# Taiwan

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**Abstract**

Taiwan straddles tropical and subtropical latitudes in the North Pacific Ocean. While shallow-water coral reefs in Taiwan have been studied for many years, mesophotic coral ecosystems (MCEs) have recently enjoyed a surge of interest because they are hypothesized to provide a refuge for some reef species in distress. The distribution of MCEs in Taiwan is influenced by numerous biophysical and environmental variables including substrate availability, temperature, light irradiance, and sedimentation. In 1991, an early survey of the diversity of MCEs off Taiwan's southern coast highlighted sedimentation and the lack of suitable substrates as important factors restricting reef communities at depths below 30 m. The steeply sloping east coast of Taiwan supports well-developed and more accessible MCEs and has therefore been the focus of recent research. Preliminary surveys have documented 18 macroalgal, 95 scleractinian, 33 octocoral, 2 antipatharian, 14 sponge, and 76 fish species. With the exception of a few scleractinians recorded for the first time and possibly restricted to mesophotic waters, the majority of species have a wide bathymetric distribution in Taiwan. However, low-light conditions at mesophotic depths in the north restrict the distribution of photosynthetic organisms to shallow waters. Only one zooxanthellate scleractinian species was found at depths below 40 m where benthic communities are dominated by fan- and whip-shaped octocorals. Historically, MCEs have received little research interest in Taiwan, and most current research is focused on descriptive studies. Future research should examine the ecological importance of these habitats and the roles they play in reef survival.

**Keywords**

Mesophotic coral ecosystems · Distribution · Reef diversity · Coral reefs · Marginal reefs

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## 14.1 Introduction

Understanding of coral reefs has been obscured by a bias in research toward shallow coral communities. Consequently, our current knowledge of their ecological dynamics and vulnerability to disturbance is based largely on a limited proportion of the coral reef habitat. Generally, past research has overlooked deeper reefs due to technical limitations; however, the democratization of technical diving and increased accessibility to remotely operated vehicles (ROVs) have progressively facilitated research into these habitats. Recent exploration has shed new light on the diversity of mesophotic coral ecosystems (MCEs, 30–150 m; Hinderstein et al. 2010) and provided insights into the role MCEs play in mitigating the worldwide degradation of coral reefs (Baker et al. 2016). While our knowledge of the biodiversity and ecology of MCEs has been greatly informed through insights derived from a few well-researched regions, cognizing a global perspective of threats on coral reefs requires further research into many other regions of the world that remain understudied (Turner et al. 2017).

Taiwan is a large island, 36,000 km$^2$ in area, situated at the transition between tropical and temperate latitudes in the North Pacific Ocean. It is located on the edge of the East China Sea continental shelf, and its east coast is bordered by steep slopes that reach depths of 1000 m within a few kilometers from shore. Taiwan therefore represents an ideal natural laboratory for testing two key hypotheses regarding the future of coral reefs: poleward migration (Burrows et al. 2011; Yamano et al. 2011) and deep reef refugia (Bongaerts et al. 2010; Bongaerts and Smith 2019). Over the past few decades, coral reef research in Taiwan has focused mainly on describing the diversity and ecology of shallow-water coral reefs (Chen 1999; Dai and Horng 2009; Ribas-Deulofeu et al. 2016). Diversity of reef organisms is high due to Taiwan's location adjacent to the Coral Triangle and in the path of the northward-flowing Kuroshio Current, but it decreases from south to north along environmental gradients (Chen and Shashank 2009; Dai and Horng 2009). At the regional scale, heterogeneity in benthic assemblages suggests that major disturbances could override regional differences (Ribas-Deulofeu et al. 2016).

MCEs in Taiwan have been mostly overlooked, with the exception of an isolated ROV survey in 1991 along the south of the island (Dai et al. 1992) and mesophotic fish surveys in 2004 (Chen 2004) and 2009–2010 (Jan and Chen 2010). Comprehensive research on MCEs began in 2014 with the first long-range scientific surveys on coral diversity below 30 m. Herein, we present a brief history of MCE research in Taiwan, its known mesophotic habitats, and available information on its dominant taxa.

### 14.1.1 Research History

Early coral reef research in Taiwan focused on developing coral species lists, comparing shallow-water diversity among localities (Yabe and Sugiyama 1932, 1941; Yabe et al. 1936; Sugiyama 1937; Kawaguti 1942, 1943, 1953; Eguchi 1968), and analyzing coral growth rates (Ma 1957, 1958, 1959). Underwater studies of coral reef communities, initiated by Jones et al. (1972), introduced SCUBA survey techniques to Taiwan and provided qualitative descriptions of reef environments and biotic communities down to 20 m. Subsequent studies by several authors described the associated reef fauna and their distributions (e.g., Yang 1985; Chen et al. 1988; Dai 1988; Chao and Chang 1989; Chen and Chang 1991), but all were confined to a maximum depth of 30 m. Dai (1988) reported coral communities in southern Taiwan at depths of up to 20–30 m, but hypothesized that corals may exist locally below this range based on observations of the bathymetric distribution of corals in the Ryukyu Islands (Yamazato 1972) and the Red Sea (Fricke and Schuhmacher 1983).

In 1991, a mesophotic survey was conducted in the coastal waters of southern Taiwan (Kenting) using an ROV to describe substrate types and the distribution of macrobenthos between depths of 35 and 120 m (Dai et al. 1992). Hermatypic scleractinian corals and macroalgae were recorded up to 70–80 m in depth. Based on this information, the combined effects of light attenuation, high sedimentation, lack of hard substrate, and water flow were suggested to influence the lower depth limits of these organisms (Dai et al. 1992). Observations of several fish species at ~30 m depth in the same region were reported in 2004 (Chen 2004) and 2009/2010 (Jan and Chen 2010).

Despite these preliminary observations, coral reef research in Taiwan focused primarily on shallow reefs until 2014, when a long-term scientific survey of coral diversity below 30 m was initiated at Ludao (Green Island). The project was motivated by a surge of interest in MCEs around the world and aimed to investigate unexplored MCEs around Taiwan. The discovery of new species records for Taiwan and the expansion of depth ranges (e.g., Denis et al. 2015) encouraged efforts to expand mesophotic research in the region. Today, this research is still in its beginnings, but aims to provide an overview of species and habitat diversity, as well as on the ecological significance of MCEs in Taiwan. In addition to documenting biodiversity, current research is focusing on regional comparisons of the composition and structure of MCE assemblages in relation to environmental factors, connectivity between shallow and mesophotic habitats, physiological responses to low-light environments, and coral reproduction and recruitment in mesophotic habitats (e.g., De Palmas et al. 2018; Soto et al. 2018).

## 14.2 Environmental Setting

Taiwan, a large continental island, is located on the edge of the continental shelf approximately 180 km off the coast of China, across the Taiwan Strait (Fig. 14.1). The main island spans the transition between tropical and temperate latitudes (between 21.90 and 25.30° N), which also constitutes the northern margin of coral reef development. Taiwan's climate is strongly influenced by the monsoon, with northeasterly and southwesterly winds producing a cold, dry season from September to April and a warm, wet season from May to August. Precipitation is particularly important during the warm, wet season when thunderstorms and frequent typhoons affect the island (i.e., 3.4 typhoons per year on average: Central Weather Bureau (2018)).

Sea surface temperature (SST) and photosynthetically active radiation (PAR, 400–700 nm) are among the main environmental parameters controlling the distribution of corals around Taiwan (Fig. 14.2). Warm waters from the Kuroshio Current flow from the southern point of Taiwan along its east coast toward the Ryukyu Archipelago (Fig. 14.2a), expanding the distribution of coral reefs and associated organisms northward into subtropical latitudes. At the western and northern coasts, reef accretion is inhibited by the frequent occurrence of winter SSTs below 18 °C (Kleypas et al. 1999; Dai and Horng 2009; Ribas-Deulofeu et al. 2016), which have occasionally caused mass mortalities of tropical organisms (Hsieh et al. 2008). PAR is highest off the southwest coast of Taiwan (Fig. 14.2b), because this region experiences clearer skies year-round (Syu et al. 2016), and decreases with increasing latitude. The whole island supports four distinct regions of coral reef development (Fig. 14.1a–d). Fringing reefs only occur off the east (Fig. 14.1b) and south (Fig. 14.1c) coasts, which are also the most diversified regions. To the west (Fig. 14.1d) and north (Fig. 14.1a), non-reefal and less-diversified coral communities occur on the basaltic substrate that forms the coastline. Depths are relatively shallow in the west and north, and the shoreline is surrounded by the continental shelf (Fig. 14.1a, d). The east (Fig. 14.1b) and, to a lesser degree, south (Fig. 14.1c) coasts are bordered by steep slopes that reach depths of 1000 m within just a few kilometers from the shore. Other coral regions include the oceanic atolls of Dongsha Atoll (20.70° N, 116.72° E; Dai et al. 1995; Jeng et al. 2008) and Taiping Island (10.38° N, 114.37° E; Dai and Fan 1996) in the South China Sea, the latter constituting the southernmost Taiwanese islet.

