Octocorals of the Indo-Pacific

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Abstract

Mesophotic coral ecosystems (MCEs), which comprise the light-dependent communities of corals and other organisms found at depths between 30 and ~150 m, have become a topic that increasingly draws the attention of coral reef researchers. It is well established that after the reef-building scleractinian corals, octocorals are the second most common group of macrobenthic animals on many shallow Indo-Pacific reefs. This chapter reviews the existing knowledge (e.g., species composition and depth of occurrence) on octocorals from selected Indo-Pacific MCEs: Okinawa (Japan), Palau, South Africa, the northern Red Sea, and the Great Barrier Reef (Australia). For all reefs, zooxanthellate taxa are not found below 65 m. We, therefore, suggest that physiological constraints of their symbiotic algae limit the depth distribution of zooxanthellate octocorals. More studies of lower MCEs (60–150 m) and their transition to deepwater communities are needed to answer questions regarding the taxonomy, evolutionary origins, and phylogenetic uniqueness of these mesophotic octocorals. New findings on mesophotic octocoral sexual reproduction indicate a temporal reproductive isolation between shallow and mesophotic octocoral populations, thus challenging the possibility of connectivity between the two populations. The existing data should encourage future studies aimed at a greater understanding of the spatiotemporal features and ecological role of mesophotic octocorals in reef ecosystems.

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38.1 Introduction

Octocorallia (Anthozoa) can be recognized from their distinctive morphological features: polyps with eight pinnate tentacles and an internal skeleton composed of microscopic calcareous sclerites (Bayer 1981; Tentori and Ofwegen 2011). Octocorals are spread across more than 40 families and feature a large variety of morphologies, sizes, and sclerite architectures (e.g., Aharonovich and Benayahu 2012). At present, Octocorallia consists of three orders: Alcyonacea, Helioporacea, and Pennatulacea. Previously, octocoral families were assigned to the orders Gorgonacea (i.e., sea fans and sea whips), Alcyonacea (i.e., the more fleshy growth forms referred to as "true" soft corals), and, two groups with stoloniferous growth forms, Stolonifera and Telestacea (Hickson 1930). With advances in knowledge, however, it became evident that intermediate forms also exist between these ordinal groups. Thus, Gorgonacea, Stolonifera, and

Telestacea are no longer used, and all species formerly assigned to those orders are now in Alcyonacea (Fabricius and Aplerslade 2001; McFadden et al. 2010). Alcyonacea is the most speciose order of Octocorallia, encompassing the vast majority of octocoral taxa on tropical coral reefs. Relatively few species belong to the other two orders, Pennatulacea (sea pens) and Helioporacea (blue corals).

Due to the limitations of underwater technologies, most coral reef studies were restricted to shallow reefs (<30 m) until the last two decades, and therefore, data on mesophotic coral ecosystems (MCEs; light-dependent communities of corals and other organisms found at depths of 30 to >150 m in tropical and subtropical regions (Puglise et al. 2009; Hinderstein et al. 2010) have been scant (Menza et al. 2007; Loya et al. 2016). Current technological advances, however, such as autonomous underwater vehicles (AUVs), remotely operated vehicles (ROVs), and closed-circuit rebreather diving, are facilitating the investigation of MCEs including their octocorals (see Kahng et al. 2010).

Octocorals have been considered the second most common group of macrobenthic animals on many shallow Indo-Pacific reefs, after the reef-building stony corals (Fabricius and Alderslade 2001). However, although members of this group have been the subject of various studies, they lag behind their scleractinian counterparts in terms of available information (Fabricius and De'ath 2008). In the overall global picture, reef-building stony corals represent only about 15% of all coral species, while octocorals comprise approximately 64% of the world's coral species (Williams and Cairns 2017). Therefore, it is important to increase the knowledge of this speciose group and understand the ecological role they play in MCEs.

Most of the theoretical concepts concerning MCEs have been derived from studies of scleractinian corals. It has been widely suggested that MCEs might serve as refugia to depth-generalist coral species (e.g., Lesser et al. 2009; Bongaerts et al. 2010; Bridge et al. 2013; Holstein et al. 2016; Loya et al. 2016) that are under threat from global climate change (e.g., Pandolfi et al. 2011; Spalding and Brown 2015). Whether these concepts are true for octocorals is unknown and should be considered.

The few studies conducted on mesophotic octocoral community composition can be divided into upper mesophotic (30–60 m) and lower mesophotic (60–150 m) zones. Most of these studies have been limited to a photographic recognition of the resident taxa, mostly at the family level, and have thus often underestimated the actual species diversity and abundance (see Shoham and Benayahu 2017). Noteworthy studies include Kahng and Kelley (2007), Bongaerts et al. (2011), Bridge et al. (2012), Appeldoorn et al. (2016), and Etnoyer et al. (2016).

In Hawaii, coral cover was demonstrated to increase for the stony coral *Leptoseris* spp. (at 90 m depth) and the inva-

sive octocoral *Carijoa riisei* (at 100 m), while the cover of other stony and soft corals decreased (Kahng and Kelley 2007). Diverse azooxanthellate octocorals were documented down to 150 m on the walls of atolls in the Coral Sea, but no taxa-level composition was presented (Bongaerts et al. 2011). Bridge et al. (2012) recorded 27 octocoral genera at 47–159 m on the Great Barrier Reef, 8 of which were absent from shallow waters, indicating that other taxa considered as rare in shallow reefs might be widespread at mesophotic depths. Etnoyer et al. (2016) addressed the impact of the Macondo oil spill (Gulf of Mexico) on gorgonian octocorals and provided data to the genus and species levels, and a study on MCEs under anthropogenic stress in Puerto Rico found that gorgonians were the only coral group present (Appeldoorn et al. 2016).

In this chapter, we compile the current knowledge on mesophotic Octocorallia of several Indo-Pacific reefs: Okinawa (Japan), Palau, South Africa, the northern Red Sea, and the Great Barrier Reef (Australia). Data are presented on aspects related to their species composition and depth distribution, community features, phylogeny, and sexual reproduction. We also compare available data on octocorals of shallow reefs with those of MCEs, highlighting the uniqueness of the latter. The gaps in our current knowledge on mesophotic octocorals present a challenge for future research to better understand their function in MCEs, their adaptive features, and the need for their conservation.

38.1.1 Research History

Studies of Indo-Pacific reef-dwelling octocorals have a long history, having begun in the Red Sea almost 250 years ago by Peter Forsskål, one of the most prominent pioneering naturalists of the eighteenth century. Forsskål's scientific legacy includes the description of the octocoral *Litophyton arboreum* Forsskål, 1775, an iconic species in the Red Sea and on many other Indian Ocean coral reefs (Ofwegen 2016). The Red Sea is considered the cradle of octocoral research based on historical research expeditions conducted in the region. Forsskål, along with the subsequent early Red Sea expeditions by Napoleon (1798) (Savigny 1817) and the Pola expedition (1895–1898) (Kükenthal 1913), provided the cornerstone for in-depth octocoral studies in the Red Sea and beyond. Among these are significant publications by Audouin (1828), Ehrenberg (1834), and Klunzinger (1877), whose studies yielded immense taxonomic knowledge, not only of the Red Sea but also of the larger Indo-Pacific region. Although not always indicated, the octocorals in those publications were collected from shallow coral reefs. Even later, much of the octocoral literature refers to Red Sea fauna obtained from a maximum depth of ~30 m (e.g., Thomson

and McQueen 1907; Kükenthal 1913; Gohar 1940, 1948; Verseveldt 1965, 1970; Verseveldt and Benayahu 1978, 1983; Benayahu 1990; Reinicke 1997; Ofwegen et al. 2013, 2016; Halász et al. 2014; Ofwegen 2016).

The taxonomic literature mostly provides the depth of collection; thus, it serves as a unique source of information on the occurrence of mesophotic octocoral species. Over a century ago, octocorals were obtained by dredging or trawling, providing records of MCE species long before the current interest in this environment began. For example, the historic Siboga expedition (1899–1900) recorded mesophotic octocorals from Indonesian reefs (Thomson and Dean 1931). Grasshoff (2000) referred to several mesophotic species, including those dredged at 70 m in 1928 by Dollfus at the entrance to the Gulf of Suez (northern Red Sea); Utinomi (1954) reported several mesophotic octocoral species on Kii Peninsula, Japan, and later (1975) reported 20 species obtained by trawling off the west coast of Australia. Octocorals were dredged in 1969 at 55–82 m in depth in the Straits of Tiran, south Gulf of Aqaba (Verseveldt and Benayahu 1978). Among these records are azooxanthellate species, which inhabit reefs below 30 m. For example, the Siboga expedition yielded several species of the genera *Acanthogorgia*, *Dendronephthya*, *Scleronephthya*, *Siphonogorgia*, and *Umbellulifera* below 30 m depth (Thomson and Dean 1931; Stiasny 1947). Verseveldt (1977) described the octocoral *Nephthyigorgia annectens* from the Great Barrier Reef dredged at 9–36 m. *Chromonephthea aurantiaca* was collected in the Philippines at ~54 m, *C. intermedia* at Salawati Island at 32 m, *C. megasclera* in Western Australia at 50 m, and *C. obscura* in Australia's Northern Territory at 55 m (Ofwegen 2005). In addition, *Dendronephthya semperi* was collected in Japan at 72 m and *D. novaezealandiae* in Aldabra at 40 m (Tixier-Durivault and Prevorsek 1959). It should be noted that at present for many Indo-Pacific reefs, such records are the only available source of information on mesophotic octocorals. Although mesophotic octocoral records are found in the taxonomic literature, in certain cases, the current status of those records requires verification in light of advances in taxonomic expertise and molecular phylogeny. Regrettably, the old taxonomic literature in many cases does not provide the depth of collection, and consequently, whether the species is from mesophotic depths cannot be confirmed.

