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Abstract

Fishes are an important component of coral reef ecosystems, and in comparison to other marine phyla, the taxonomy of fishes is relatively robust. Some of the earliest explorations of mesophotic coral ecosystems (MCEs) involving both submersibles and rebreather diving focused on fishes. Since 1968, over 400 publications have documented fishes on MCEs, ~75% of which were published since 2011. Most fish species inhabiting MCEs belong to families and genera typical of shallow coral reefs, and many new species remain to be discovered and described. Species richness generally peaks at a depth of 30 m and declines with increasing depth. The composition of the fish communities on MCEs includes a mixture of species restricted to MCEs and species with broad depth ranges. Patterns of species turnover and composition vary depending on geographic location, ecological characteristics, and method of study. Nearly 70% of MCE fish research has occurred within the tropical western Atlantic and Hawai'i. Not enough is known about global distributions to infer broad biogeographical patterns, but there seems to be higher representation by endemic species and individuals on MCEs, and the eastward attenuation of diversity of shallow Pacific reefs does not appear to apply to fishes within MCEs. Analyses of nearly 900,000 occurrence records of reef fishes at depths of 1–200 m reveal patterns of diversity that are mostly consistent with controlled studies. Future work should

emphasize basic exploration and documentation of diversity in under-sampled geographic regions and hypothesis-driven studies in areas where logistics facilitate MCE research.

Keywords

Mesophotic coral ecosystems · Biodiversity · Endemism · New species · Technical diving

40.1 Introduction

Coral reefs and associated habitats are home to approximately one-quarter of all fishes. Tens of millions of people around the world depend on reef fishes for nourishment and livelihood, and their dazzling array of colors, behaviors, and other characteristics have attracted a broad range of scientific investigation and aesthetic appeal (Pyle 1993; Spalding et al. 2001). The presence of reef fishes may also be used as an indicator of coral reef ecosystem health (Hourigan et al. 1988; Reese 1994; Crosby and Reese 1996; Reese and Crosby 1999). Among marine organisms, fishes have relatively high species diversity, extensive existing data, and a rich potential for new species discoveries. Initiatives such as the Catalog of Fishes and FishBase have generated tremendous digital resources for nomenclature and a wide spectrum of integrated data from multiple sources. Such resources have provided ichthyologists access to robust data content. However, as compounding factors of climate change, ocean acidification, coastal development, and over-harvesting continue to imperil coral reef ecosystems at escalating rates, the future health of reef fish diversity and populations remains in question (Pandolfi et al. 2011; Hughes et al. 2017).

Mesophotic coral ecosystems (MCEs) are light-dependent coral ecosystems found at depths from 30–40 m to over 150 m in tropical and subtropical regions (Hinderstein et al. 2010). The upper boundary for this definition is largely based

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on historical limitations of diving technology, rather than evidence-based demarcations of biological zones. A more thorough discussion of the problems of how the term “MCE” has been defined, applied, and subdivided is discussed in Pyle and Copus (2019).

Knowledge of fishes inhabiting MCEs goes back for centuries, with specimens collected by hook and line, traps, and trawls. The advent of SCUBA and its application in ichthyological research began in the 1950s and played a key role in documenting reef fish diversity (Sale 1991). Many intrepid divers throughout the 1950s–1990s used conventional SCUBA to reach depths in excess of 30 m to collect fish specimens. John E. Randall, the most active and prolific ichthyologist of the twentieth century, is credited with discovering more new species of fishes than anyone in history and mostly with conventional SCUBA (including many from depths below 30 m). Among the Bishop Museum fish collection are nearly 2000 specimens (including nearly 400 type specimens) collected by Randall from MCEs going back to the 1950s.

Despite early efforts using conventional SCUBA and historical methods of collecting fish specimens, the majority of MCEs and their corresponding ichthyofauna remained poorly explored and documented. In particular, almost all of these deep excursions were limited to a maximum depth of about 75–80 m. Even with a few open-circuit, mixed-gas dives to greater depths, these efforts were severely limited in how much time could be spent conducting research at depth.