## 14.3 Habitat Description

Despite historical ROV surveys in Kenting, the majority of information on mesophotic reef habitats in Taiwan comes from recent surveys at Ludao, with some recent information from Kenting. Vertical profiles of PAR, temperature, and salinity in coastal reef waters were recorded using a Seabird 19 SPlus CTD (Sea-Bird Electronics, USA) mounted with a QSP-200 L PAR sensor (Biospherical Instruments, USA). Profiles were recorded in February 2016 and repeated in March 2017 at Ludao (CTD site: 22.63038° N, 121.46884° E), and in May 2017 at Kenting (CTD site: 21.95906° N, 120.69420° E). These preliminary surveys were not recorded under similar surface environmental conditions, and thus, comparisons need to be made cautiously. However, they provide some insight into the physical environment of mesophotic habitats around Taiwan. Light penetration is a key determinant of the bathymetric range of hermatypic corals (Fricke and Schuhmacher 1983), and the depth at which light is reduced to 1% of PAR often defines the lower limits of hermatypic coral distribution (Fricke and Meischner 1985). This 1% threshold often occurs around 90–100 m depth (Yamazato 1972; Fricke and Schuhmacher 1983). Winter SSTs below 18 °C are usually considered the limit for coral development (Kleypas et al. 1999), and prolonged exposure to <14 °C or low salinity is usually lethal for corals (Veron and Minchin 1992). These environmental parameters in conjunction structure the species composition of mesophotic habitats around Taiwan.

### 14.3.1 Kenting (Southern Taiwan)

Nanwan Bay at Kenting exhibits a gentle slope that gradually reaches 100 m depth within ~5 km from the coast. Topography is steeper to the east and, particularly, to the west of Kenting, where mesophotic depths can be reached within a few hundred meters off the coast. Temperature decreases gradually with depth, but salinity remains relatively constant (Fig. 14.3a, b). Winter temperatures have been estimated to remain above 20 °C at 70 m in depth in Nanwan Bay (Su et al. 1984). Three major rivers located on the west, south, and east coasts of Kenting often result in relatively turbid waters, especially during the rainy season from May to August. This turbidity substantially reduces light intensity, and the 1% PAR threshold is reached at depths <80 m (Fig. 14.3c). High sedimentation rates result in the predominance of sandy substrates below 40 m in southern Taiwan (Dai et al. 1992; Fig. 14.4). In Kenting, coral reefs are very narrow and fore-reef slopes terminate at depths between 20 and 30 m, with no extensive reefs or coral communities found below 40 m (Dai et al. 1992). Blocks and boulders of various sizes were found scattered on sandy bottom from 40 to 100 m in depth, and these occasional hard substrates support relatively rich communities in terms of diversity and biomass (Dai et al. 1992; Fig. 14.5). The 1991 survey of mesophotic habitats in Kenting (Dai et al. 1992) revealed fan- and whip-shaped octocorals, as

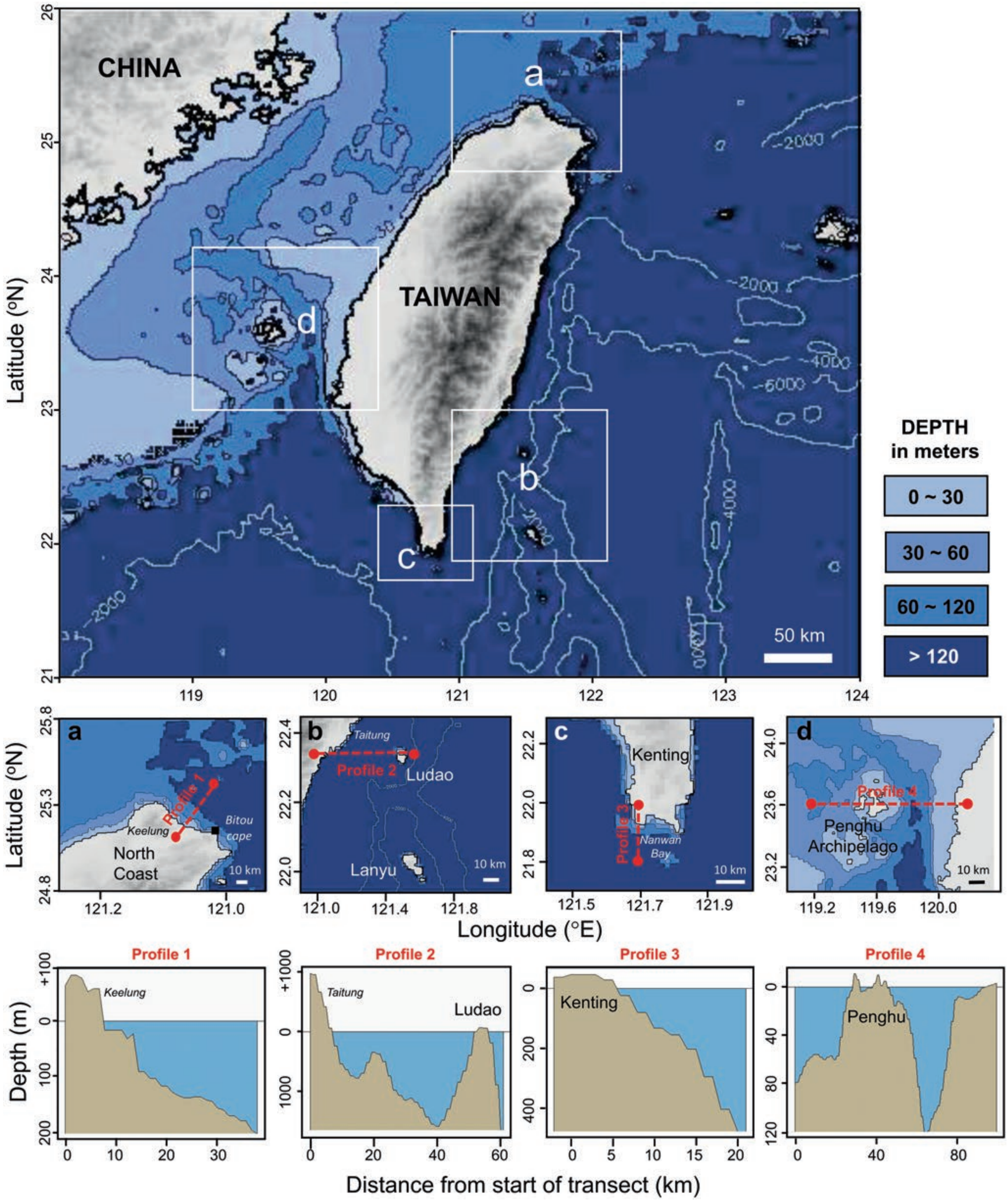


**Fig. 14.1** Locations of the four main regions of coral development around Taiwan (**a**–**d**), with a focus on their respective bathymetry and underwater topography: North (**a**), East (**b**), South (**c**), and West (**d**) Bathymetric data was derived from ETOPO1 databases of the US National Oceanic and Atmospheric Administration and accessed via the marmap R package (Pante and Simon-Bouhet 2013)

