinawa Island in the southern Central Ryukyus and Irabu Island in the South Ryukyus (Humblet and Iryu 2014; Humblet et al. 2009b). Keeping in mind the limitations of the data currently available, we can identify some general features of fossil deep coral assemblages. The fossil MCEs described in these three locations share a common characteristic of being mainly composed of thin laminar morphologies, i.e., encrusting, platy, or foliaceous. *Porites* and/or *Montipora* (not always distinguishable in the fossil record) appear to be important components of these assemblages. *Turbinaria* also seems to be widespread. There are however notable differences among deep coral assemblages described in the three islands. For example, *Echinophyllia* was found only in fossil MCEs on Irabu and Kikai Island. *Galaxea astreata* and *Pachyseris speciosa* are significant species in southern Okinawa and Kikai Island, respectively. *Stylocoeniella* (potentially confused with a *Montipora* species) and *Leptoseris* are common on Irabu Island. The diversity of merulinids also varies from one site to another. Surprisingly no mesophotic *Acropora* species has yet been reported from the fossil record. Differences in community structure of MCEs described in the fossil record likely reflect the spatial or depth-related variations in taxonomic compositions displayed by modern mesophotic communities.

10.5 Sexual Reproduction of Mesophotic Corals in Okinawa

Scleractinian corals release their gametes (eggs and sperm) or shed their planula larvae into the water column (see Chap. 7). After their planula larvae disperse and settle onto the substrata, they metamorphose into polyps and start their sessile life. While there are numerous studies on sexual reproduction of shallow corals, little is known on the reproduction of mesophotic corals (but see Holstein et al. 2015, 2016; Prasetia et al. 2016, 2017a, b; Eyal-Shaham et al. 2016). Sexual reproduction plays an important role in maintaining and extending coral distribution. In the context of the Deep Reef Refugia Hypothesis (DRRH, see Sect. 10.6), the main possibility for deep corals to recolonize degraded shallow reefs is through larval dispersal (Bongaerts et al. 2010). It is therefore crucial to study and understand the sexual reproduction of mesophotic corals including fecundity, reproductive seasonality, timing of spawning and larval characteristics (such as behavior and settlement competency periods), and vertical connectivity between shallow and mesophotic reefs.

In Indo-Pacific region and the Ryukyu archipelago in particular, *Acropora tenella* was the first mesophotic spawning coral species to be studied for its reproductive biology

Fig. 10.6 (a) Egg bundles of *Acropora tenella* (in the background) spawn in aquarium in June 2016, (b) planula of *Seriatopora hystrix* released from a 40 m depth colony, the white bar represents 400 μm , (c) 11 months old juvenile colony of *S. hystrix* deployed in a shallow reef (about 3 m depth) on Sesoko Island, intervals between marks on the scale represent 0.5 mm (Photographs b, c courtesy of R. Prasetia)



(Prasetia et al. 2016, 2017a). It is also the first investigation on sexual reproduction in the genus *Acropora* at mesophotic depths in the world. This species is a hermaphrodite with oogenesis and spermatogenesis occurring for 11–12 and 5–6 months, respectively. The gametogenesis is relatively longer compared to shallow *Acropora* species, probably because of lower seawater temperature in spring and summer and lower light intensity compared to shallow water (Prasetia et al. 2016). In addition, the fecundity (number of eggs per polyps) and the gonad index (number of eggs per square centimeter) are among the lowest reported for an acroporid coral. The longer gametogenesis and lower reproductive yields may reflect the limited energy available at the depths where this species is found (around 40 m). Except for the longer gametogenesis, the reproductive behavior of *A. tenella* is not significantly different from other shallow *Acropora* species. The rapid maturation of gametes at the end of spring seems to be correlated with a rapid increase in seawater temperature. The spawning is expected to occur at night in both June and July, like shallow acroporid corals in the same area, (around Sesoko Island, northern Okinawa). Although there is no record on in situ spawning, aquarium observations showed that released eggs are positively buoyant (Prasetia et al. 2017a) (Fig. 10.6a). This observation raises questions on how gametes fertilize at the surface of the ocean and how larvae return to the deeper part of the reef. Larval dispersal ranges of corals are controlled by their settlement competency period, position in the water column, and currents that actually deliver the larvae (Harri and Kayanne 2003). In shallow reefs, eggs of many corals including *Acropora* are positively buoyant due to their high lipid contents (Arai et al. 1993; Harri et al. 2007) and flushed by wind-driven current (Willis and Oliver 1990; also see

Chap. 7). The potential challenges of fertilization 40 m above the spawning origin combined to the reported low fecundity and low gonad index may explain the rarity of this species and its absence from most mesophotic sites investigated in the region.