The first technological breakthrough to overcome the limitations of diving technology was in the late 1960s with the invention and development of the first electronically controlled, closed-circuit, mixed-gas rebreather by Walter Starck II and John Kanwisher (Tzimoulis 1970; Starck and Starck 1972; Starck 1973). Primarily due to limitations of available electronics technology and oxygen sensors, as well as some unfortunate diving accidents, such rebreathers were not widely adopted for use in exploring and conducting scientific research within MCEs until decades later (Pyle 2019a).

Instead, submersibles served as the primary tool for studying fishes on MCEs, beginning with a series of test dives in the mid-1960s using the submersible *Asherah* in the Hawaiian Islands (Brock and Chamberlain 1968; Strasburg et al. 1968). The use of submersibles to explore MCEs continued through the next two decades (Colin 1974, 1976; Nelson and Appeldoorn 1985; Randall et al. 1985; Parker and Ross 1986; Thresher and Colin 1986; Dennis and Bright 1988; Moffitt et al. 1989; Shinn and Wicklund 1989; Itzkowitz et al. 1991; Gilmore and Jones 1992; Tyler et al. 1992; Chave and Mundy 1994), and to a lesser extent, into the present (Locker et al. 2016; Pyle et al. 2016a; Tornabene et al. 2016a; Armstrong et al. 2019). Submersibles have several key limitations, including difficulty conducting quantitative fish assessments (Fig. 40.1) and the general restriction of study sites to facili-

ties with submersible operations nearby (Fricke and Knauer 1986). As a result, most of the submersible research on MCEs has taken place in just a few localities in the tropical western Atlantic, central Pacific (Hawaiian Islands and adjacent regions), and the Red Sea. Many researchers have also encountered difficulties collecting specimens and confirming identifications of observed species using submersibles (Strasburg et al. 1968; Colin 1974; Colin et al. 1986). Cryptic and small fishes are especially difficult to see, resulting in datasets biased toward larger, conspicuous fishes (Thresher and Colin 1986). Despite these limitations, some recent research on MCEs has been successfully conducted with submersibles. For example, submersibles owned and operated by the Hawai‘i Undersea Research Laboratory at the University of Hawai‘i (*Makali‘i*, *Pisces IV*, and *Pisces V*) have conducted extensive observations on fishes within MCEs for decades (e.g., Randall et al. 1985; Colin et al. 1986; Pyle et al. 2016a; Spalding et al. 2019), including the use of rotenone and a suction device for collecting fishes. The *Curasub* submersible, with similar capabilities, has been used successfully and extensively for MCE research in Curaçao and Bonaire (Baldwin and Robertson 2013; Hoeksema et al. 2014; Baldwin et al. 2016; Tornabene et al. 2016b).

Some work documenting fishes in MCEs has involved the use of various remote forms of underwater camera systems, such as drop and towed camera systems (Blyth-Skyrme et al. 2013; Easton et al. 2017), remotely operated vehicles (ROVs; Pereira-Filho et al. 2011; Blyth-Skyrme et al. 2013; Bryan et al. 2013; Reed et al. 2017; Ajemian et al. 2015a, b; Cánovas-Molina et al. 2016; Simon et al. 2016; Streich et al. 2017; Easton et al. 2017; Armstrong et al. 2019), and baited remote underwater video stations (BRUVS; Blyth-Skyrme et al. 2013; Pearson and Stevens 2015; Andradi-Brown et al. 2016, 2017; Lindfield et al. 2016; Asher et al. 2017a, b). Autonomous underwater vehicles (AUVs) have also been utilized for MCE research, but they have mostly focused on characterizing sessile benthic fauna (Armstrong and Singh 2012; Armstrong et al. 2011, 2019; Bridge et al. 2011). While these systems have provided valuable insights on general patterns of conspicuous fish diversity on MCEs, similar to submersibles they are limited in their ability to document small, cryptic species or collect specimens for taxonomic identification (Simon et al. 2016).