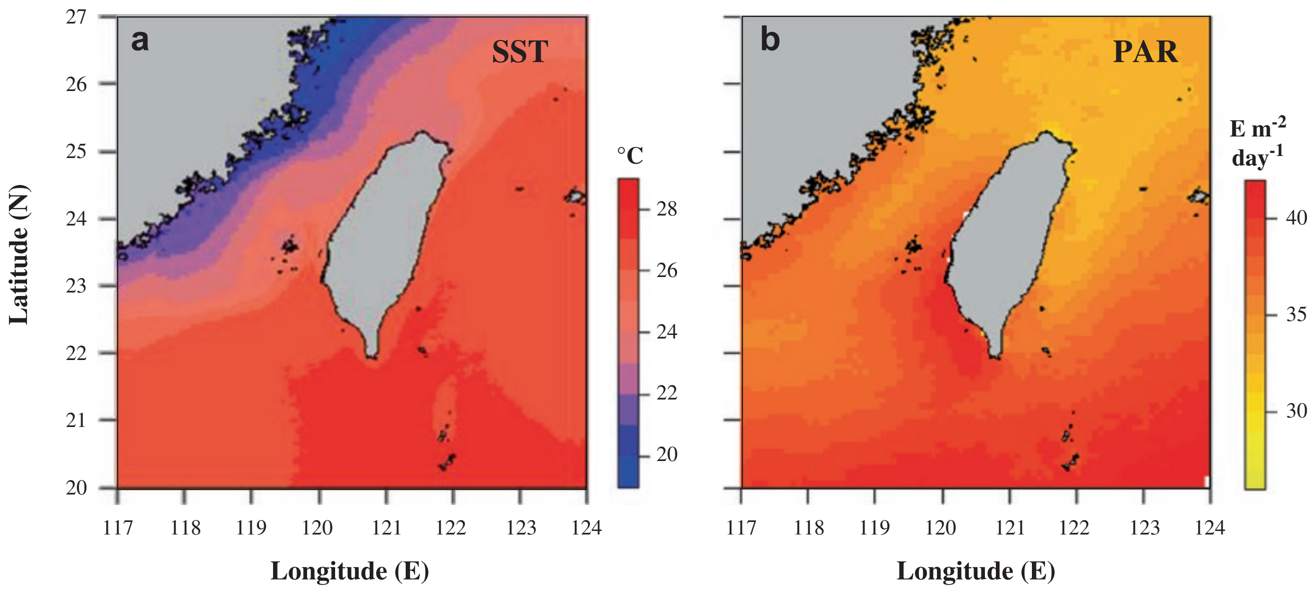


**Fig. 14.2** Daily average SST (**a**) and PAR (**b**) for Taiwan's waters. SST (°C) is based on monthly average MODIS aqua 4 km resolution data (11 µm) at night for the 2003–2016 period. PAR (E $m^{-2}$ $d^{-1}$) is based on monthly average SeaWiFS 9 km resolution data for 1997–2010 period

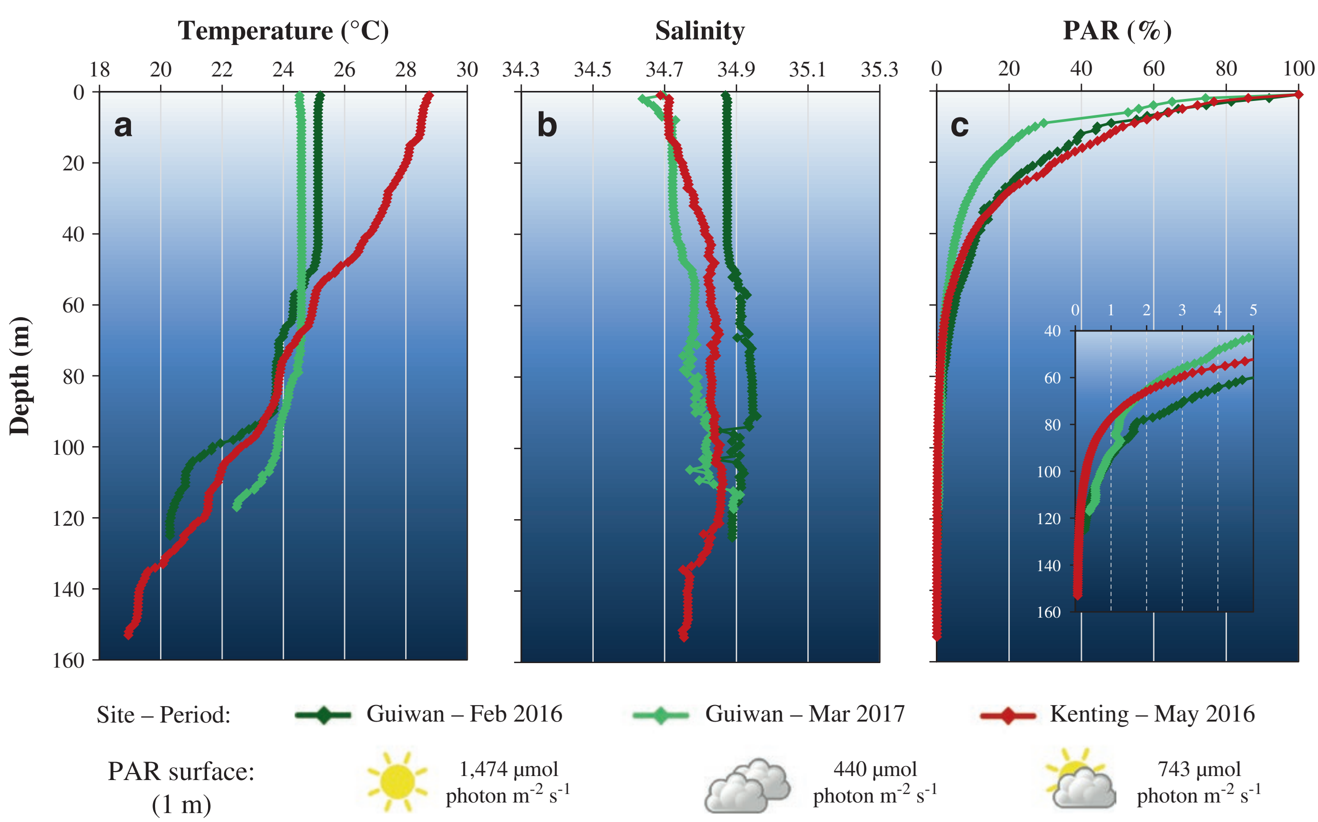


**Fig. 14.3** Depth profiles of (**a**) temperature (°C) (**b**) salinity, and (**c**) PAR (% of surface PAR) at Guiwan (22 February 2016 and 14 March 2017) and Kenting (21 May 2016). PAR surface indicates environmental conditions at the time of records. The inset shows the light attenuation values for mesophotic depths from 40 to 160 m. Data represents a single CTD cast for each date recorded using a Seabird 19 SPlus CTD (Sea-Bird Electronics, USA)

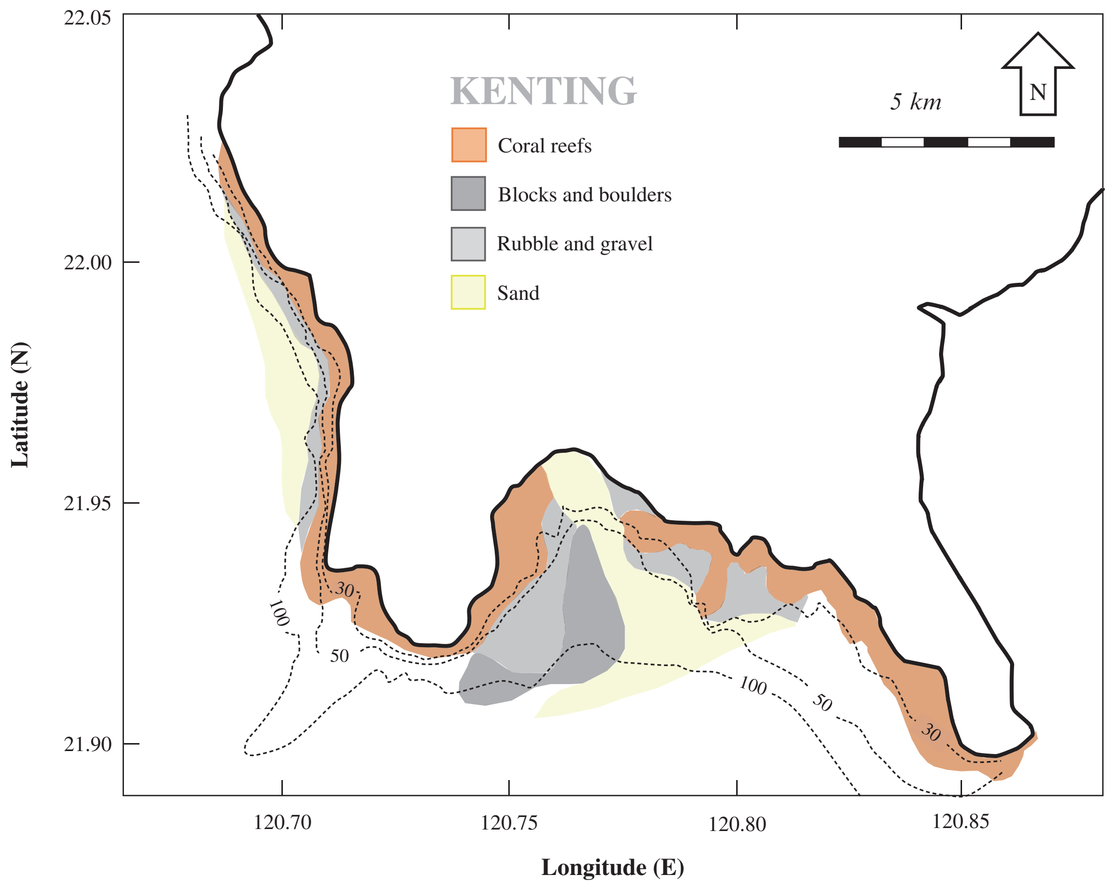


**Fig. 14.4** Distribution of three substrate types and living coral reefs around Kenting. Adapted and modified from Dai et al. (1992). Depth contours adapted from Chen et al. (1974)

well as antipatharians to be the dominant taxa on these substrates. Additionally, sparse representatives of a diverse fauna and flora, including Scleractinia, Porifera, Bryozoa, Ascidians, Crinoids, Ophiuroids, and crustose coralline algae, were also observed. The abundance of suspension feeders in MCE communities in this habitat suggests that deepwater environments in southern Taiwan may be rich in nutrients. In areas less affected by siltation, mesophotic benthic assemblages on hard substrates in southern Taiwan are associated with large patches of encrusting coralline algae, and scleractinians become more abundant.