The azooxanthellate octocoral genera noted above also frequently occur in shallower reefs (<30 m) (e.g., Benayahu and Loya 1985; Benayahu et al. 2003). It should be noted that shallow Indo-Pacific reefs are inhabited by both zooxanthellate and azooxanthellate octocorals, occasionally living side by side in well-lit habitats. Some azooxanthellate octocorals are found growing in shallow-reef crevices or overhangs (e.g., Benayahu et al. 2003). Thus, some azooxanthellate octocoral taxa are depth-generalists and exhibit a wide depth

distribution ranging from shallow waters down to mesophotic depths.

As octocorals at mesophotic depths have been poorly studied, discoveries abound. *Sinularia mesophotica*, a zooxanthellate octocoral, was recently described from Eilat's MCEs (Fig. 38.1a; Benayahu et al. 2017a). Similarly, *Altumia delicata* n. gen. n. sp. (Fig. 38.1b), an azooxanthellate octocoral, was also discovered (Benayahu et al. 2017b). These discoveries highlight the need for an in-depth study of MCE octocoral diversity.

38.2 Species Composition and Community Features

38.2.1 Okinawa, Japan

The shallow octocorals of Okinawa Island, as well as of other reefs of the Ryukyu Archipelago, have been studied quite intensively (see Benayahu 1995, 2002; Ofwegen and Benayahu 2006 and references therein). Those studies focused on shallow-reef fauna, but it should be noted that *Ceeceenus quadrus* was collected at 32 m. Other than this report, the mesophotic octocorals there have remained unstudied.

In the course of prospecting for bioactive molecules from marine organisms in Okinawa, it was realized that conventional *scuba* diving does not allow researchers to explore the full potential of reef biodiversity. Consequently since 2005, trimix rebreather diving has been adopted for that purpose. Extensive photographic records of mesophotic octocorals were made during collection trips to Zampa, Maeda, Manza, Seragaki, and Hedo on Okinawa Island.

Okinawa is surrounded by fringing reefs, featuring a drop-off to the upper mesophotic zone at 30 to ~45 m, mainly on the northern side of the island, and then followed by a deeper moderate sandy slope. Most of the octocoral surveys conducted were from the bottom of the reef wall down to the sandy slope, to a maximal depth of 60 m. The photographic records enabled identification of some octocorals to the genus level. Adjacent to the bottom of the wall, *Scleronephthya* (Fig. 38.2a) and *Siphonogorgia* colonies are commonly found growing under overhangs, with the colonies hanging downward. Although the sandy slope is considered an unlikely habitat for octocorals, fragments of stony coral debris and drifted gravel have provided attachment sites for colonies of zooxanthellate genera of the families Alcyoniidae, *Sinularia* (Fig. 38.2b); Clavulariidae, *Knopia* (Fig. 38.2c); Nephtheidae, *Litophyton*; and Xeniidae, *Cespitularia* and *Xenia* (Fig. 38.2d) along with the more abundant azooxanthellate genera Alcyoniidae, *Paraminabea* (Fig. 38.2e); Anthothelidae, *Solenocaulon* (Fig. 38.2f); Clavulariidae, *Carijoa*; Ellisellidae, *Ellisella* and *Junceella*; and
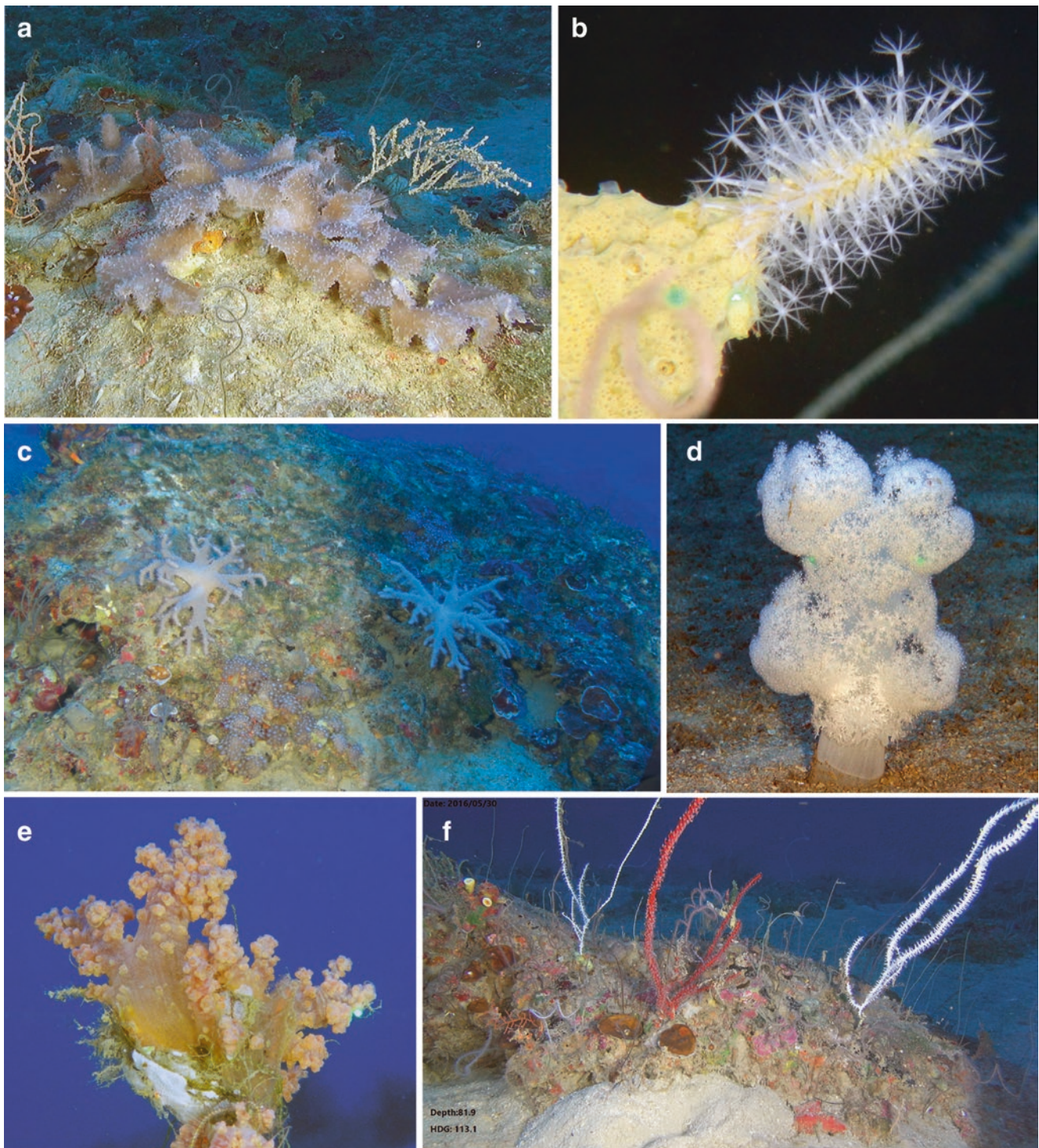
Fig. 38.1 Underwater photographs of Eilat's (Gulf of Aqaba, northern Red Sea) mesophotic octocorals. (**a**) Colonies of *Sinularia mesophotica*, 62 m; (**b**) *Altumia delicata*, 102 m; (**c**) *Sinularia eilatensis*, 55 m; (**d**) *Dendronephthya* sp., 75 m; (**e**) *Scleronephthya lewinsohni*, 82 m; and (**f**) rocky patch with octocorals, 83 m. (Photo credits: Yehuda Benayahu and Erez Shoham)