Beginning in the mid- to late 1980s (two decades after Starck and Kanwisher invented the electronically controlled, closed-circuit rebreather), mixed-gas diving technology finally experienced an increase in use among civilian, noncommercial divers. These practices came to be known as “technical diving” (Hamilton 1990; Menduno 1991a, b) and were exploited by freshwater cave divers, wreck divers, and researchers studying MCEs. Most early technical diving involved open-circuit, mixed-gas systems incorporating trimix (i.e., breathing mixtures containing helium, nitrogen, and oxygen) and oxygen-

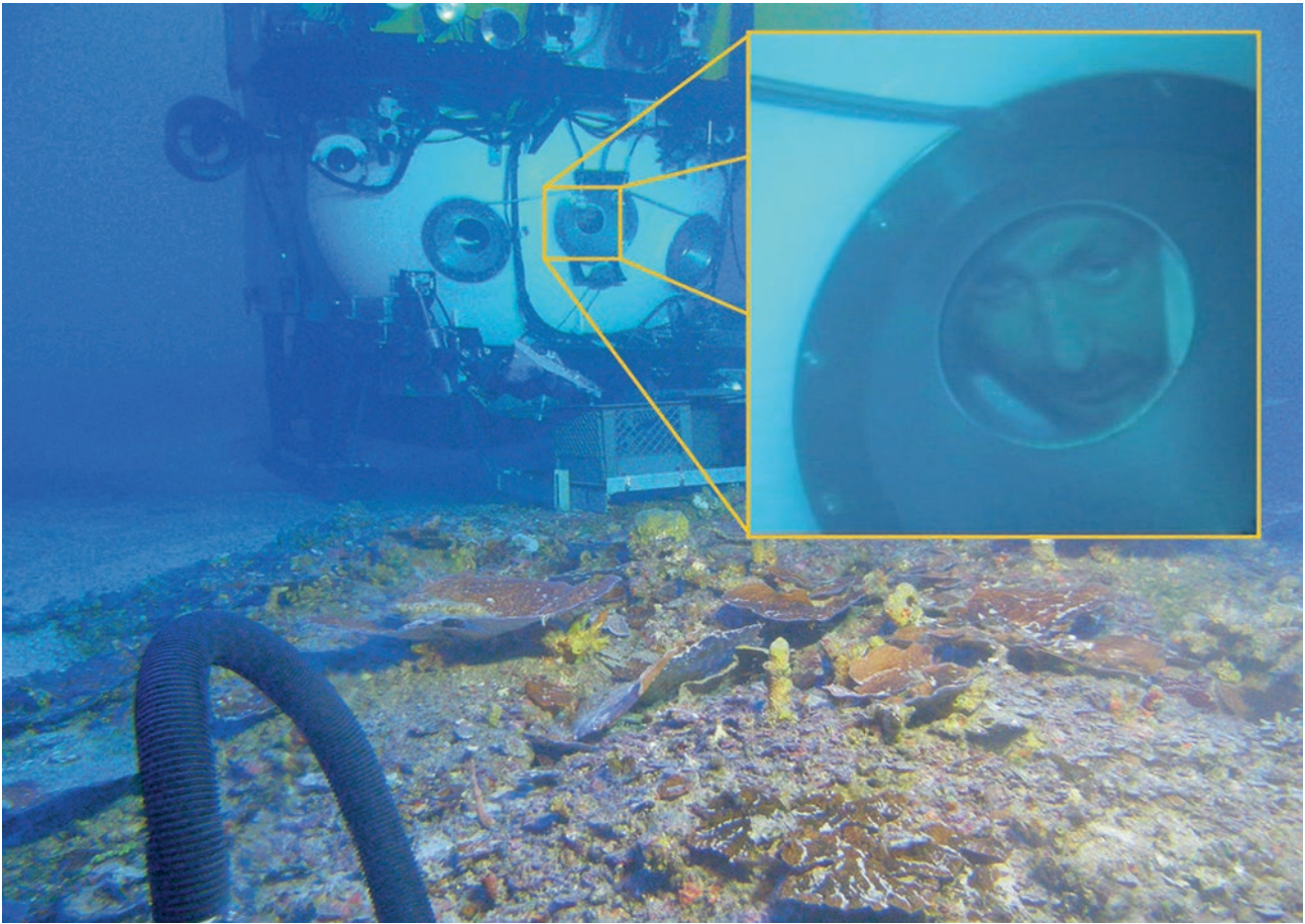


Fig. 40.1 Researcher Anthony Montgomery peers through the porthole of the *Pisces V* submersible on a MCE off Maui, Hawai‘i. Submersibles are extremely effective for MCE research but impose limits on collecting fishes and documenting cryptic motile diversity. (Photo credit: NOAA Hawai‘i Undersea Research Laboratory, can be reused under the CC BY license)

enriched mixtures for decompression. Such equipment has been used for MCE research involving fishes (Pyle 1991, 2019a; Pereira-Filho et al. 2011; Kane et al. 2014; Meirelles et al. 2015; Simon et al. 2016), but requires relatively large quantities of helium and oxygen, limits dives to relatively short bottom times, and is generally inefficient compared to closed-circuit, mixed-gas systems (Parrish and Pyle 2002).

During the mid-1990s, methods to collect fish specimens from MCE habitats using closed-circuit rebreather technology, particularly in remote locations, were developed and refined (Pyle 1996a, b, 1998, 1999a, 2000; Pence and Pyle 2002; Weiss 2017). Although much of the initial work involved the discovery and documentation of new fish species (e.g., Gill et al. 1996; Earle and Pyle 1997; Randall and Pyle 2001a, b; Pyle et al. 2008), rebreather technology was soon adopted by scientists for conducting a wide variety of MCE research (e.g., Sherman et al. 2009; Fricke et al. 2010; García-Sais 2010; Bejarano et al. 2011; Lesser and Slattery 2011). Since 2012, at least 30 publications have reported on research involving closed-circuit rebreather technology to

study fishes within MCEs. As rebreather technology continues to improve (Pyle 2016) and as the number of institutions supporting technical diving increases (Jessup 2014; Pollock et al. 2016), closed-circuit rebreathers are becoming an increasingly important tool in MCE research, perhaps as important as conventional SCUBA has been for shallow reef exploration (Sale 1991; Pyle 2019a).