### 14.3.2 Ludao (Eastern Taiwan)

Ludao (also named Green Island) is a volcanic island with a steep coastline where mesophotic depths are easily accessible from the shore (Fig. 14.1b). Salinity remains relatively stable along the depth gradient (Fig. 14.3b), while water temperatures decline sharply (up to 4 °C) at depths between 90 and 110 m (Fig. 14.3a). PAR declines to <1% of the available surface radiation at ~90 m depth (Fig. 14.3c), suggesting that the clear waters at Ludao contribute to the wide bathymetric distribution of photosynthetic organisms. Southeastern Ludao has been the focus of most mesophotic research. Habitats are clearly differentiated between shallow fringing reef structures down to 30 m, and an extensive zone between 30 and at least 60 m, where hard substrates emerge from large rubble areas and support diverse mesophotic communities. Extreme storm events commonly affect the area, generating reef rubble and sediment in shallow waters that is transported downslope, a phenomenon also observed in Palau (Colin 2016). Patch reefs dominated by turf algae and crustose coralline algae support diverse assemblages of scleractinian corals, sponges, and soft corals (Fig. 14.6). Rubble areas extending between patch reefs are character-

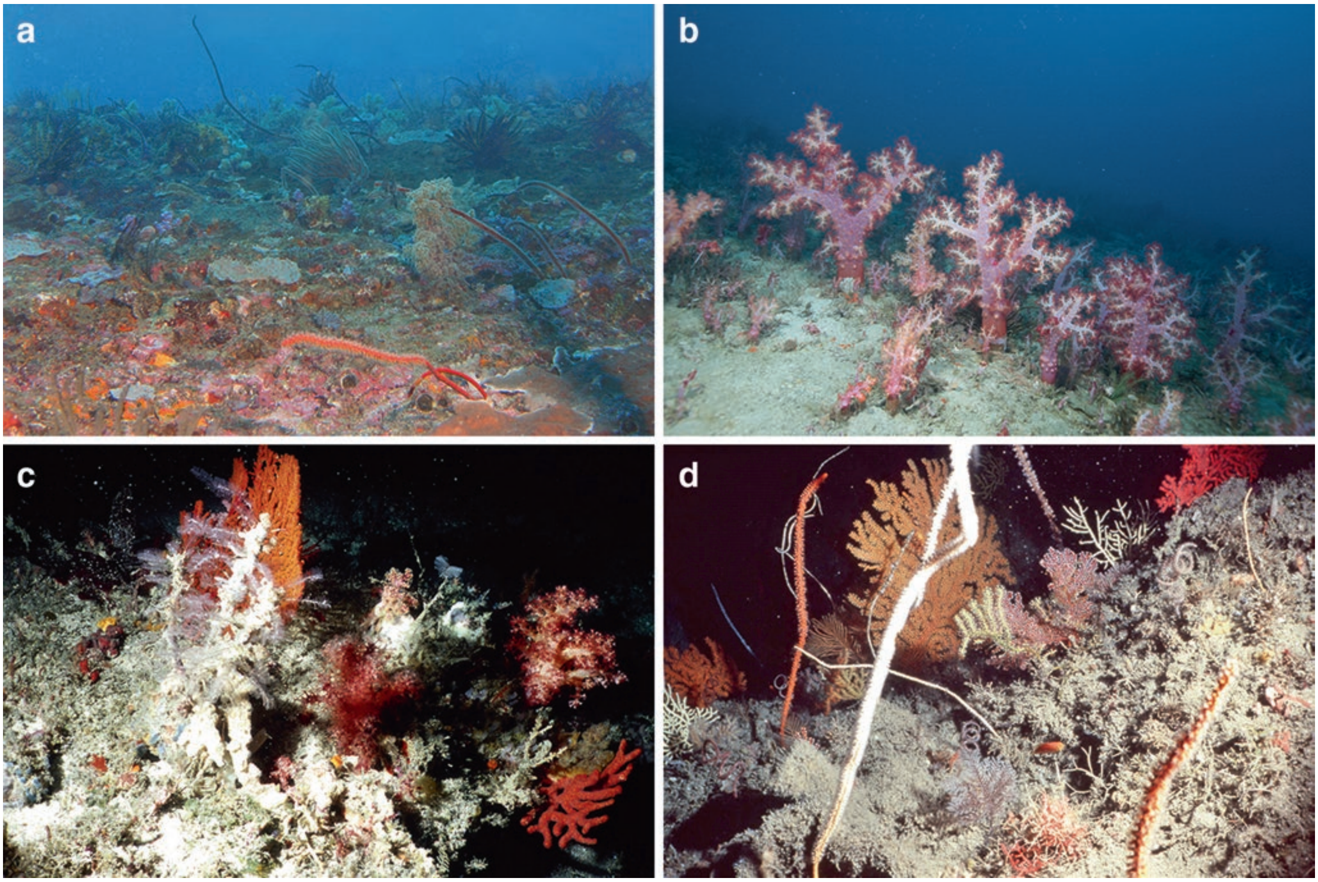


**Fig. 14.5** MCEs around Kenting. (**a**) Nanwan Bay, Maobitou, 40 m depth (Photo credit: Vianney Denis), (**b**) West of Kenting, Hejie, 36 m depth (Photo credit: Chang Feng Dai), and (**c**) and (**d**) Nanwan Bay from the 1991 ROV survey (Dai et al. 1992), 75 m depth (Photo credit: Chang Feng Dai)

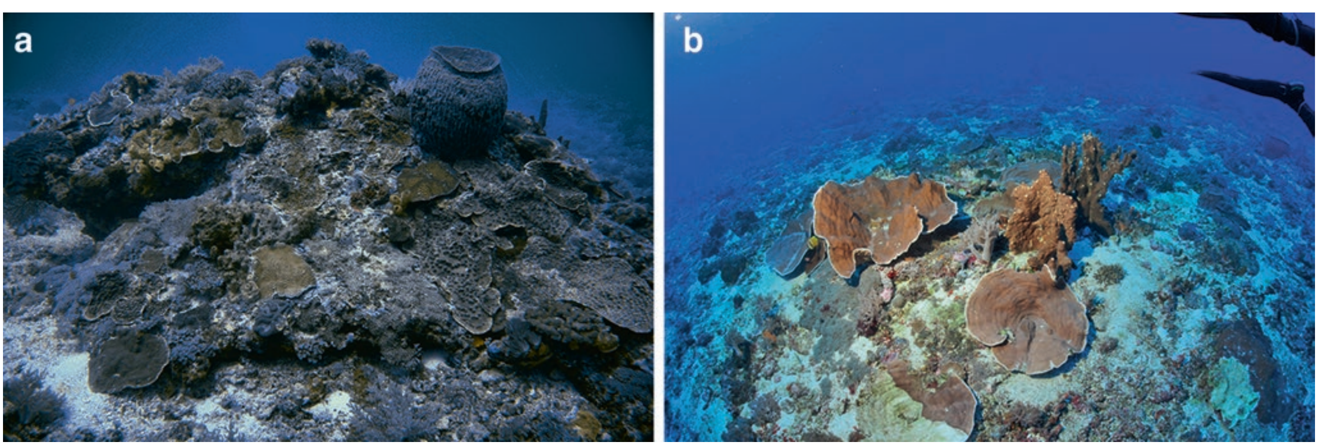


**Fig. 14.6** MCEs at Ludao at 50 m depth. (**a**) Dabaisha (Photo credit: Vianney Denis) and (**b**) Guiwan (Photo credit: Chao-Yang Kuo)