Nephtheidae, *Dendronephthya* and *Umbellulifera.* *Paraminabea* colonies are rather common in deep cave formations and appear to have yielded interesting natural products (Uddin et al. 2011). Although no quantitative data have been obtained on the species composition, the photographic records indicate a prevalence of azooxanthellate octocorals in Okinawa's upper mesophotic zone, as opposed to its shallow reefs that are dominated by zooxanthellate octocorals, primarily of the genera *Lobophytum*, *Sarcophyton*, and *Sinularia* (Benayahu 1995, 2002).
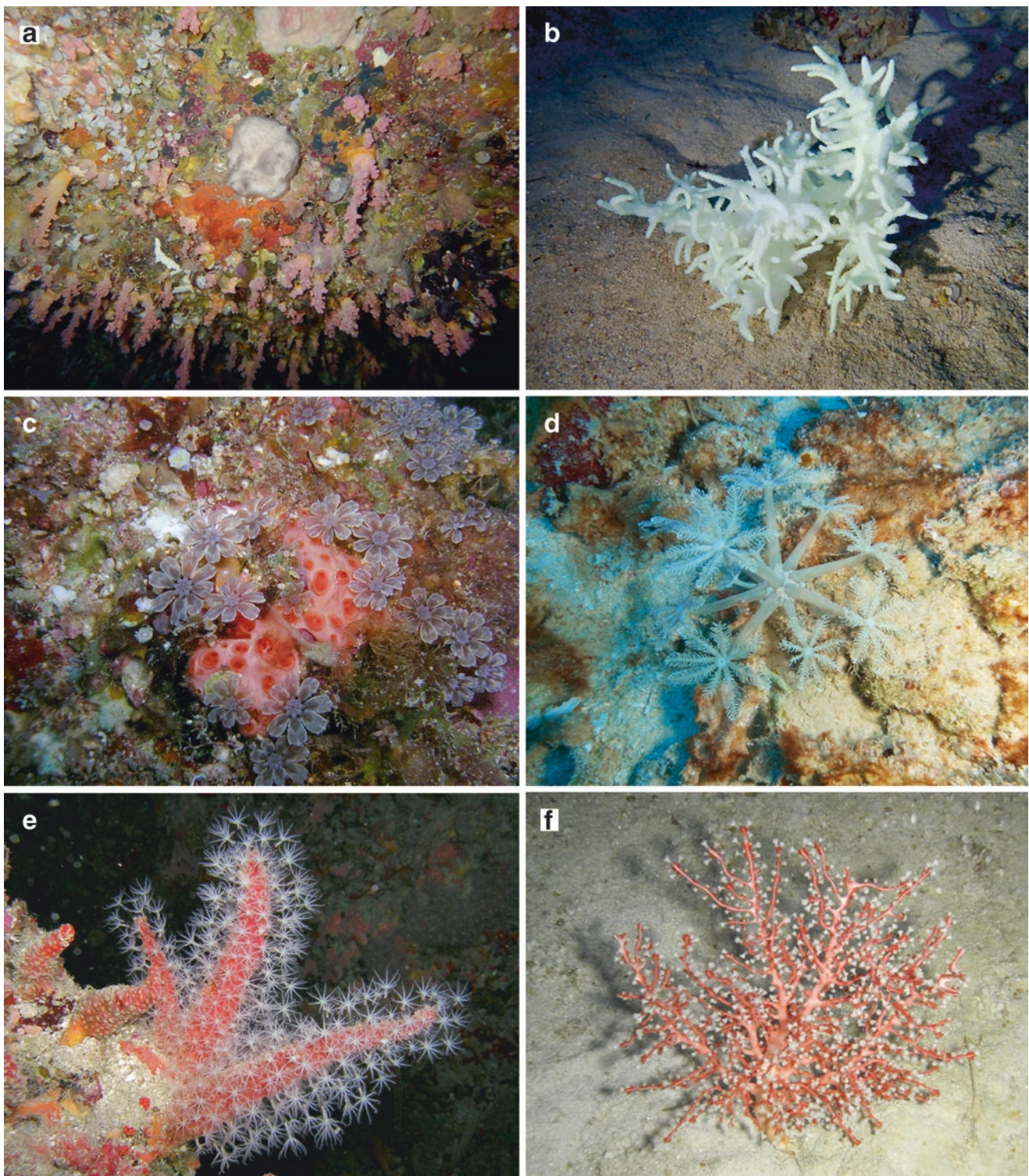
Fig. 38.2 Underwater photographs of Okinawa (Ryukyu Archipelago, Japan) mesophotic octocorals. (**a**) *Scleronephthya* sp., 35 m; (**b**) *Sinularia* sp., 50 m; (**c**) *Knopia* sp., 30 m; (**d**) *Xenia* sp., 50 m; (**e**) *Paraminabea* sp., 40 m; and (**f**) *Solenocaulon* sp., 50 m. (Photo credits: Junichi Tanaka)

38.2.2 Palau

Octocorals have constituted an important group collected by the Coral Reef Research Foundation for natural product research by the US National Cancer Institute.

Extensive efforts were made in Palau to obtain a complete sampling of the fauna, and all organisms encountered were identified to genus/species level. An early listing was presented in Fabricius et al. (2007), but additional species have been found since. Some aspects of the sea

fans and sea whips of Palau are included in Sanchez et al. (2019).

Palau has a highly diverse octocoral fauna in shallow waters of ~150 species with some areas dominated by them (e.g., Ofwegen 2008; McFadden et al. 2014). Ninety of these species can be considered as fleshy octocorals, while the remainder are largely sea fans and sea whips. Considering the 45 Indo-Pacific octocoral genera listed by Fabricius and Alderslade (2001), about 16 are likely to have mesophotic members. Of those, 14 genera, roughly 30 species, have been recorded from Palau. Palau's mesophotic octocorals include diverse azooxanthellate taxa recorded at a wide depth range and only a couple of zooxanthellate species such as *Klyxum* sp. inhabiting the upper mesophotic zone (Figs. 38.3 and 38.4) and *Sarcophyton glaucum*.

A small research submersible, the *DeepWorker 2000*, as well as deep mixed-gas diving was used in Palau to sample the lower mesophotic octocoral fauna. As a result, a number of new species, yet to be described, were discovered, and new occurrence records were documented for known species. In addition to the mesophotic outer slope, some channel and lagoon areas of Palau also have MCEs, with octocorals occurring there (Colin 2009).

38.2.3 South Africa

High-latitude coral communities occur along South Africa's east coast between 26°54′ and 27°56′. They comprise an extension of the more typical, accretive reef system found along the East African coast, forming the marginal, southern-most African distribution of this fauna in KwaZulu-Natal province (see Williams 1992; Riegl et al. 1995; Schleyer 2000). Their occurrence is mediated by the Agulhas Current, which originates primarily from the East Madagascar Current, forming one of the strongest of the warm, western boundary currents (Lutjeharms 2006).

These coral reef communities are found primarily in what is known as the Delagoa Bioregion in the iSimangaliso Wetland Park. Octocorallia, rather than Scleractinia, are preponderant in most of the coral communities, with this being attributable to the marginal nature of the reefs and prevailing turbulence (Schleyer 2000). The octocorals are prolific on the shallower reefs and range in depth from ~8 to 25–27 m. While there is a natural break in the reef structure at this depth, the distribution of corals beyond this appears to be largely light-limited (Schleyer 2000), as hard substrata also occur in the upper margin of the upper mesophotic zone (28 to ~40 m). However, the shallower reefs present a more varied profile than the deeper habitat, which is flat and mostly covered by a thin layer of sediment. Two-mile Reef is typical of such South African reefs and hosts a lush mix of octocorals, mainly zooxanthellate species (Benayahu and Schleyer 1993). Offshore of this reef lies a flat, featureless upper MCE extending down to 38 m and known as Sponge Reef due to its abundance of large Porifera. This is similar to other isolated areas off South Africa in which slightly elevated areas on deeper reefs support a lower abundance of octocorals, covering only 6.3% of this reef's surface.

The octocoral community in this upper mesophotic zone comprises a distinct "spillover" from the adjacent shallower reef (see Ramsay et al. 2006; Celliers and Schleyer 2007). Several zooxanthellate Alcyoniidae can be found here (e.g., *Lobophytum depressum*, *L. latilobatum*, *Sarcophyton* sp., and *Sinularia brassica*), but they are far less abundant than the azooxanthellate *Dendronephthya* sp., *Parasphaerasclera aurea* (Fig. 38.5a), *Homophyton verrucosum* (Fig. 38.5b) and *Leptogorgia* sp. The zooxanthellate species have encrusting morphologies and, thus, are able to utilize the limited light available, as well as shed sediment.

38.2.4 Northern Red Sea

The northern Red Sea octocorals have been extensively studied, albeit mostly shallower than 30 m, and included studies on their community structure (e.g., Benayahu and Loya 1977, 1981), life history (e.g., Kahng et al. 2011 and references therein; Mandelberg and Benayahu 2015), recruitment capability (e.g., Perkol-Finkel and Benayahu 2004, 2005), and taxonomy. While these studies have revealed a vast shallow-water octocoral richness in the northern Red Sea, mesophotic octocorals have remained poorly studied.