These advances in technology and easier access to greater depths, along with a renewed interest in studying deeper habitats, has vastly increased our understanding of MCEs. (Hinderstein et al. 2010; Baker et al. 2016; Loya et al. 2016; Pyle and Copus 2019). This chapter summarizes and synthesizes what is known about the diversity of fishes on MCEs in comparison to shallow reef fishes in three sections: Taxonomy, Biogeography, and Analysis and Information Gaps (see also Sinniger et al. 2016). The first two sections review existing literature to capture a broad picture of what has been documented. The third analyzes two databases of fish occurrence records spanning 1–200 m in depth and identifies gaps in our knowledge.

40.2 Taxonomy

Compared with most taxonomic groups inhabiting coral reefs (including MCEs), the taxonomy of fishes is relatively robust, stable, and complete. Although many new species of reef fishes are discovered and described each year and taxonomic revisions continue to provide new insights into inferred phylogenetic relationships (Betancur et al. 2017), most fish specimens, unlike most other taxa, can be reliably identified to taxonomic family and genus and usually to species. Therefore, documentation of fishes on MCEs can be put into a more robust taxonomic context than many other organisms, which has allowed the comparison of fish communities across depth gradients and geographic regions.

The global understanding of coral reef fishes in general is greatly facilitated by a number of recent and relatively complete field guides, particularly in the tropical Indo-Pacific (e.g., Myers 1999; Randall 2005, 2007; Allen and Erdmann 2012). Each of these includes information on many species that are either typical of or restricted to MCE habitats. However, whereas the coverage of species inhabiting shallow reefs is robust and mostly complete, coverage of species restricted to MCE habitats is primarily limited to those species that can be found in depths of 60 m or shallower and species that can be readily collected using remote sampling methods. As such, coverage of the true complement of MCE ichthyofauna is incomplete and largely inadequate.