Seriatopora hystrix is another common mesophotic species that is the focus of several studies in Okinawa in regard to the DRRH (see Sect. 10.6). This species is widely known as a brooder in shallow reefs (Atoda 1951) and is a good model to examine shallow reef recovery from mesophotic populations by larval dispersal. *S. hystrix* from 40 m offshore Sesoko Island has been observed to release planula larvae at least during the summer months (Prasetia et al. 2017b, Fig. 10.6b). Preliminary results suggest that larvae can survive at least up to several months in shallow reef conditions (Fig. 10.6c), although light intensity appears to be a strongly limiting parameter for direct transplant from upper mesophotic to shallow reefs.

These first studies on mesophotic coral reproduction open the path to further research on the larval behavior, dispersal, and genetic connectivity in order to understand better the true potential of MCEs to contribute to shallow reef recovery and also to understand the interactions between different MCEs and their evolution through time.

10.6 Deep Reef Refugia Hypothesis

One of the major drivers of the fast-growing upper mesophotic research effort in the last years comes from the Deep Reef Refugia Hypothesis (DRRH). The hypothesis initially stated that several environments, including deep reefs, could serve as refuge for shallow species threatened by ocean

warming (Glynn 1996). The deeper waters being less affected by seasonal temporary extreme warming events, shallow coral species may be able to survive catastrophic warming events in these remote habitats. The hypothesis was further refined by stating that to serve as refugia, MCEs should be also serving as a source of recolonization for shallow reefs (Bongaerts et al. 2010). Recent studies (Serrano et al. 2016; Bongaerts et al. 2017; Holstein et al. 2015, 2016) suggest that the potential for mesophotic corals to reseed shallow reefs differs between species and locations, and investigations on the physiological adaptation and depth specialization, symbiotic association and vertical connectivity are contributing to estimate the potential and the challenges of a mesophotic source of larvae for shallow reefs.

The Ryukyu archipelago and especially the main Island of Okinawa and neighboring locations such as Sesoko Island were strongly affected by massive coral bleaching events occurring in 1998 and 2001 (Loya et al. 2001). These events lead to a long-term reorganization of the coral species assemblages in the shallow reefs (van Woesik et al. 2011). One of the species concerned is *S. hystrix*. In Okinawa, *S. hystrix* is normally relatively common in shallow reefs. However, being a species highly sensitive to bleaching, it is strongly threatened by global warming. As a result, *S. hystrix* disappeared from the shallow reefs around Sesoko Island following the massive bleaching events of 1998 and 2001 (van Woesik et al. 2011). The frequent occurrences of *S. hystrix* at mesophotic depths in the archipelago, especially near Sesoko Island (Sinniger et al. 2013, 2017) (Fig. 10.4c), provide an excellent model to test the ecological role of MCEs in Okinawa. Although fine scale population genetics to assess connectivity between shallow and deep *S. hystrix* is still ongoing, first observations of various morphotypes and genotypes do not support the hypothesis of a clonal deep population and the observation of larval release in deep colonies suggest an active sexual reproduction of deep colonies (Sinniger et al. 2017, also Sect. 10.5). Therefore, the first part of the DRRH can be validated as this species actually survived in deeper parts of the reef. However, as *S. hystrix* was not yet found again in the shallow reefs around Sesoko Island, it remains to be seen if and how deep refuge populations can recolonize depleted shallow reefs. Such research will define whether Okinawan deep reefs are more likely to act as refugia or as traps from which species cannot get out.