The first quantitative reference to mesophotic octocorals in Eilat (Gulf of Aqaba, northern Red Sea) was by Eyal (2014). He found octocorals to cover 8% of the benthic habitat at 40 m, decreasing to 1% at 60 m, and assigned the documented taxa to three families: Alcyoniidae, Melithaeidae, and Xeniidae. Shoham and Benayahu (2017) compared octocoral communities off Eilat at two upper mesophotic reefs (30–45 m) and two shallow reefs (reef flat and upper fore reef) and found higher species richness in the upper mesophotic reefs. Each reef type revealed a unique octocoral species composition and distinct community structure, with only 16% of the species shared by both MCEs and shallower reefs. This study also revealed an almost exclusive dominance of zooxanthellate species in the upper mesophotic reefs, thus indicating an adequate light regime for photosynthesis to take place there.
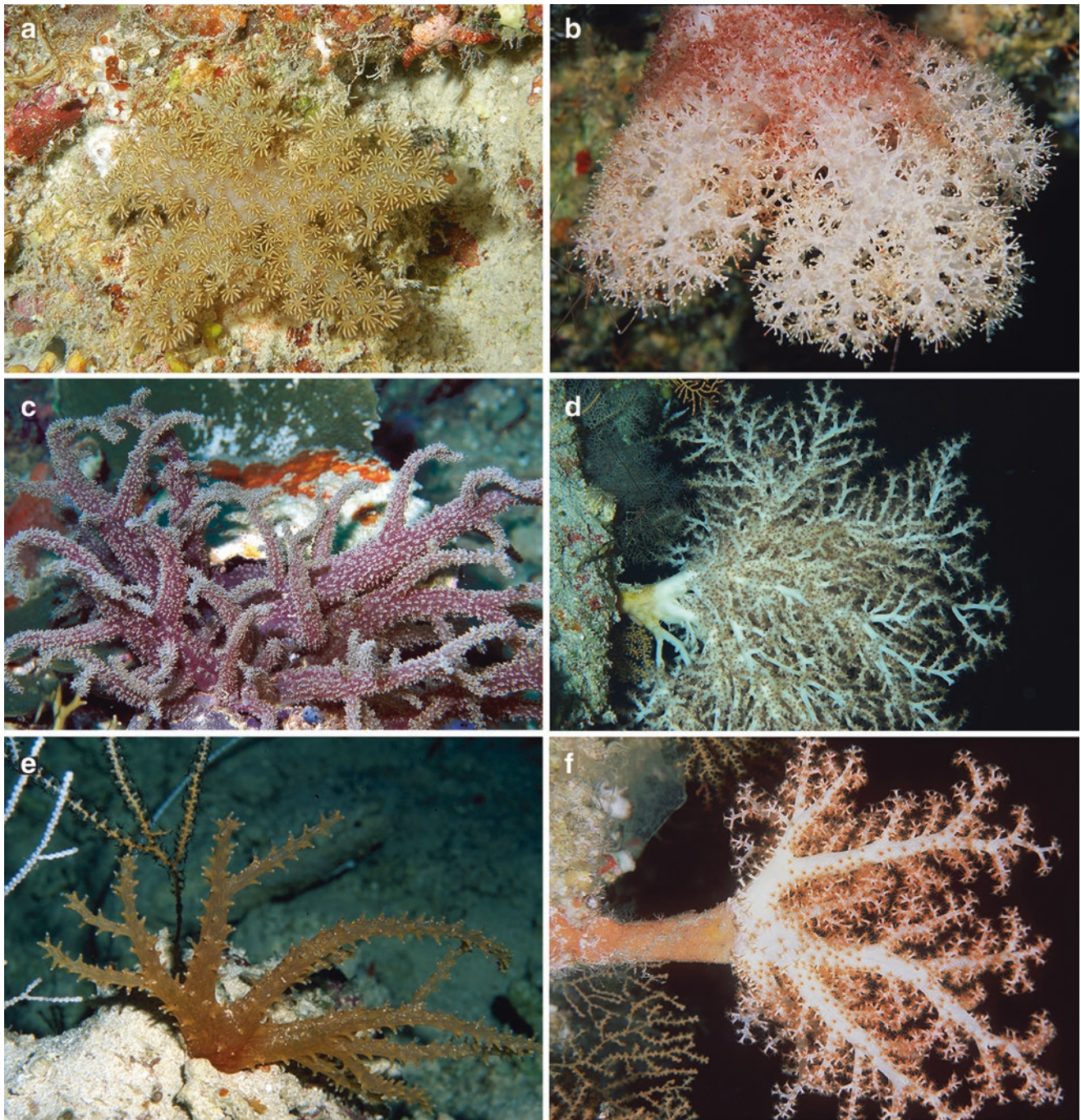
Fig. 38.3 Underwater photographs of Palau mesophotic octocorals. (**a**) *Klyxum* sp., 38 m, is an upper mesophotic species; (**b**) *Dendronephthya* sp., 100 m, is one of the several members of this genus in Palau; (**c**) probably *Stereonephthya* sp., 35 m, in a deep channel; (**d**) *Chironephthya* sp., 120 m, is common on the outer slope; (**e**) *Nephthyigorgia* sp., 110 m, is common on the outer slope; and (**f**) *Scleronephthya imbricans*, 110 m, is common starting at ~75 to 120 m. (Photo credits: Coral Reef Research Foundation)
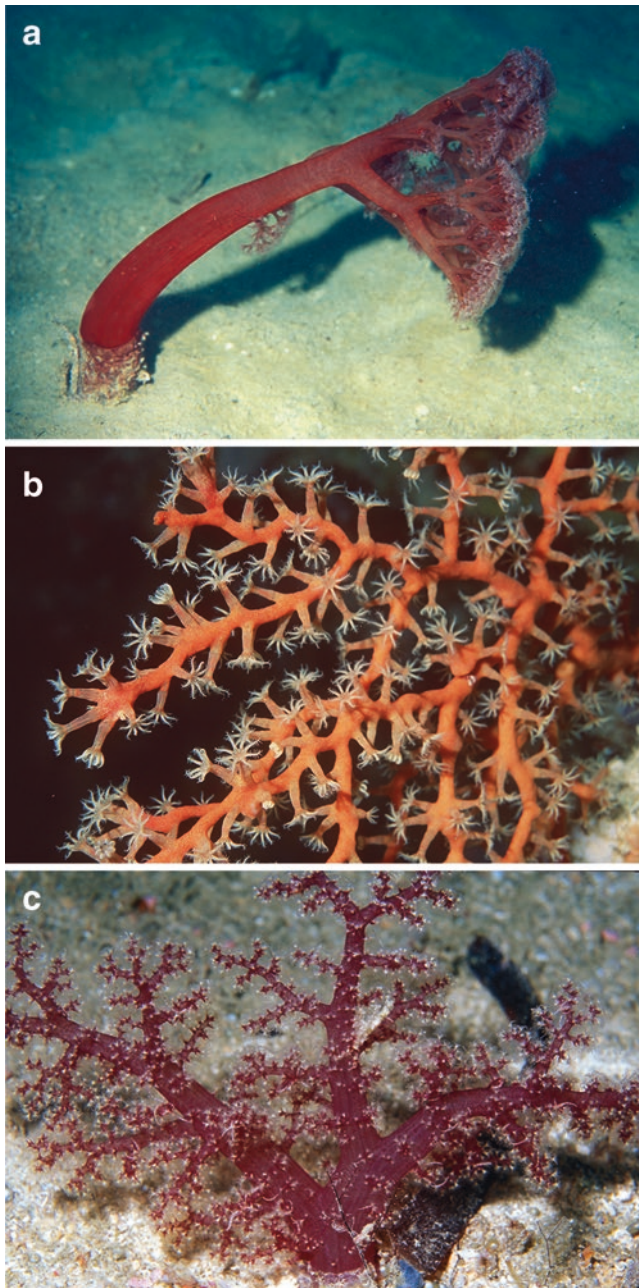
Fig. 38.4 Underwater photographs of Palau's mesophotic octocorals. (**a**) *Umbellulifera* sp., 80 m, is one of a variety of color forms; (**b**) *Iciligorgia* sp., 80 m, is found in the 75–100 m depth range; and (**c**) probably *Nephthyigorgia* sp., 85 m, occurs in clusters of colonies on the slope. (Photo credits: Coral Reef Research Foundation)

Eilat's lower MCEs (60–150 m) were documented using an ROV[1] in 2016–2017 (Benayahu unpubl. data). The ROV

[1]Samples were collected by ROV (ECA H800) operated from the R/V *Sam Rothberg*. In situ photography used a low-light black and white camera VS300 (Eca Robotics) and 1CAM Alpha HD camera (SubCimaging). Octocoral samples were collected using a manipulator arm on the ROV, and fragments of colonies were carefully preserved in 100% ethanol for molecular work. The original samples were placed in

surveys revealed a rather continuous reef at the lower margins of the upper mesophotic zone (45–70 m), which is composed of hard substrate that is occasionally separated by sandy patches. The deeper seascape, between 70 and 150 m, is comprised of scattered hard bottom patches that decrease in abundance with depth (see also Fricke and Hottinger 1983). These patches, especially those at greater depth, vary in size but mostly cover several square meters. They are low at their periphery, with a mounded center and a complex morphology occasionally featuring some crevices and overhangs.

Table 38.1 summarizes the known octocoral families and species recorded in Eilat, northern Gulf of Aqaba, according to reef zone: reef flat, upper fore reef, and upper MCE (based on Shoham and Benayahu 2017) and lower MCE of the northern Red Sea (based on the 2016–2017 ROV dives presented herein, the octocoral collection of Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, and Grasshoff (2000)). The highest number of species (45) was recorded from the upper mesophotic zone (30–45 m) followed by a decrease with depth, reaching a minimum of only 7 species at a depth of >105 m (Table 38.1). As patches of hard substrate become sporadic in the deepest mesophotic zone, along with an increased percentage of sandy seabed, it is suggested that the decrease in octocoral diversity is associated with this transition. Further MCE studies will confirm whether this low value is a bias derived from a limited sampling or indeed reflects the true octocoral diversity there.

Zooxanthellate octocorals are dominant on Eilat's reef table and upper fore reef (Table 38.1; Shoham and Benayahu 2017). These species also comprise a major faunistic component of the upper mesophotic zone down to 45 m, after which their abundance and diversity sharply decrease. The zooxanthellate octocorals of the family Alcyoniidae are dominant including the speciose genus *Sinularia*, *Sarcophyton*, *Rhytisma*, and *Cladiella*. No *Sinularia* colony was recorded below 65 m, with *S. eilatensis* (Fig. 38.1c), *S. humesi*, *S. gardineri*, *S. leptoclados*, *S. querciformis*, and *S. vrijmoethi* documented at the lower edge of the upper mesophotic zone.

Only sparse zooxanthellate colonies of a few species were found at 50–65 m and none deeper. The zooxanthellate depth-generalist octocorals whose distribution extends from the reef flat to the deepest margins of the upper mesophotic zone are *Litophyton* sp., *Rhytisma fulvum fulvum*, *Sinularia leptoclados*, and *S. humesi*. The zooxanthellate species of the families Alcyoniidae and Nephtheidae are highly abundant on the reef flat and upper fore-reef zone, massively contributing to the octocoral diversity there. At the upper mesophotic