40.2.1 Species Composition

Among the first to explore MCEs, Strasburg et al. (1968) noted shallow reef fishes were present on MCEs, as did Colin (1974). From 1986 to 2017, more than 6000 occurrences of fishes collected or photographed were made during 60 expeditions to 30 locations throughout the tropical Indo-Pacific, at depths ranging from 30 to 150 m. Of the 733 species represented, all except 3 belong to families associated with shallow coral reefs (Sinniger et al. 2016). For example, on three expeditions to Rarotonga (1989), Papua New Guinea (1995), and Palau (1997), the 20 most species-rich families of fishes on MCEs were typically associated with shallow reefs, and only one specimen represented a non-shallow reef family (Symphysanodontidae; Pyle 2000; Sinniger et al. 2016). Additionally, the top five most diverse families reported on MCEs (Gobiidae, Serranidae, Labridae, Pomacentridae, and Apogonidae) coincide with the five most diverse families found on shallow coral reefs (Pyle 2000).¹ Similar results

¹These data were primarily obtained through specimens collected with hand nets and the ichthyocide rotenone. Thus, they are biased against larger predatory species, such as Jacks (Carangidae) and snappers (Lutjanidae), both of which are well represented on shallow reefs and MCEs.

were found for quantitative analyses of fishes in Brazil, where the most species-rich families were Carangidae, Gobiidae, Lutjanidae, Labridae, Serranidae, and Haemulidae (Feitoza et al. 2005). Thus, at the family level, coral reef fish communities typical of shallow reefs in the tropical Indo-Pacific extend down to depths of at least 150 m.

Some early MCE researchers (Colin 1974, 1976; Thresher and Colin 1986) noted that although several fish species occur on both shallow reefs and MCEs, many species were restricted to MCEs (i.e., confined to depths of about 60–120 m). Thresher and Colin (1986) found that the fish community on MCEs in the Marshall Islands was composed of a higher proportion of non-shallow-water species than the fish community at shallower (30–60 m) or greater (>150 m) depths. This would imply that there are a greater number of species restricted to the 60–150 m depth zone than there are shallower or deeper than MCEs. Similar patterns, involving certain species limited to shallow reefs, some species with broad depth ranges, and some species being restricted to deep environments only, have likewise been documented by more recent studies (e.g., Feitoza et al. 2005; Bejarano et al. 2011, 2014; Wagner et al. 2014; Fukunaga et al. 2016, 2017a, b; Pinheiro et al. 2016; Pyle et al. 2016a).

40.2.2 New Species

Many species found on MCEs are new to science. In Jamaica and Belize, of 21 fishes observed from 60 to 150 m in depth, 7 (33%) represented undescribed species (Colin 1974). Similarly, of 50 fish species recorded from Eniwetok Atoll, 20 (40%) could not be identified to species and were likely undescribed (Thresher and Colin 1986). Since the late 1980s, over 70 new fish species have been described from specimens collected on MCEs (see Fig. 40.2 and figures in Pyle (2019b) and Pyle et al. (2019)). Of these, at least 22 new fish species have been described in the past few years alone (e.g., Copus et al. 2015a, b; Stiller et al. 2015; Anderson et al. 2016; Baldwin et al. 2016; Carvalho-Filho et al. 2016; Pyle and Kosaki 2016; Pyle et al. 2016b; Tea et al. 2016; Tornabene et al. 2016b; Anderson and Johnson 2017; Conway et al. 2017; Gill et al. 2017; Hastings and Conway 2017; Krishna et al. 2017; Motomura et al. 2017; Prokofiev 2017; Rocha et al. 2017; Tornabene and Baldwin 2017; Walsh et al. 2017; Winterbottom 2017). Moreover, dozens of fish species discovered on MCEs are awaiting formal description (R.L. Pyle, unpubl. data).