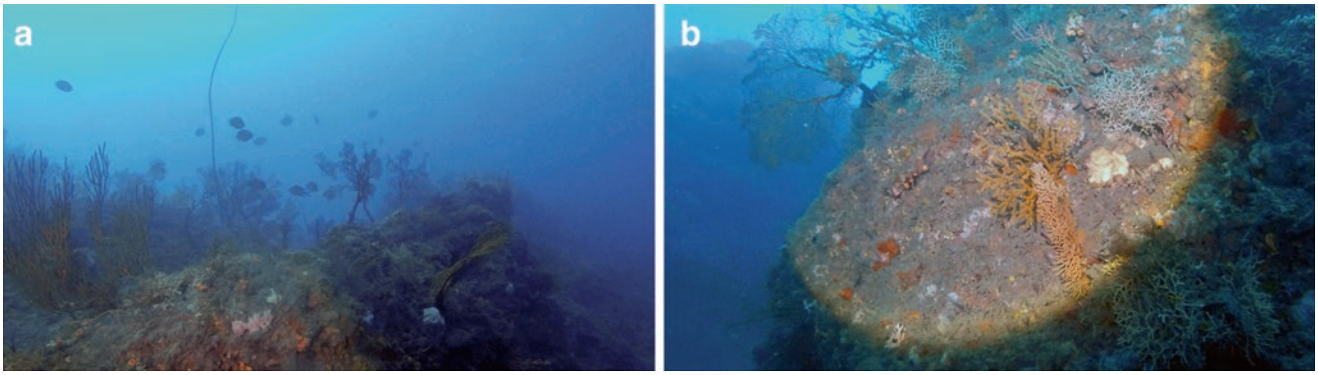


**Fig. 14.7** Mesophotic benthic communities at Bitou Cape, 50 m depth. (**a**) Horizontal platform and (**b**) wall. (Photo credit: Phil Hsieh)

ized by unattached coral colonies associated with unidentified plumose hydroids, encrusting sponges, and turf algae. Generally, environmental conditions in Ludao seem suitable for the occurrence of scleractinian corals and other associated organisms such as algae, octocorals, sponges, and fishes across a wide depth range. However, the availability of hard substrates could represent a limitation for the development of extensive coral assemblages, such as those observed at nearby Okinawa Island (White et al. 2013, 2017; Sinniger et al. 2019). Nevertheless, a relatively tiny proportion of the coastline around Ludao has been surveyed, and additional investigations are needed.

### 14.3.3 Bitou Cape (Northern Taiwan)

The shallow continental shelf along the northern coast of Taiwan makes access to MCEs more difficult, but depths >30 m can be reached around islets or where the shore projects into the sea (e.g., Bitou Cape: 25.12894° N, 121.92473° E). Light irradiance generally attenuates sharply in the first few meters due to high turbidity. While no vertical profiles of PAR or temperature are currently available for this area, our preliminary investigation indicates a low-light environment with frequent surges of cold water in winter (<18 °C). Octocorals dominate benthic assemblages, with diverse, but unidentified fan- and whip-shaped octocoral species as the most abundant faunal group (Fig. 14.7). They are accompanied by antipatharians, bryozoans, and sponges, which become more abundant in steeper and less silted areas. The contribution of scleractinian corals to local benthic communities is unknown. Overall, deep habitats in northern Taiwan appear unsuitable for most shallow-water coral species and for most light-dependent organisms. The region may represent an interesting location for investigating environmental factors controlling reef distribution but may actually be better characterized as a temperate mesophotic ecosystem (e.g., Bo et al. 2011; Gori et al. 2011; Richmond and Stevens 2014).

## 14.4 Biodiversity

Information on mesophotic biodiversity is compiled from Dai et al. (1992) and other recent mesophotic surveys around Taiwan. All surveys used enriched-air or mixed-gas technical diving. Since 2014, eight surveys have examined the diversity of scleractinian corals at three upper mesophotic sites (40–60 m) at Ludao: Gongguan (22.67750° N, 121.49415° E), Guiwan (121.48113° N, 22.64022° E), and to a lesser extent Dabaisha (121.49026° N, 22.63678° E). Site selection was strongly influenced by safety considerations, since the currents around Ludao can be particularly strong and unpredictable. Each specimen was photographed in situ and collected for further skeletal identification. Mesophotic investigations initially attempted to maximize the number of specimens collected, but later surveys were taxa-specific and prioritized problematic groups. In 2016, preliminary surveys at 40 m in Kenting (Longkeng, 120.86932° N, 21.93487° E; Hongchaikeng, 120.70994° N, 21.96487° E; Xiaowan, 120.79052° N, 21.92707° E; and Maobitou, 120.73765° N, 21.91722° E) and Bitou Cape provided additional information on scleractinian diversity. Other taxonomic groups, such as macroalgae, soft corals, and sponges, have only been examined in detail at Guiwan, Ludao (40 m depth) in February 2017. Common species were photographed in situ and sampled. In the laboratory, specimens were photographed and subsampled for museum records. Identification based on morphology was

**Table 14.1** Mesophotic algae of Taiwan

| Phylum | Family | Species |
|---|---|---|
| Rhodophyta | Corallinaceae | *Amphiroa* sp. (L) |
| | | *Jania* sp. (L) |
| | Cystocloniaceae | *Hypnea caespitosa** (L) |
| | Galaxauraceae | *Dichotomaria obtusata* (L) |
| | | *Galaxaura* sp. (K) |
| | | *Tricleocarpa fragilis* (L) |
| | Nemastomataceae | *Predaea* sp. (L) |
| | Peyssonneliaceae | *Peyssonnelia* sp.* (L) |
| | Pterocladiaceae | *Pterocladiella* sp.* (L) |
| | Rhodomelaceae | *Neurymenia fraxinifolia* (K) |
| Chlorophyta | Dichotomosiphonaceae | *Avrainvillea* sp. (K) |
| | Udoteaceae | *Udotea* sp.* (L) |
| | Valoniaceae | *Valonia aegagropila* (L) |
| | | *Valonia ventricosa* (L) |
| Ochrophyta | Dictyotaceae | *Dictyota* sp. |
| | | *Lobophora* sp. (L) |
| | | *Spatoglossum stipitatum* (L) |
| | Sargassaceae | *Sargassum* sp. (K) |

*L* Ludao, species having DNA barcode confirmation are labeled with an asterisk (*); *K* Kenting, data from Dai et al. (1992) with the exception of *Neurymenia fraxinifolia* recorded in April 2016

supported by DNA barcoding for some taxa, such as macroalgae. Information on benthic diversity recorded in Taiwan MCEs is accessible at www.dipintothereef.com/diversity.html.

Information on fish diversity was obtained from high-definition video transects recorded at 40 m at four sites near Kenting (Hongchaikeng, Longkeng, Maobitou, and Xioawan), three sites at Ludao (Dabaisha, Guiwan, and Shihlang: 121.47098° N, 22.64776° E), and Keelung Island in northern Taiwan (121.781996° N, 25.188805° E). At each site, 5 × 20 m belt transects (~5 m wide) were used to identify dominant species. The diets of each fish species identified were extracted from FishBase (Froese and Pauly 2017), and trophic structures (composition in feeding guilds) were compared to shallow-water surveys using similar methods where data was available.

### 14.4.1 Macroalgae

In total, 18 macroalgal species have been identified to date from MCEs in Taiwan (Table 14.1). The diversity of key groups, such as crustose coralline algae (CCA), remain unknown due to the challenge of morphological identification and the lack of DNA-assisted identification at the species level. CCA, together with other forms of crustose algae (e.g., *Peyssonnelia* spp. and *Lobophora* spp.), are often the dominant component of benthic communities in mesophotic habitats because of their ability to tolerate or adapt to low light, high water motion, and high sedimentation conditions (reviewed in Ballesteros 2006; Sinniger et al. 2016). The clear waters at Ludao allow macroalgae to occur over a broad depth range, and diverse algal assemblages including representatives of Chlorophyta (e.g., *Valonia*) were common at 40 m depth. At Kenting, the lower depth limit for turf algae, green filamentous algae, brown algae, and articulated calcareous algae occurred at 35–45 m. *Neurymenia fraxinifolia* was the dominant alga at some sites at 40 m. This alga tolerates high sedimentation and was found living beneath a layer of sediment. In northern Taiwan, mesophotic depths were devoid of macroalgae. Light penetration into mesophotic depths is probably the major factor limiting the depth range of algae in this region.

### 14.4.2 Anthozoans

#### 14.4.2.1 Scleractinia

At least 96 scleractinian coral species have been recorded at mesophotic depths. This number is likely an underestimate because diverse genera such as *Fungia* or *Acropora* have yet to be identified to species level. However, there are important regional differences in coral community composition related to contrasting environmental conditions among regions. The diversity of scleractinian corals from Taiwanese MCEs and their depth ranges are given in Table 14.2 for complex corals (42 species) and robust corals (54 species).

At Ludao, more than one-third of the 250 known shallow-water scleractinian corals (Dai 2006) have been documented at 40–60 m depth. Encrusting and foliose corals such as *Mycedium elephantotus*, *Pavona varians*, and *Pachyseris speciosa*, together with bushy colonies of *Pocillopora verrucosa*, *Seriatopora* cf. *caliendrum*, and *S.* cf. *hystrix*, constitute the dominant scleractinian species and structure the mesophotic coral assemblage where hard substrates are available. Unattached colonies of *Acropora tenella*, *Anacropora pillai*, *Anacropora matthai*, and *Psammocora stellata* prevail in rubble areas extending between patch reefs. Since 2014, investigations of the mesophotic zone have expanded the list of scleractinian corals recorded from Taiwan by at least 12 (possible or confirmed) species. The discovery of species such as *A. tenella*, *Trachyphyllia geoffroyi*, and *Catalaphyllia jardinei* in Taiwan's MCEs is not surprising because they are known to occur in the Philippines and Japan (Nishihira and Veron 1995; Veron 2000). The record of *P. stellata* in Taiwan was unexpected and considerably extended the known distribution and depth range of this species (Denis et al. 2015). As observed for macroalgae, mesophotic depths at Ludao appear suitable for many depth-generalist species that also occur in shallow waters. Nonetheless, the relatively small number of mesophotic sites examined suggests that total diversity and maximum depth limits of coral species will increase as more areas are studied.