70% ethanol for taxonomic identification and deposited at the Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies.
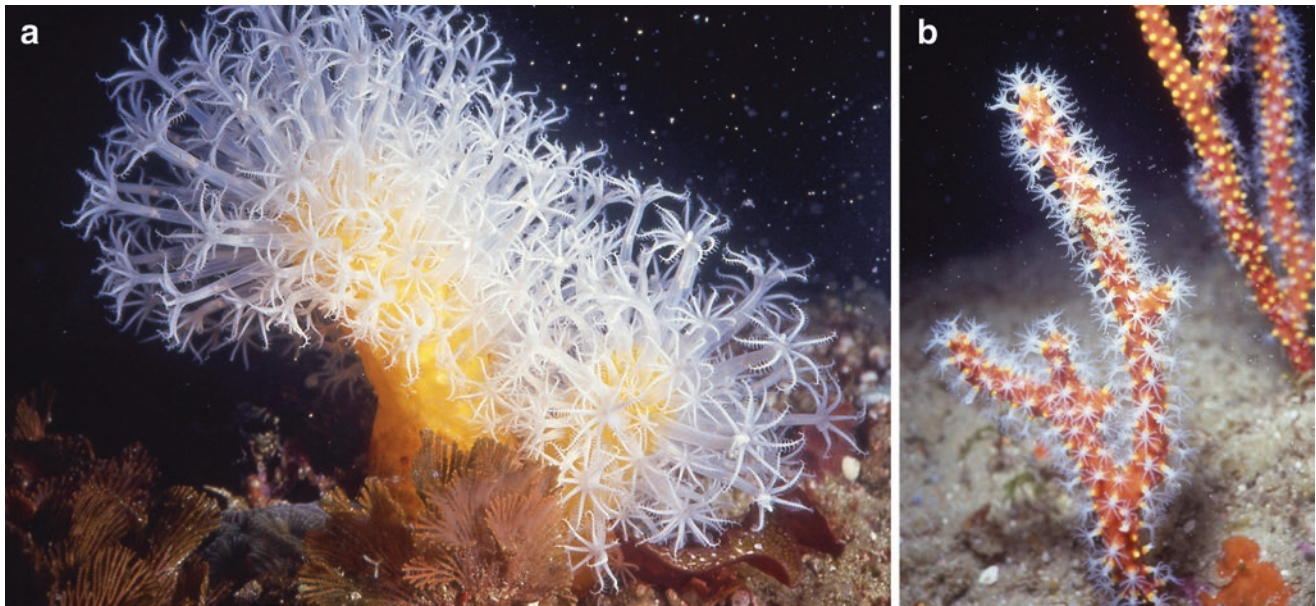
Fig. 38.5 Underwater photographs of South Africa's mesophotic octocorals. (**a**) *Parasphaerasclera aurea*, 35 m, and (**b**) *Homophyton verrucosum*, 32 m. (Photo credits: Michael H Schleyer)

zone (30–45 m), members of these two families occur, along with frequently occurring patches of the Xeniidae (Table 38.1; Shoham and Benayahu 2017). Only sparse xeniid colonies were encountered deeper than 50 m. These findings indicate that zooxanthellate octocorals do not inhabit the lower mesophotic zone, in stark contrast to some zooxanthellate stony corals which occur at 120 m (references in Shoham and Benayahu 2017). Such differences in the distributional patterns of these two coral groups may arise from physiological constraints of the octocoral symbiotic algae, which cannot cope with the low solar irradiance even in Eilat's clear waters.

The azooxanthellate genera of the Nephtheidae, *Dendronephthya* (Fig. 38.6d) and *Scleronephthya* (Fig. 38.6e), inhabit both the upper and lower mesophotic zones (Table 38.1). The Nidaliidae are typically mesophotic inhabitants, with some being very rare in Eilat, such as *Nephthyigorgia* sp. and *Nidalia* sp. It is worth noting that both genera are new records for the Red Sea.

Table 38.1 indicates that among octocorals, sea fans and sea whips are the most common inhabitants of Eilat's lower mesophotic zone (Fig. 38.6f), comprising eight families. There, they replace the other zooxanthellate fleshy genera, becoming the prominent octocoral group, along with some azooxanthellate Nephtheidae and Nidaliidae. Notably, there are a large number of sea fan and sea whip species known and described from the Red Sea, especially from its northern part (Grasshoff 2000). Grasshoff (2000) provided an extensive and almost conclusive overview of this fauna, including historical records of MCE species from the Dolffus expeditions to the Gulf of Suez, as well as others collected by Dr.

Cyril Crossland during the Mabahith expedition (Stiasny 1938, 1940, 1959). Grasshoff's study also reexamined the type material collected from many of these species, originally described from the Red Sea, and described new ones from old collection material, as well as more recent ones.

The recent ROV collections in Eilat yielded >35 samples comprising 6 families and 13 genera of sea fan and sea whip species and branched members of the family Nidaliidae. Among these samples were specimens of *Discogorgia erythraeensis*, a species previously only known from the holotype. The holotype specimen was collected at 70 m and the newly acquired material at 97 and 100 m. These new findings represent depth extensions for this species. Another plexaurid, *Bebryce inermis*, was discovered for the first time in the Red Sea. This species is known from the Gulf of Oman (Samimi Namin and Van Ofwegen 2010) but has now been discovered at 78 m in Eilat, which is also a new depth record. Other new depth distribution records are *Acanthogorgia* cf. *spinosa* (62 m), *Euplexaura rhipidalis* (108 m), *Melithaea sinaica* (65 m), *Subergorgia rubra* (108 m), *Verrucella klunzingeri* (152 m), *Villogorgia nozzolea* (159 m), and *Viminella junceelloides* (82 m) (Table 38.1). It should be noted that all the above taxa are azooxanthellate, thus portraying the octocoral fauna of the lower mesophotic zone as typically azooxanthellate. Octocorals of the family Nidaliidae were encountered in Eilat's MCE at a depth range of 55–120 m and represented mostly by the genera *Chironephthya*, *Nephthyigorgia*, *Nidalia*, and *Siphonogorgia*. Species of these genera have a branched morphology and were frequently encountered at mesophotic depths.

Table 38.1 Octocoral families and species recorded in Eilat, northern Gulf of Aqaba, according to reef zone: reef flat (<1 m), upper fore reef (1–5 m), upper mesophotic (30–45 m and 45–65 m, based on Shoham and Benayahu 2017), and lower mesophotic (65–85 m, 85–105 m, and >105 m; based on Benayahu unpubl. data, octocoral collection of Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, and Grasshoff (2000))

	Reef flat	Upper fore reef	Upper mesophotic		Lower mesophotic		
Depth (m)	~1	<5	30–45	45–65	65–85	85–105	>105
Taxa							
Family Acanthogorgiidae							
Acanthogorgia spinosa				+			
Acanthogorgia sp.				+			
Anthogorgia caerulea[a]			+				
Anthogorgia gubalensis[a]				+	+		
Anthogorgia sp.				+			
Muricella sayad[a]					+		
Family Alcyoniidae							
Cladiella pachyclados	+		+				
Klyxum utinomii			+	+			
Klyxum sp.				+			
Lobophytum depressum			+				
Lobophytum patulum				+			
Metalcyonium verseveldti				+			
Rhytisma f. fulvum	+	+	+				
Sarcophyton auritum	+	+					
Sarcophyton gemmatum			+				
Sarcophyton glaucum			+	+			
Sarcophyton pauciplicatum				+			
Sarcophyton sp.				+			
Sinularia cruciata	+	+					
Sinularia eilatensis			+	+			
Sinularia erecta	+	+					
Sinularia gardineri			+	+			
Sinularia heterospiculata			+				
Sinularia hirta			+				
Sinularia humesi	+	+	+				
Sinularia levi	+	+					
Sinularia leptoclados	+	+	+	+			
Sinularia licroclados			+				
Sinularia mesophotica				+			
Sinularia polydactyla	+	+					
Sinularia portieri	+	+					
Sinularia querciformis		+		+			
Sinularia recurvata	+		+				
Sinularia terspilli		+	+				
Sinularia vrijmoethi		+	+				
Family Briareidae							
Briareum hamrum			+				
Family Clavulariidae							
Altumia delicata							+
Family Ellisellidae							
Ellisella dollfusi[a]			+	+	+		
Ellisella marisrubri[a]				+	+		

(continued)

Table 38.1 (continued)

	Reef flat	Upper fore reef	Upper mesophotic		Lower mesophotic		
Depth (m)	~1	<5	30–45	45–65	65–85	85–105	>105
Junceella juncea[a]			+				
Verrucella gubalensis[a]				+	+		
Verrucella klunzingeri				+	+	+	+
Viminella erythraea					+	+	+
Viminella junceelloides			+	+	+		
Nicella alba[a]							+
Family Gorgoniidae							
Rumphella torta[a]			+				
Family Plexauridae							
Acanthomuricea dina[a]				+	+		
Astrogorgia jiska[a]					+		
Astrogorgia lea[a]			+				
Astrogorgia milka[a]					+		
Bebryce inermis					+		
Bebryce sulfurea[a]			+				
Discogorgia erythraeensis						+	
Euplexaura rhipidalis				+	+	+	+
Villogorgia mabahith[a]					+		
Villogorgia nozzolea [a]					+		+
Menella kanisa[a]					+	+	
Lapidogorgia batseba[a]							
Paracis chawwa[a]			+				
Family Melithaeidae							
Melithaea biserialis[a]							+
Melithaea pulchra[a]			+				
Melithaea splendens[a]			+	+	+		
Melithaea rubrinodis[a]				+			
Melithaea sinaica				+			
Melithaea sp.						+	
Melithaea erythraea			+				
Family Nephtheidae							
Dendronephthya hemprichi					+		
Dendronephthya pharonis					+		
Dendronephthya sinaiensis				+	+		
Dendronephthya sp.				+	+	+	+
Litophyton arboreum					+		
Litophyton sanderi			+	+			
Litophyton sp.	+	+	+	+			
Paralemnalia thyrsoides			+	+			
Scleronephthya corymbosa			+				
Scleronephthya imbricans							+
Scleronephthya lewinsohni			+	+	+	+	
Scleronephthya sp.				+			
Stereonephthya cundabiluensis			+				

(continued)

Table 38.1 (continued)

Depth (m)	Reef flat ~1	Upper fore reef <5	Upper mesophotic 30–45	45–65	Lower mesophotic 65–85	85–105	>105
Stereonephthya imbricans				+	+		
Stereonephthya sp.				+		+	
Umbellulifera oreni				+			
Family Nidaliidae							
Siphonogorgia mirabilis				+			
Siphonogorgia sp.			+	+	+	+	+
Chironephthya sp.				+	+		+
Nephthyigorgia sp.						+	
Nidalia sp.				+			
Family Parisididae							
Parisis fruticosa[a]					+		
Family Subergorgiidae							
Annella reticulata			+				
Subergorgia rubra			+	+	+		+
Subergorgia suberosa[a]					+		
Family Tubiporidae							
Tubipora musica	+	+	+				
Family Xeniidae							
Anthelia sp.			+				
Heteroxenia coheni			+				
Heteroxenia fuscescens			+				
Ovabunda sp.			+				
Ovabunda ainex			+				
Ovabunda biseriata				+			
Ovabunda faraunensis			+				
Ovabunda impulsatilla			+				
Ovabunda macrospiculata				+			
Xenia hicksoni			+				
Xenia umbellata			+				
Xenia sp.			+				
Family Keroeididae							
Keroeides erythraea[b]							