New fish species discovered per unit effort (NSPUE) was calculated for four expeditions to MCEs in the Pacific Ocean (Table 40.1; Pyle 2000, 2019b). Discovery rates ranged from 4.3 new species per hour of exploration time in Rarotonga up to an average of >11 new species per hour in Fiji. The data from Fiji are the most reliable, as they involved a series of

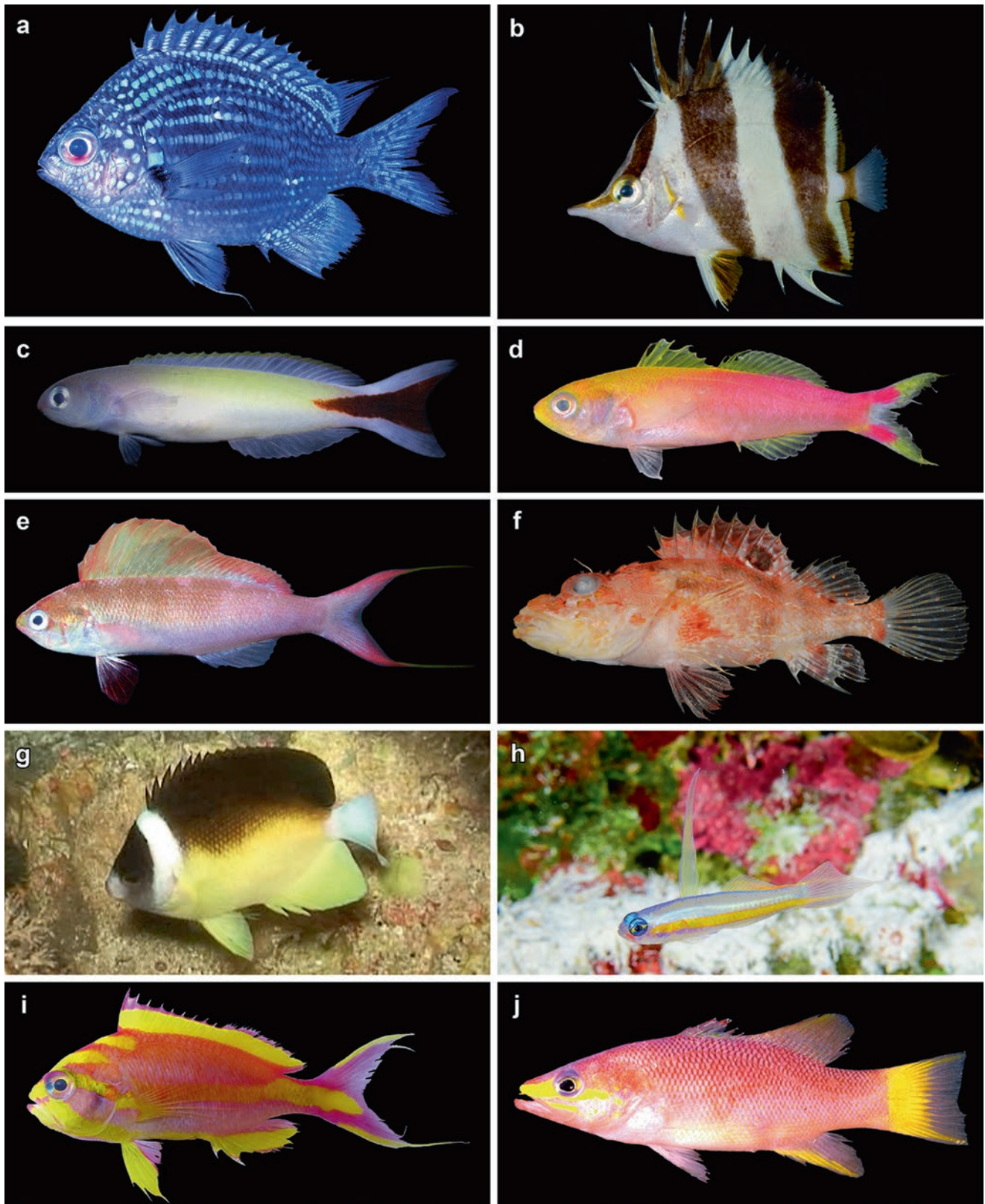


Fig. 40.2 Examples of recently discovered fish species from MCEs. (a) *Chromis abyssus* Pyle Earle and Greene 2008, (b) *Prognathodes geminus* Copus, Pyle, Greene and Randall 2019, (c) *Hoplolatilus* n. sp. (Christmas Island, Line Islands), (d) *Luzonichthys seaver* Copus Ka'apu-Lyons and Pyle 2015a, (e) *Rabaulichthys* n. sp. (Christmas Island, Line Islands), (f) *Scorpaenopsis* n. sp. (Hawaiian Islands), (g) *Centropyge abei* Allen, Young & Colin, 2006, (h) *Antilligobius nikkiae* Van Tassell & Colin, 2012, (i) *Tosanoides annepatrice* Pyle, Greene, Copus and Randall 2018, (j) *Liopropoma* n. sp. (throughout tropical Pacific) (Photo credits: R.L. Pyle (a, b, f, j), B.D. Greene (c, d, e, i), J.L. Earle (g), and L.A. Rocha (h); composite image by R.L. Pyle, can be reused under the CC BY license)

Table 40.1 Summary of new fish species discovered on MCEs based on collections at four locations, with calculated NSPUE

Locality	New fish species	Collecting effort (h)	NSPUE
Rarotonga	12	2.8	4.3
Papua New Guinea	16	3.2	5.0
Palau	27	3.9	6.9
Fiji	>46	4.1	>11.2

Data from Pyle (2000, 2019b)

All expeditions, except to Rarotonga, used closed-circuit rebreathers for extended bottom times. Additionally, the Palau and Fiji collections involved the use of rotenone

controlled stations at various depths. In the deepest zone (105–120 m), the rate of discovery was 27 new species per hour. Extrapolating from these Fiji data, it was estimated that 1800–2700 fish species are still to be discovered in the Pacific Ocean (Pyle 2005), representing approximately 30–50% of the total