At Kenting, less than 30 of the 280 scleractinian corals documented in shallow waters in southern Taiwan (Dai 2007) were found during surveys at 40 m depth. Among them, four encrusting scleractinians (*Merulina ampliata*, *Echinophyllia aspera*, *Montipora foveolata*, and *Porites* spp.) were recorded on the upper surfaces of rocks down to 76 m, constituting the deepest recorded scleractinian corals in Taiwan (Dai et al. 1992). Sedimentation in Kenting strongly reduces light penetration and limits the vertical distribution of most scleractinian corals to the

**Table 14.2** Mesophotic scleractinian corals. Diversity and known depth ranges in northern (blue), eastern (green), and southern (red) Taiwan

| Family | Species | | Depth (m) 0-5 | 5-15 | 15-30 | 30-60 | >60 |
|---|---|---|---|---|---|---|---|
| **Acroporidae** | *Acropora* | cf. *clathrata* | | | | | |
| | | cf. *cytherea* | | | | | |
| | | cf. *granulosa* | | | | | |
| | | *solitaryensis* | | | | | |
| | | cf. *tenella* * | | | | | |
| | | cf. *valida* | | | | | |
| | *Anacropora* | cf. *matthai* | | | | | |
| | | cf. *pillai** | | | | | |
| | *Astreopora* | cf. *myriophthalma* | | | | | |
| | | cf. *randalli* | | | | | |
| | *Isopora* | *palifera* | | | | | |
| | *Montipora* | cf. *aequituberculata* | | | | | |
| | | cf. *danae* | | | | | |
| | | cf. *exesa** | | | | | |
| | | *foveolata* 76 | | | | | |
| | | cf. *grisea* | | | | | |
| | | cf. *millepora* | | | | | |
| **Agariciidae** | *Gardineroseris* | *planulata* | | | | | |
| | *Leptoseris* | cf. *amitoriensis** | | | | | |
| | | cf. *explanata* | | | | | |
| | | cf. *hawaiinensis* | | | | | |
| | | cf. *mycetoseroides* | | | | | |
| | | *papyracea** | | | | | |
| | | cf. *scabra* | | | | | |
| | *Pachyseris* | *rugosa* | | | | | |
| | | *speciosa* | | | | | |
| | *Pavona* | *duerdeni* | | | | | |
| | | *varians* | | | | | |
| **Coscinaraeidae** | *Coscinarea* | cf. *crassa* | | | | | |
| **Dendrophyllidae** | *Tubastraea* | *aurea / coccinea* 52 | | | | | |
| | | *faulkneri* | | | | | |
| | | *micrantha* | | | | | |
| | *Turbinaria* | *reniformis* | | | | | |
| **Euphylliidae** | *Catalaphyllia* | *jardinei** | | | | | |
| | *Euphyllia* | *ancora* | | | | | |
| | | *glabrescens* | | | | | |
| | *Galaxea* | *fascicularis* | | | | | |
| **Fungiidae** | *Fungia* | undetermined spp | | | | | |
| | *Leptastrea* | cf. *purpurea* | | | | | |
| | *Polyphylia* | *talpina* | | | | | |
| | *Psammocora* | *profundacella* | | | | | |
| | | *stellata** | | | | | |
| | *Sandalolitha* | *robusta* | | | | | |
| | *Zoopilus* | *echinatus** | | | | | |
| **Lobophylliidae** | *Cynarina* | *lacrymalis* | | | | | |
| | *Echinophyllia* | cf. *aspera* 76 | | | | | |
| | | cf. *echinata* | | | | | |
| | *Lobophyllia* | cf. *corymbosa* | | | | | |
| | | cf. *hataii* | | | | | |
| | | cf. *hemprichii* | | | | | |
| | | cf. *valenciennesii* | | | | | |
| | *Oxypora* | cf. *lacera* | | | | | |
| | *Symphyllia* | cf. *agaricia* | | | | | |
| **Merulinidae** | *Cyphastrea* | *chalcidicum* | | | | | |
| | | *microphthalma* | | | | | |
| | | *serailia* | | | | | |

(continued)

**Table 14.2** (continued)

| Family | Species | | Depth (m) 0-5 | 5-15 | 15-30 | 30-60 | >60 |
|---|---|---|---|---|---|---|---|
| **Merulinidae** | *Dipsastraea* | cf. *favus* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *lizardensis* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *matthai* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *maxima* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *pallida* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *rotumana* | B/G/R | B/G/R | B/G/R | G | |
| | *Echinopora* | cf. *lamellosa* | | B/G/R | B/G/R | G/R | |
| | *Favites* | cf. *flexuosa* | | B/G/R | G/R | G | |
| | | cf. *halicora* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *pentagona* | B/G/R | B/G/R | B/G/R | G/R | |
| | | cf. *rotundata* | B/G/R | B/G/R | B/G/R | G | |
| | | cf. *russelli* | B/G/R | B/G/R | B/G/R | G | |
| | | *valenciennesi* | B/G/R | B/G/R | B/G/R | G | |
| | *Goniastrea* | cf. *favulus* | B/G/R | B/G/R | B/G/R | G | |
| | *Hydnophora* | *microconos* | | B/G/R | B/G/R | G | |
| | *Leptoria* | cf. *irregularis* * | | | | G | |
| | *Merulina* | cf. *ampliata* **76** | | B/G/R | G/R | G/R | R |
| | *Mycedium* | *elephantotus* | B/G/R | B/G/R | G/R | G/R | |
| | | *robokaki* | | G/R | G/R | G | |
| | *Oulophyllia* | *crispa* | | B/G/R | B/G/R | G | |
| | *Paragoniastrea* | cf. *australensis* | B/G/R | B/G/R | B/G/R | G | |
| | *Pectinia* | *lactuca* | B/G/R | B/G/R | B/G/R | G | |
| | | *paeonia* | B/G/R | B/G/R | B/G/R | G | |
| | *Platygyra* | cf. *ryukyuensis* | B/G/R | B/G/R | B/G/R | G | |
| | *Trachyphyllia* | *geoffroyi** | | | | G | |
| **Plesiastreidae** | *Cyathelia* | *axillaris** | | | B | B | |
| | *Blastomussa* | *wellsi* | | B | B/G/R | G | |
| | *Physogyra* | *lichtensteini* | | R | R | G | |
| **Pocilloporidae** | *Pocillopora* | *damicornis* complex | B/G/R | B/G/R | G | G | |
| | | *eydouxi* | | G/R | G/R | G | |
| | | *verrucosa* | B/G/R | B/G/R | G/R | G | |
| | *Seriatopora* | cf. *hystrix* | G/R | G/R | G | G | |
| | | cf. *caliendrum* | G/R | G/R | G/R | G | |
| | *Stylocoeniella* | *guentheri* | B | B/G/R | G/R | G/R | |
| **Poritidae** | *Alveopora* | cf. *excelsa** | | | | G | |
| | | cf. *spongiosa* | | G/R | G/R | G | |
| | *Goniopora* | *lobata* | | B/G/R | G | G | |
| | *Porites* | *lichen* | B/G/R | B/G/R | G/R | G | |
| | | *lobata* | B/G/R | B/G/R | B/G/R | G | |
| | | *lutea* | B/G/R | B/G/R | B/G/R | G | |

* *Potential new record in Taiwan*

Maximum depths are given next to species names if previously identified (Dai et al. 1992)

shallowest part of the reef. Recent and past surveys both suggest that actual reefs at Kenting do not extend below 40 m.

Our surveys at the northern coast of Taiwan show that diversity in scleractinian corals at 40 m is low compared to both shallow waters (134 species; Dai et al. 2004) and mesophotic sites further south. Only four species have been recorded: an uncommon *Leptoseris* sp. (the only zooxanthellate species) and the azooxanthellate corals *Tubastrea aurea/coccinea*, *T. faulkneri*, and *Cyathelia axillaris* (a new record for Taiwan). Further research should be conducted in this region, where basic information, such as the location of potential mesophotic habitats, is lacking.