Bottom of table provides number of recorded species per reef zone. Presence of species at a given depth is indicated by +
[a]Indicates Red Sea record derived from Grasshoff (2000)
[b]Suspected mesophotic distribution (although specific depth not mentioned)

The changes in octocoral taxa composition from the shallow reef flat and upper fore-reef zone to the upper MCE and then to the lower MCE were associated with respective transitions from zooxanthellate autotrophs to azooxanthellate heterotrophs. In addition, there was a corresponding change from the encrusting, flattened colony morphology of the zooxanthellate species to an upright branching morphology of the azooxanthellate species. It is suggested that such changes reflect a change in the mode of feeding, where the flat colonies (e.g., *Sarcophyton* spp., *Sinularia* spp., and *R. f. fulvum*) are well adapted to expose their algal symbionts to the light needed for photosynthesis, while an upright branching morphology (e.g., *Dendronephthya* spp., *Scleronephthya* spp., and *Siphonogorgia* sp.) enables exposure to water currents and enhances the capture of planktonic food by the asymbiotic taxa.

38.2.5 Great Barrier Reef, Australia

Octocorals are a key component of benthic ecosystems on the Great Barrier Reef (GBR) and in the adjacent Coral Sea (Bridge et al. 2012, 2019). Azooxanthellate octocorals representing a diverse range of genera dominate the lower mesophotic depths along the GBR shelf edge, while zooxanthellate octocorals, particularly from the family Xeniidae, are dominant components of the upper mesophotic coral communities at some locations (Bridge et al. 2011a). Octocoral
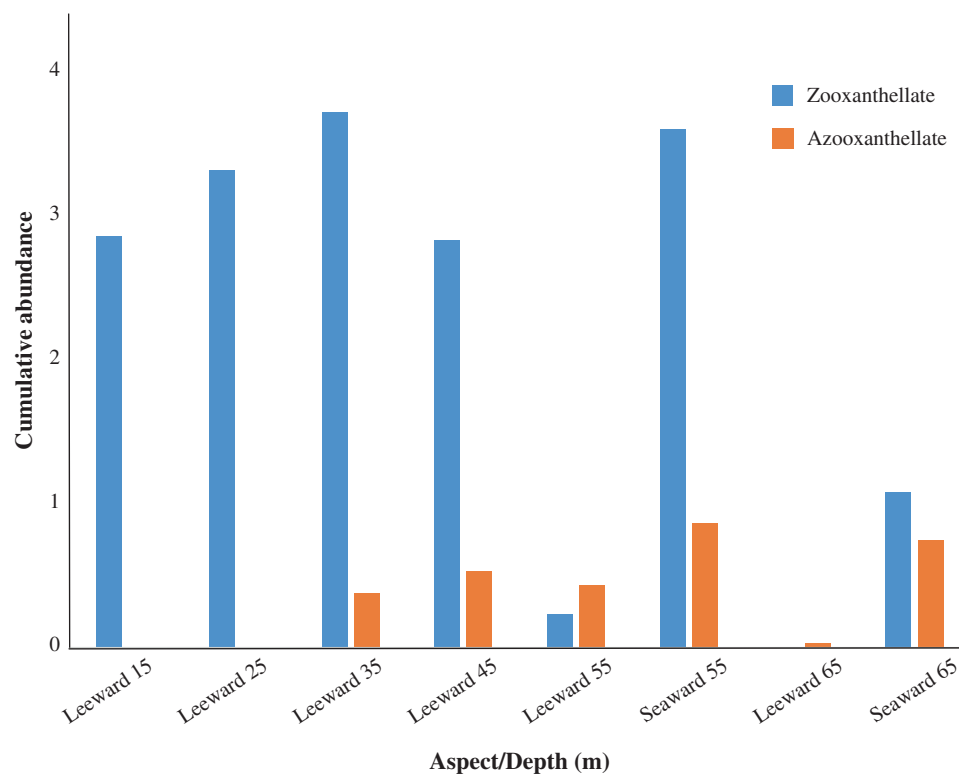
Fig. 38.6 Total octocoral abundance for each aspect/depth combination at Hydrographers Passage. Abundance (y-axis) is measured as summed mean of relative abundance scores across all images at each site (i.e., the sum of the mean relative abundance score for each taxon on the 0–5 scale at each aspect/depth combination)

collections from mesophotic depths, since 2007, are housed in the collections of the Queensland Museum. Most specimens have been identified to genus level, although a few taxa have been identified to species. The most extensive survey of mesophotic octocorals in 2007 recovered at least 24 azooxanthellate genera, approximately a quarter of which represented new records for the region (Bridge et al. 2012). Zooxanthellate octocorals were less diverse at mesophotic depths but were abundant at upper mesophotic depths at some sites. Specimens collected included new records for the region, such as *Lohowia koosi*, which was described in 2003 from Lord Howe Island in the South Pacific.

Octocoral abundance was analyzed from benthic surveys conducted using the AUV *Sirius* (Williams et al. 2010) along a depth gradient from 15 to 75 m at Hydrographers Passage on the outer shelf of the central GBR (Beaman et al. 2011; Bridge et al. 2011b).[2] The results indicated that octocorals

were abundant from shallow to upper mesophotic depths (Fig. 38.6). On the leeward side of the shoals, their abundance declined rapidly below 45–50 m. On the seaward side, octocorals remained abundant to 55–60 m but declined substantially below 60 m. Community composition also changed considerably among depths (Fig. 38.7). Shallow sites (<30 m) were dominated by *Efflatounaria*-like colonies, while deeper sites were generally dominated by

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[2] The AUV collected geo-referenced, stereo images with a footprint of 1.5 × 1.2 m at a rate of ~1 image pair every 50 cm. We randomly selected 30 images separated by at least 2 m (to avoid double counting from image overlap) from within 6 depth bins (10–20, 20–30, 30–40, 40–50, 50–60, and 60–70 m) representing shallow to mesophotic depths. Images were further divided into "seaward" and "leeward" aspects, depending upon their location. The GBR outer shelf supports long, linear lines of submerged shoals along the shelf edge with tops at ~15 m water depth (Hopley et al. 2007), and these features are common
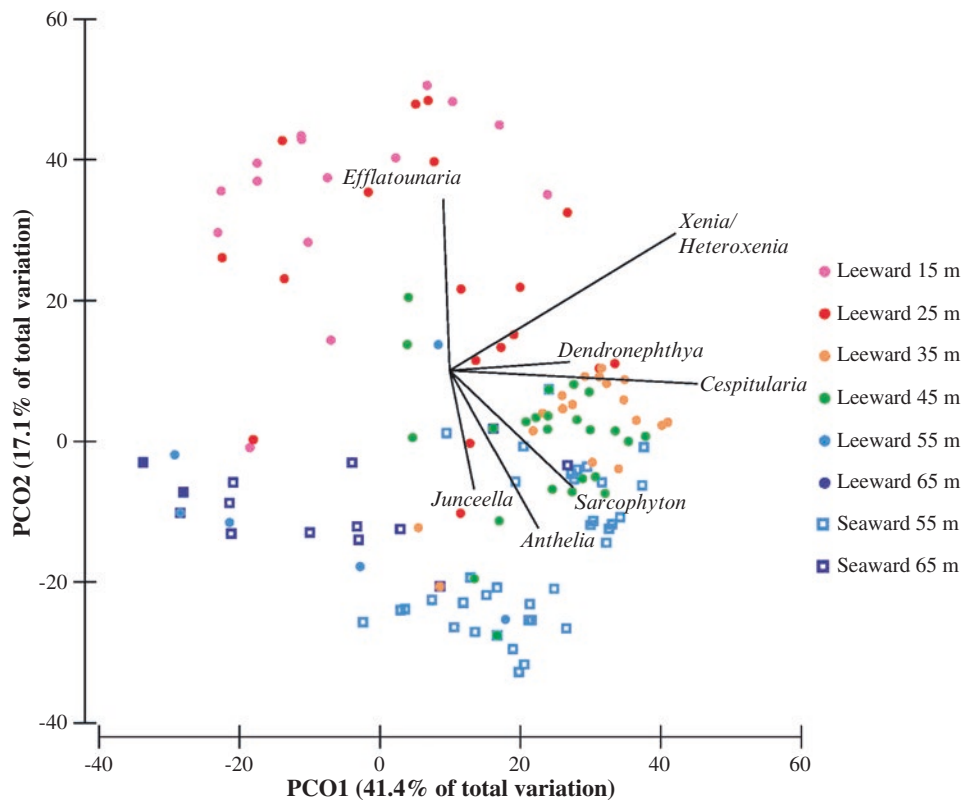
at Hydrographers Passage (Beaman et al. 2011). In this study, "leeward" aspect sites were considered as those occurring on the leeside of these shoals, while "seaward" aspect sites were those on the seaward side. Not all depth bins contained enough images to fulfill all the selection criteria, although each aspect/depth combination contained at least 22 images for analysis.