known coral reef fishes of the region. Whether or not these numbers are representative of how many species actually remain to be discovered on the MCEs of the Pacific will require substantially more exploration. It is worth noting that of the 70 new species described from MCEs since the 1980s, only 1 represents a new genus (Conway et al. 2017). Although more new genera may be established as more new species from small, cryptic groups (particularly Gobiidae) are discovered and described; this trend further emphasizes the general affinities of MCE fish fauna to their shallow-water counterparts, even if the actual species may differ.

40.2.3 α Diversity

Many researchers have sought to compare patterns of overall species richness (α diversity) across different depths. Strasburg et al. (1968) documented over 100 species from 50 submersible dives in the Hawaiian Islands and provided the first data on diversity changes with depth, recording 23 species at 0–30 m depth, 80 (31–60 m), 57 (61–91 m), 55 (92–121 m), 33 (122–152 m), 22 (153–182 m), and 15 (182–192 m). Although they did not specify sampling effort within each depth zone, they did note that the depth ranges from 0–30 m and 183–192 m were not sampled thoroughly.

Some early attempts to characterize the diversity of fishes on MCEs described them as depauperate shallow-water communities (Itzkowitz et al. 1991). Brokovich et al. (2008) found a peak in total species richness at 30 m (attributed in part to a mixing zone where both shallow species and deep species overlap), with a decline in species richness with increasing depth. Similar results were documented in Puerto Rico and Curaçao, with high species richness at depths of 40–70 m (Bejarano et al. 2014; Pinheiro et al. 2016). However, other early studies comparing fish species diversity across a range of depths found high species richness at

depths of 60–90 m in the western Atlantic and the Pacific Oceans (Parker and Ross 1986; Thresher and Colin 1986).