#### 14.4.2.2 Octocorallia and Antipatharia

In Taiwan's MCEs, 33 octocoral and two antipatharian (black coral) species have been recorded (Table 14.3). All species have been previously reported in shallow waters, indicating a wide bathymetric distribution for members of these groups. In terms of abundance, Nephtheidae represents the dominant soft coral taxon at Ludao (40 m in depth), with numerous small colonies of *Clavularia inflata*, *Anthelia* sp., *Stereonephthya* sp., *Xenia* sp., and *Conglomeratusclera coerulea*. Fan- and whip-shaped octocorals including *Astrogorgia* sp., *Ellisella* sp., *Melithaea* sp., and *Juncella* sp. are conspicuous and grow up to 1 m in height.

At Kenting, Nephtheidae and fan- or whip-shaped octocorals are commonly found at 40 m along with occasional alcyoniid colonies. In rubble and gravel areas that often border the lower edges of living coral reefs between 35 and 45 m in depth, alcyonacean corals and *Dendronephthya* spp. occur frequently on the surfaces of scattered rocks and boulders (Dai et al. 1992). Fan-shaped octocorals such as *Annella* spp. (previously *Subergorgia* spp.) and *Melithaea* spp. prevail at depths between 50 and 70 m, while whip-shaped octocorals and antipatharians such as *Juncella fragilis*, *J. juncea*, *Ellisella maculata*, *E. robusta*, and *Cirrhipathes* spp. are more common below 80 m (Dai et al. 1992).

To the north of Taiwan, a range of unidentified fan- and whip-shaped octocorals dominate benthic assemblages (Fig. 14.7). Octocorals (e.g., *Dendronephthya* spp.) and antipatharians are interspersed, with the latter becoming locally dominant in some locations and colonies reaching more than 1 m in diameter. Interestingly, these benthic

**Table 14.3** Mesophotic octocorals and antipatharians of Taiwan

| Order | Family | Species |
|---|---|---|
| Alcyonacea | Acanthogorgiidae | *Acanthogorgia vegae*[a] (L) |
| | Alcyoniidae | *Lobophytum hsiehi* (L) |
| | | *Protodendron repens* (L) |
| | | *Rhytisma* sp.[a] (L) |
| | | *Sarcophyton* sp. (L) |
| | | *Sinularia mollis* (L) |
| | | *Sinularia slieringsi* (L) |
| | | *Sinularia* sp. (L) |
| | Briareidae | *Briareum violaceum* (L) |
| | Clavularidae | *Clavularia inflata* (L) |
| | | *Clavularia viridis*[a] (L) |
| | Ellisellidae | *Ellisella maculata* (K) |
| | | *Ellisella robusta*[a] (L, K) |
| | | *Ellisella* sp. (L) |
| | | *Junceella fragilis* (L, K) |
| | | *Junceella juncea*[a] (L, K) |
| | | *Junceella* sp. (L) |
| | Helioporidae | *Heliopora coerulea* (L) |
| | Melithaeidae | *Melithaea* sp. (L, K) |
| | Nidaliidae | *Siphonogorgia* sp. (K) |
| | Nephtheidae | *Capnella* sp.[a] (L) |
| | | *Dendronephthya* sp. (L, K) |
| | | *Lemalia* sp. (L) |
| | | *Nephthea* sp.[a] (L) |
| | | *Stereonephthya* sp. (L) |
| | Plexauridae | *Astrogorgia* sp. (L) |
| | Subergorgiidae | *Subergorgia* sp. (K) |
| | Tubiporidae | *Tubipora musica*[a] (L) |
| | Xeniidae | *Anthelia glauca*[a] (L) |
| | | *Anthelia* sp. (L) |
| | | *Conglomeratusclera coerulea* (L) |
| | | *Heteroxenia* sp.[a] (L) |
| | | *Xenia* sp. (L) |
| Antipatharia | Antipathidae | Anthipathidae sp. (L) |
| | | *Cirrhipathes* sp. (L, K) |

Data from Dai et al. (1992) at Kenting
*L* Ludao, *K* Kenting
[a]Unconfirmed species

assemblages exhibit similar characteristics to temperate mesophotic assemblages (e.g., Bo et al. 2011; Gori et al. 2011) but differ from the few existing descriptions of subtropical mesophotic assemblages (e.g., Richmond and Stevens 2014).

### 14.4.3 Sponges

Sponges are common in mesophotic habitats where they can be abundant and sometimes form large, erect structures. In the north, encrusting and branching sponges intersperse with octocorals and represent a dominant component of the benthic assemblage. Together with large sclerosponges, they are especially common on the surfaces of rocks scattered between 40 and 70 m in depth at Kenting (Dai et al. 1992), but less frequent at greater depths (Dai et al. 1992). Detailed information on the diversity of mesophotic sponges is only available from Ludao, where 14 species of demosponges have been recorded (Table 14.4). The large barrel sponge *Xestospongia testudinaria* is characteristic of deeper habitats, where it can reach heights greater than 1 m. Together with massive sponges such as *X.* cf. *vansoesti* and one unknown species of Thorectidae, they intersperse with corals and can form remarkable formations.

### 14.4.4 Fishes

Seventy-six reef fish species have been recorded during our surveys of mesophotic depths (40 m deep). Table 14.5 lists fish diversity recorded during our survey of northern, eastern, and southern Taiwan. All species also inhabit shallow-water reefs around Taiwan. Diversity at mesophotic depths is generally lower when compared to shallow waters, especially in Kenting where trophic structure reveals the absence of herbivorous fish at 40 m in depth (Fig. 14.8).

### 14.4.5 Other Biotic Components

Diversity surveys have focused on taxa contributing significantly to the benthic assemblage. Diverse and numerous minor taxa remain overlooked but warrant further study. Dai et al. (1992) reported the occurrence of the feather-like hydroids *Macrorhynchia* (previously *Lytocarpus*) and *Aglaophenia* (Aglaopheniidae) at 60 m at Kenting. An unidentified *Leptothecata* hydroid was also dominant in rubble areas associated with unattached coral colonies at depths of 40–60 m at Ludao. The encrusting hydrozoan *Millepora exaesa* was also observed associated with mesophotic coral assemblages at Ludao.

To the north, unidentified large foliose and branching bryozoan colonies become an important component of the benthic assemblage, where they share available hard substrates with fan- and whip-shaped octocorals and sponges. Locally, they represent the dominant taxa. Past (Dai et al. 1992) and recent surveys (V. Denis, unpubl. data) also show that crinoids and the holothurian *Colochirus robustus* are commonly found in MCEs at Kenting. Several nudibranch species were observed during our surveys at Kenting and at Ludao. Furthermore, a new association between goblet worms (phylum Entoprocta) and xeniid corals has recently been reported in mesophotic reefs at Ludao (Denis et al. 2019) and represents the first known occurrence of this phylum in Taiwan.

**Table 14.4** Mesophotic sponges of Ludao

| Order | Family | Species |
|---|---|---|
| Agelasida | Agelasidae | *Agelas nemoechinata* |
| | | *Agelas cavernosa* |
| Bubarida | Dictyonellidae | *Acanthella cavernosa* |
| Dictyoceratida | Spongiidae | *Hippospongia* sp. |
| | | *Coscinoderma* sp.[a] |
| | Thorectidae | One unknown species |
| Haplosclerida | Callyspongiidae | *Callyspongia confoederata* |
| | Niphatidae | *Dasychalina fragilis* |
| | Petrosiidae | *Petrosia* sp. |
| | | *Xestospongia testudinaria* |
| | | *Xestospongia* aff. *vansoesti*[a] |
| Scopalinida | Scopalinidae | *Stylissa carteri* |
| Suberitida | Suberitidae | *Aaptos suberitoides* |
| Verongiida | Aplysinellidae | *Suberea* sp. |