Each image was visually inspected for soft corals, and the abundance of each genus is recorded using scale of relative abundance (sensu DeVantier et al. 1998). Relative abundance of each genus was scored as 1, 1–10% cover; 2, 11–30%; 3, 31–50%; 4, 51–75%; and 5, 76–100%. Taxonomic identifications based on images were informed by specimens collected from the same region concomitantly with the AUV surveys. In addition, very small colonies (<10 cm in diameter) were excluded from our analysis. Changes in community composition were assessed using multivariate techniques in PRIMER V6 (Clarke and Gorley 2006). Analyses were performed on an untransformed Bray-Curtis similarity matrix, and the relationship between images in all aspect/depth combinations was visualized using principal coordinates analysis (PCO), with Spearman rank correlation vectors showing the relationship between the dominant taxa and sites.

Fig. 38.7 Principal coordinates (PCO) plot based on a Bray-Curtis similarity matrix showing the relationship between images for each aspect/depth group

Xenia/Heteroxenia and *Cespitularia*. *Anthelia* was also common at lower mesophotic depths on seaward sites but less common on leeward sites. Other genera, including *Lobophytum*, *Sarcophyton*, and *Sinularia*, appeared in a relatively high number of images across many seaward and leeward depth groups but were not particularly abundant in any one location.

The current findings confirm that octocorals are a key component of the benthos at mesophotic depths on the GBR. Zooxanthellate octocorals, predominantly xeniids, are particularly abundant at upper mesophotic depths, and octocoral cover at these mesophotic depths exceeds 50% in some locations. Zooxanthellate octocorals become rare in the lower mesophotic zone, even in the exceptionally clear waters of the GBR outer shelf.

38.3 Phylogeny

Little is known about the phylogenetic affinities and origins of the mesophotic octocoral fauna. Is there an overlap between phylogenetically distinct shallow-water and deep-water lineages of octocorals, or do species that comprise MCEs represent unique evolutionary lineages adapted spe-

cifically to that environment? Throughout the tropical Indo-Pacific, shallow-reef octocoral communities are typically dominated by species belonging to the families Alcyoniidae, Nephtheidae, and Xeniidae (Fabricius and Alderslade 2001), a majority of which are zooxanthellate. While members of these clades extend to the upper mesophotic zone (Bridge et al. 2012; Shoham and Benayahu 2017), it is not clear whether the species that occur at greater depth are the same as those that are found on the shallow reef. Soft corals are extremely challenging to identify to species level, and our understanding of species concepts and species boundaries in these groups is in flux (e.g., Ofwegen et al. 2013, 2016; McFadden et al. 2017). In most genera, genetic data are necessary to confirm and support species-level identifications made on the basis of morphology (McFadden et al. 2014).

The very few genetic datasets that exist for mesophotic octocorals suggest that some of the same species that occur in shallow-water reefs do extend into the MCEs (Fig. 38.8; McFadden unpubl. data), but there are also species that occur only in MCEs. The northern Red Sea at Eilat, Israel, is one of the only locations to date where contiguous shallow-reef and mesophotic octocoral communities have been sampled genetically (Fig. 38.8). Here, some of the same octocoral
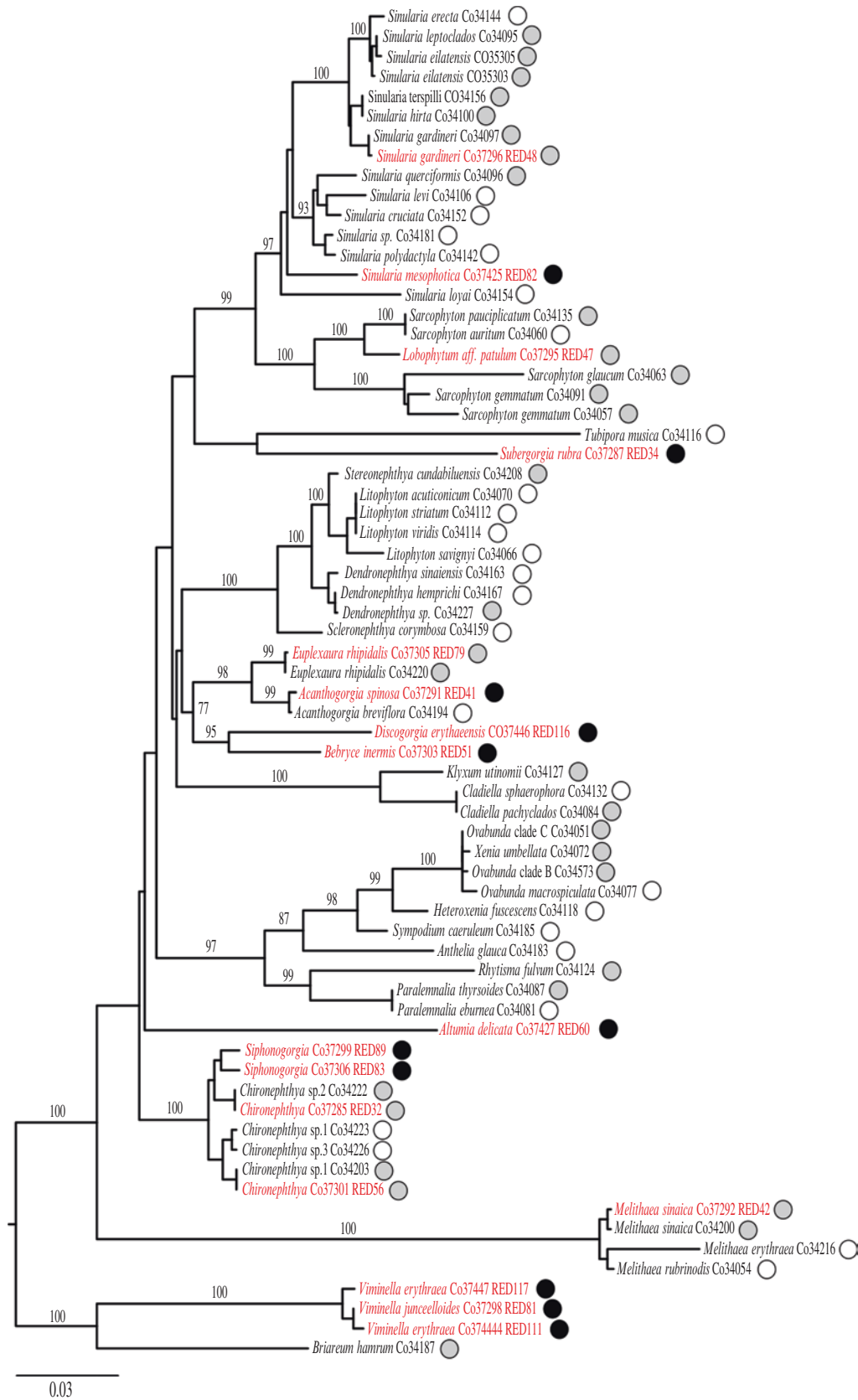
Fig. 38.8 Maximum likelihood reconstruction of phylogenetic relationships among shallow-reef and mesophotic octocorals from Eilat, Israel (Red Sea). Tree constructed using PhyML (Guindon and Gascuel 2003) with a GTR+I+G model of evolution applied to concatenated sequence alignment (total length = 1781 bp) of mitochondrial *mutS* (*mtMutS*), cytochrome-oxidase subunit I (COI) plus an intergenic spacer (*igr1*). Species highlighted in red were collected from >30 m depth, all others <30 m. Open circles, species recorded only above 30 m; filled circles, species recorded only below 30 m; shaded circles, species recorded above and below 30 m. The numbers on nodes represent bootstrap values; values >70% are shown for major clades (genera or recognized clades within genera) only

species that are found in shallow waters extend into the upper mesophotic zone, with the same mitochondrial haplotypes.

There are, however, several phylogenetically distinct lineages that so far have only been found in the MCEs. These include the recently described *Sinularia mesophotica*, a species that diverges genetically from all other members of that speciose shallow-water genus (Benayahu et al. 2017a), as well as *Altumia delicata*, a new genus of the subordinal group Stolonifera (Benayahu et al. 2017b). Although the few sea fan genera that occur on the shallow reef at Eilat (*Melithaea*, *Euplexaura*, and *Acanthogorgia*) also extend into MCEs, a number of additional clades of both sea fans and sea whips have to date only been found in the MCEs. These include several genera of Ellisellidae (e.g., *Viminella* and *Verrucella*), Plexauridae (e.g., *Bebryce* and *Discogorgia*), and *Subergorgia*.

Although the lower depth limits of most shallow-reef species at Eilat have been surveyed, the lower limits of those species that have only been found in MCEs remain unknown. Consequently, it remains to be determined whether species that appear to be unique to MCEs are indeed restricted to those communities or whether they are primarily deepwater species whose upper range limits extend into mesophotic depths. Considerably more studies of the lower MCEs and their transition to deepwater communities are needed to answer questions about the evolutionary origins and phylogenetic uniqueness of the mesophotic octocorals. The answers to such questions are important to our understanding of the potential of MCEs to serve as refugia for shallow-water lineages imperiled by climate change.

38.4 Reproduction

For octocorals, sexual reproductive processes are fundamental to maintaining populations and influencing macroevolutionary processes (Kahng et al. 2011). Their sexuality and mode of reproduction have been investigated in numerous species, but to date no study has dealt with a mesophotic species. The question of whether MCE organisms, octocorals included, reproduce despite environmental constraints and can, thus, replenish the larval supply to shallow reefs is of particular interest (e.g., Slattery et al. 2011; Van Oppen et al. 2011; Holstein et al. 2016). Previous studies have demonstrated that in the northern Gulf of Aqaba, some common octocorals reproduce sexually at 27–30 m (*Rhytisma fulvum fulvum*, Benayahu and Loya 1983; *Ovabunda macrospiculata*, Benayahu and Loya 1984a, b; *Sarcophyton glaucum*, Benayahu and Loya 1986). Shoham and Benayahu (2017) noted that 16% of the overall octocoral species occur in both the shallow and upper mesophotic reefs in Eilat. Hence, if their sexual reproduction in

MCEs can be validated, it is conceivable that mesophotic octocorals may also contribute gametes and/or propagules to the shallow reefs.