10.7 Threats on Mesophotic Coral Ecosystems in Japan

In addition of providing refuge to shallow corals during thermal stress, MCEs also have been suggested to be less affected by powerful storms and destructive wave action. However, the effect of typhoons on deeper reef communities may be

significant in the Pacific, for example, through mechanical destruction of coral communities by massive coral colonies and boulder tumbling down reef slopes during typhoons (Harmelin-Vivien 1994). More recently typhoon-induced damages have been observed in the Great Barrier Reef in Australia (Bongaerts et al. 2013). In Okinawa, extensive damages have been reported for a mesophotic *Acropora horrida* community offshore of Kume Island as well as at the upper edge (31 m) of a mesophotic *Pachyseris* community on the west coast of Okinawa Island.

In Kume Island, the typhoons #2 (Songda) and #9 (Muifa) tracked near/passed over a dense *A. horrida* community (see Sect. 10.2) on the 28th of May and between the 4th and 6th of August 2011, respectively. A survey conducted 1 month after this event showed extensive damages resulting in a loss of coral cover (from over 90 % to 20–30 %) and the invasion of dead corals by filamentous cyanobacteria (Fujita et al. 2012). However, Fujita et al. (2012) also found surviving fragments already reattached to the substrate or fused with other coral branches. This finding combined to the absence of bleaching and burial by sediments suggests a strong potential for rapid recovery of this community.

On the west coast of Okinawa Island, typhoon #16 (Jelawat) passed hit Ryugu Reef (see Sect. 10.2) on the 29th of September 2012. White et al. (2013) found that the “deep” (32 m) community of foliose *Pachyseris* corals suffered more damages than the shallower (25 m) and more diverse coral community. While the dominance of *Pachyseris* at the deeper site may have hindered observable community composition shifts, at the shallower site branching *Acropora* coverage was reduced and the proportion of fungiids increased. At both deep and shallow site, coral rubbles covered extensive area of the reef. However, as was the case in Kume Island 1 year earlier, a few months after the typhoon passage, signs of recovery could be observed in the *Pachyseris* community.

These two studies in Okinawa demonstrate that, while MCEs can be heavily impacted by typhoons, they show a strong resilience and recovery potential. Whether this conclusion holds MCEs in general or reflects the relative remoteness of these MCEs from anthropogenic influences remains to be tested. But these two studies already provide a good baseline to evaluate the impact of typhoons on mesophotic corals and their subsequent recovery.

Other threats are likely endangering MCEs in Okinawa, such as the impact of *Acanthaster* (crown of thorns sea star, see Chap. 9), sedimentation, nutrient enrichment, or shoreline modifications, and climate change. However, until now no study investigated these threats on mesophotic corals in Japan.

Considering the paucity of knowledge on how human activities (e.g., coastal development, pollution) affect MCEs and the rapid development of the islands of the archipelago (including landfills for various uses), a proactive conserva-

tion approach should be applied until adequate knowledge on the distribution, biodiversity, ecology, and connectivity of MCEs is acquired. Failing to do so may lead to the dramatic destruction of these ecosystems due to our ignorance as to how they respond to environmental changes or even where they are located.

10.8 Future Perspectives for Japanese Mesophotic Research

As highlighted in the recent UNEP report on MCEs (Baker et al. 2016), the priority for mesophotic research is to locate and identify MCEs to allow understanding the conditions required by such rich ecosystems to develop and survive. This is especially important in Japan in regard to the area suitable for mesophotic habitats. The high diversity of MCEs encountered until now in the Ryukyu archipelago would suggest the presence of a high biodiversity of mesophotic organisms in these ecosystems. In this respect, large multidisciplinary biodiversity surveys, across a broad depth range similar to the Kumejima Expedition 2009, or focusing on mesophotic depths, are highly needed to identify the biodiversity of these remote ecosystems. Identifying the organisms inhabiting these ecosystems is an absolute pre-requisite to any further study on the biology or ecology of mesophotic corals and associated organisms.

In regard to the Deep Reef Refugia Hypothesis, while it was shown that some species could be relatively protected from massive bleaching occurring in shallow reefs, the role of these corals can play in the recovery of shallow reefs is not yet known. Research on the physiological adaptation of deep corals to shallow reef conditions, horizontal, and vertical connectivity are highly needed in order to understand the real potentials of MCEs to contribute to shallow reef recovery. Moreover, Japanese mesophotic corals being likely connected to other MCEs in the West Pacific, international collaborations are essential in order to obtain the most complete and accurate knowledge on these mysterious ecosystems.

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