[a]Unconfirmed species

**Table 14.5** Mesophotic reef fishes of Taiwan

| Order | Family | Species |
|---|---|---|
| Beryciformes | Holocentridae | *Myripristis botche* (L) |
| Perciformes | Acanthuridae | *Acanthurus mata* (L) |
| | | *Acanthurus nubilus* (L) |
| | | *Acanthurus olivaceus* (L) |
| | | *Ctenochaetus binotatus* (L) |
| | | *Zebrasoma flavescens* (L) |
| | Caesionidae | *Caesio lunaris* (L) |
| | | *Pterocaesio digramma* (K) |
| | Chaetodontidae | *Coradion altivelis* (N) |
| | | *Chaetodon argentatus* (K, L) |
| | | *Chaetodon auriga* (L) |
| | | *Chaetodon auripes* (L) |
| | | *Chaetodon kleinii* (K, L) |
| | | *Chaetodon lunulatus* (L) |
| | | *Chaetodon unimaculatus* (L) |
| | | *Chaetodon vagabundus* (K) |
| | Cirrhitidae | *Cirrhitichthys falco* (L) |
| | | *Cyprinocirrhites polyactis* (K, L) |
| | Labridae | *Anampses melanurus* (L) |
| | | *Bodianus bilunulatus* (L) |
| | | *Bodianus bimaculatus* (L) |
| | | *Bodianus perditio* (K) |
| | | *Choerodon jordani* (L) |
| | | *Cirrhilabrus rubrimarginatus* (L) |
| | | *Coris dorsomacula* (K) |
| | | *Cymolutes torquatus* (L) |
| | | *Halichoeres chrysus* (K, L) |
| | | *Labroides dimidiatus* (K, L) |
| | | *Labropsis manabei* (L) |
| | | *Macropharyngodon negrosensis* (K, L) |
| | | *Oxycheilinus bimaculatus* (K) |
| | | *Oxycheilinus digramma* (L) |
| | | *Oxycheilinus unifasciatus* (L) |
| | | *Stethojulis bandanensis* (L) |
| | Malacanthidae | *Malacanthus latovittatus* (L) |
| | Microdesmidae | *Nemateleotris magnifica* (K,L) |
| | | *Ptereleotris evides* (K) |
| | Mullidae | *Parupeneus indicus* (K) |
| | | *Parupeneus multifasciatus* (K, L) |
| | Nemipteridae | *Scolopsis bilineata* (K) |
| | | *Scolopsis xenochroa* (L) |
| | Pinguipedidae | *Parapercis clathrata* (K, L) |
| | | *Parapercis millepunctata* (K) |
| | | *Parapercis pulchella* (K) |
| | | *Parapercis schauinslandii* (L) |
| | | *Parapercis tetracantha* (K) |
| | Pomacanthidae | *Apolemichthys trimaculatus* (L) |
| | | *Centropyge bicolor* (L) |
| | | *Centropyge heraldi* (L) |
| | | *Genicanthus semifasciatus* (L) |
| | | *Pomacanthus imperator* (K) |
| | | *Pygoplites diacanthus* (L) |
| | Pomacentridae | *Amblyglyphidodon aureus* (K) |
| | | *Chromis albomaculata* (L) |
| | | *Chromis alleni* (L) |
| | | *Chromis analis* (N) |
| | | *Chromis fumea* (N) |
| | | *Chromis margaritifer* (K, L) |
| | | *Chromis ovatiformes* (L) |
| | | *Chrysiptera starcki* (K, L) |
| | | *Dascyllus trimaculatus* (K, L) |
| | | *Pomacentrus amboinensis* (L) |
| | Scaridae | *Scarus forsteni* (L) |
| | Serranidae | *Diploprion bifasciatum* (N) |
| | | *Pseudanthias hypselosoma* (K) |
| | | *Pseudanthias luzonensis* (N) |
| | | *Pseudanthias squamipinnis* (K, L, N) |
| | Zanclidae | *Zanclus cornutus* (L) |
| Tetraodontiformes | Balistidae | *Balistoides conspicillum* (L) |
| | Tetraodontidae | *Canthigaster valentini* (K) |

*K* Kenting, *L* Ludao, *N* North

## 14.5 Ecology

MCE research in Taiwan provides an overview of environmental conditions in these habitats and their associated diversity. To date, mesophotic research has been largely descriptive – an essential and important first step toward obtaining a better understanding of changes in ecological communities and processes with depth. Nonetheless, the observed patterns provide interesting

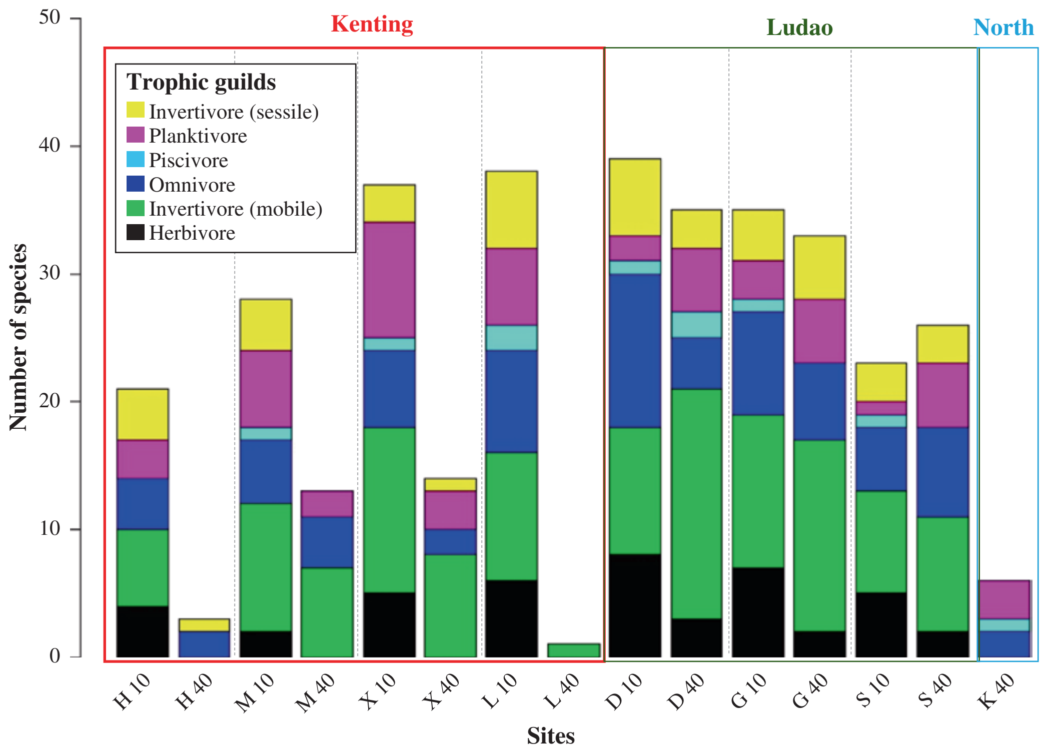


**Fig. 14.8** Comparison of trophic structure between shallow (10 m deep) and mesophotic (40 m deep) fish assemblages. *H* Hongchaikeng, *M* Maobitou, *X* Xiaowan, *L* Longkeng, *D* Dabaisha, *G* Guiwan, *S* Shihlang, *K* Keelung Island. The numbers 10 and 40 are the depths surveyed in meters

information on environmental parameters influencing the distribution of reef organisms and the role that MCEs could play in their survival when facing disturbances. In particular, our work highlights important regional differences specific to a particular latitudinal or geomorphological context. In Kenting, reef communities are limited by substrate availability and sedimentation and do not reach mesophotic depths. Low scleractinian coral diversity below 30 m suggests that mesophotic depths are unlikely to contribute to the dynamics of shallow-water reefs in Taiwan. However, sponges, octocorals, and other benthic taxa could constitute a distinctive community associated with boulders and rocks found at these depths. In contrast, we recorded substantial overlap in faunal diversity between shallow and mesophotic depths at Ludao, and further studies should investigate connectivity between deep and shallow populations.

Mesophotic communities in northern Taiwan exhibit characteristics of temperate mesophotic ecosystems, with a dominance of octocorals and the presence of a few, mainly azooxanthellate, scleractinian species. The differences with shallow-water communities in northern Taiwan, where scleractinian corals are abundant (Yang and Dai 1982; Ribas-Deulofeu et al. 2016), suggest two very distinctive communities. However, species overlap in major taxa other than hard corals requires further investigation.

The trophic structure of Taiwanese reef fish fauna reveals that invertivores, omnivores, and planktivores are the dominant feeding guilds (Fig. 14.8), a pattern consistently reported in mesophotic fish assemblages (Pyle et al. 2016). The unusually low abundance of piscivores could reflect high fishing pressure on this guild, which is usually one of the first to decline in fished areas (Friedlander and DeMartini 2002). Piscivores, as well as herbivores, decrease with depth and are totally absent at 40 m in depth at Kenting and in northern Taiwan. The decline of herbivores with depth is likely to be associated with changes in habitat complexity, shifts in benthic primary productivity sources, and/or changes in algal composition and their overall nutritional value, which constrain herbivores to shallow waters (Brokovich et al. 2008, 2010; Kahng et al. 2010; Asher et al. 2017).

## 14.6 Threats and Conservation Issues

Although threats on MCEs have not yet been assessed in Taiwan, they are likely to be impacted by the same natural and human disturbances already affecting shallow reefs in Taiwan, such as typhoons and overfishing. Conservation actions have never focused specifically on mesophotic depths in Taiwan, probably because of the limited amount of ecological knowledge on this ecosystem. However, MCEs sometimes benefit from protections targeting shallow waters. For example, the Marine Ecology Protection Zone of Kenting

National Park in southern Taiwan and Dongsha Atoll National Park in the South China Sea do extend to depths of about 200 m, which includes MCEs. Current research aims to uncover the diversity of this habitat in Taiwan while acknowledging regional differences for better integration of these ecosystems into future ecological management efforts. It also provides a baseline upon which MCEs may be integrated into long-term ecological research currently restricted exclusively to shallow-water reefs.

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