R. f. fulvum is an encrusting zooxanthellae octocoral found on Eilat's reefs along a wide depth gradient including the upper MCE (Shoham and Benayahu 2017); its deepest distribution is at ~50 m. It is a gonochoric surface brooder, whose fertilization takes place inside the polyp cavity and spawning occurs in the summer months (June to July) corresponding to the lunar phase (Benayahu and Loya 1983). Upon release, embryos remain on the surface of the female colonies entangled in the maternal mucus until the planula development is completed 6 days later.

In Eilat from January 2016 to August 2017, the annual gonadal development (results not shown) and breeding activity of *R. f. fulvum* in shallow (5–10 m) and upper mesophotic (38–45 m) populations were studied.[3] It was found that the shallow colonies (5–10 m) spawned 5 days prior to the July full moon, and colonies with surface-brooded embryos were subsequently observed for 6–7 successive days in ~50% of the colonies (Fig. 38.9), corresponding to their 1:1 sex ratio. No surface brooding occurred in any of the upper MCE colonies until 2 weeks later. On day 4 prior to the new moon, colonies with embryos were observed at 38–45 m. As opposed to the yellow-brown color morphs commonly found on the shallow reef and featuring yellow embryos (Fig. 38.10a), the vast majority of the upper mesophotic depth colonies were the gray-brown morphs with bright, almost white embryos and planulae (Fig. 38.10b). Similarly, the percentage of colonies with surface-brooded embryos corresponded to the male-biased sex ratio at that depth (~2:1). These results demonstrate a distinct temporal reproductive isolation of 2 weeks difference between the shallow and the upper mesophotic *R. f. fulvum* colonies. Although the former colonies breed earlier than the latter, both feature a highly synchronized spawning activity, each during a different moon phase.

If the upper mesophotic *R. f. fulvum* population is indeed to prove to be a viable source of planulae to replenish the shallow reefs, then it must produce a sufficient amount of propagules. Our findings indicate a difference in the sex ratio between the shallow and upper mesophotic populations (see also Benayahu and Loya 1983). However, the mesophotic populations feature a relatively low reproductive potential, which may reduce the chances of a massive propagule transfer to shallow reefs. The planulae of *R. f. fulvum* are benthic,

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[3] During the breeding season, colonies were monitored almost daily underwater in marked 30 × 1 m belt transects in both depth zones. Each day, when encountered, the number of *R. f. fulvum* colonies with surface-brooded embryos or planulae was recorded and their percentage of the total number of colonies was calculated.
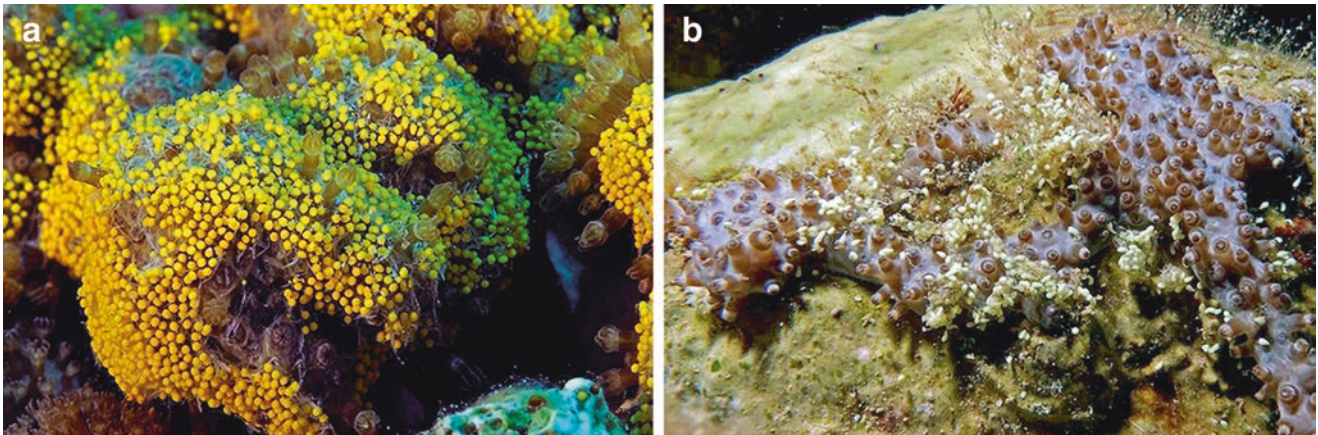
Fig. 38.9 Surface brooding of *Rhytisma fulvum fulvum*: (**a**) shallow yellow color morph and (**b**) mesophotic gray morph. Both feature brooded planula larvae entangled in a thick mucus layer during surface brooding. (Photo credits: Tom Shlesinger)
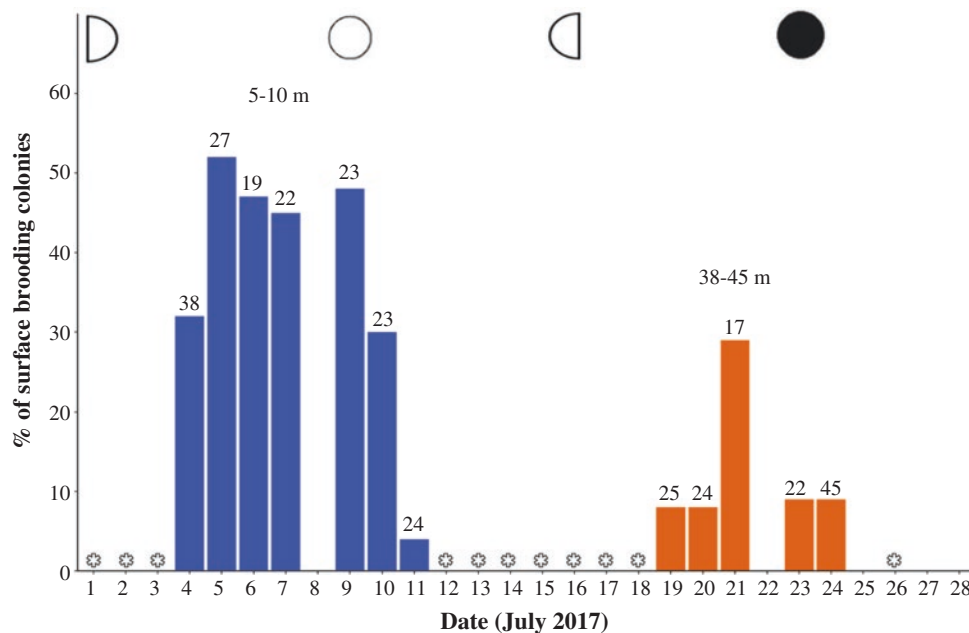

Fig. 38.10 Daily percentage of colonies of *Rhytisma fulvum fulvum* with surface-brooded planula larvae on shallow reef (5–10 m) and in the upper mesophotic reef (38–45 m); the number (appearing above bars) of reproductive colonies is provided relative to moon phase (July 2017). Asterisk indicates dates when no surface-brooded colonies were observed

exhibiting limited drift capabilities or movement but tending rather to settle adjacent to the parent colonies (Benayahu and Loya 1983). This behavioral feature, along with the temporal reproductive isolation that occurs between the two reef zones, would tend to minimize an exchange of genetic material between them and, indeed, enhance their genetic separation. The prevalence of two distinct color morphs (yellow vs. gray) on the shallow reefs and in the upper mesophotic, respectively, also raises doubts concerning connectivity between the two extremes of *R. f. fulvum*'s depth distribution. Thus, the reproductive features of this species greatly reduce the potential of connectivity between the shallow and mesophotic populations, favoring instead spatial separation between the two. Further studies on the reproductive biology of depth-generalist octocorals, including both broadcasters and brooders, are required to determine whether the "deep reef refugia" hypothesis (Bongaerts et al. 2010) holds true for octocorals. Such studies will shed light not only on theoretical aspects regarding the life history of mesophotic octocorals but also on conservation issues related to the members of this group.

38.5 Conclusions

The foundations of our knowledge of mesophotic octocorals were established in the late eighteenth century, with dredging and trawling samples acquired from this depth for taxonomic purposes. During the last decade, MCEs have gained scientific interest, but few studies have been conducted on the octocoral fauna in the Indo-Pacific region. Basic data on species composition of mesophotic octocorals, their depth distribution, population structure, abundance, and habitat preferences are still lacking (see also Loya et al. 2016). The findings presented herein indicate that zooxanthellate octocorals do not occur in the lower mesophotic zone, while azooxanthellate ones feature a wide depth distribution in all reef zones down to the deepest fringes of the lower mesophotic zone. It is still too early to generalize concerning the precise factors governing mesophotic octocoral distribution along a depth gradient.

The scarce data available on mesophotic octocorals, along with recent findings, will hopefully stimulate studies aimed at answering key questions concerning their biological function in MCEs, as well as the factors that determine their spatial occurrence. There are still major gaps in our knowledge of their phylogenetic affinities and degree of similarity to the shallow-water and/or deepwater octocorals. The level of endemism of mesophotic octocorals is still unknown, as is the horizontal and vertical connectivity between their populations in the different mesophotic depth zones. Data on the life history traits and physiology of mesophotic octocorals are needed to elucidate their biological adaptations to the prevailing environmental conditions, especially in view of climate change. Studies on mesophotic octocorals should be based on solid taxonomic and phylogenetic knowledge, thus providing comparative quantitative data at a species-level resolution of communities from shallow reefs to the mesophotic depths. A greater spatiotemporal knowledge of mesophotic octocorals will contribute to their management and conservation throughout the Indo-Pacific region.

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