40.2.4 β Diversity

Several studies have attempted to quantify fish species turnover (β diversity) across shallow coral reefs and MCEs, and while generally similar patterns were documented worldwide, some details differed. In the northern Red Sea, data from quantitative visual and video transects at 0–65 m were compared, and there was a high degree of species turnover below 30 m (Brokovich et al. 2008). The change in fish community was highly correlated with both depth and the abundance of branching corals, and the pattern was largely driven by a replacement of damselfishes (Pomacentridae) in shallow habitats with sea basses (Serranidae) and wrasses (Labridae) in deeper habitats. In the Solitary Islands Marine Park (New South Wales, Australia), changes in reef fish assemblages were also strongly correlated with depth, with distinct assemblages on reefs <25 m, 25–50 m, and >50 m (Malcom et al. 2011). In Puerto Rico, Bejarano et al. (2014) reported that a major faunal break for fishes, corals, and algae was found at 60 m, below which herbivory and light were reduced. Using BRUVs off eastern Australia at 30–82 m, Pearson and Stevens (2015) documented a relatively high proportion (15–45%) of species restricted to within each of four depth bands (30–34, 46–51, 62–65, and 79–82 m).

Examining depth distributions of 95 species of Caribbean gobies, Tornabene et al. (2016a) found that species richness decreases with increasing depth. They also found that the most prominent bathymetric break in depth distributions was 50–70 m. Using a similar analysis, 445 Hawaiian reef fish species with known depth ranges between 30 and 200 m were analyzed, and 87% were found to also occur at shallower depths (<30 m; Pyle et al. 2016a). Additionally, the most substantial turnover in species was in the depth ranges of 20–30 m and 110–120 m, with the least turnover in the ranges of 40–50 m and 50–60 m.

Fukunaga et al. (2016) analyzed transect data from 1 to 67 m in the Northwestern Hawaiian Islands and found gradual changes in the structure of fish assemblages with depth, noting that the mid-depth zone (27–40 m) seemed to be a transition between shallow reefs and MCEs. In a follow-up study, different fish assemblages on MCEs at different geographic locations along the Hawaiian Archipelago were found, suggesting these differences may be related to latitudinal temperature changes (Fukunaga et al. 2017a, b).

In a study spanning all taxa (including fishes) in the Gulf of Mexico, Semmler et al. (2017) analyzed data for over 9000 benthic and suprabenthic species in the Gulf of Mexico, at depths ranging from 0 to 300 m. Their results suggested that the MCE depth range (30–150 m) did not represent a

distinct community as a whole. Rather, they found clusters of taxa at 0–70, 60–120, 110–200, and 190–300 m. Similar to the findings in Puerto Rico (Bejarano et al. 2014), they found an important break in the benthic community and actinopterygian fishes at approximately 60 m. Their analysis showed that peak diversity for fishes was somewhat lower in the depth range of 0–50 m, compared to results for all taxa, with the break occurring at 60 m.

Depth is not the only correlate with fish species turnover on MCEs. In Puerto Rico at depths of 15–50 m, direct diver observation surveys of fish populations associated with reef habitats found that fish species richness was positively correlated with live coral cover (García-Sais 2010). Certain fish species were most abundant or only present at stations >30 m, including *Centropyge argi*, *Chaetodon aculeatus*, *Chromis insolata*, *Halichoeres cyanocephalus*, *Sparisoma atomarium*, and *Xanthichthys ringens*, suggesting that these species could represent “indicator species” of transition into MCE habitats. In Florida, a comparison of low-relief substrate to high-relief reefs on sunken vessels or “vessel reefs” between 50 and 120 m revealed distinct fish assemblages on each (Bryan et al. 2013). Fish assemblages on vessel reefs more closely resembled those found at similar depths in high-relief natural areas elsewhere than assemblages associated with adjacent low-relief habitat. Using visual census techniques to quantify reef fish communities at depths up to 80 m in Bermuda and 130 m in Curaçao, Pinheiro et al. (2016) compared both depth and habitat type (coral reefs, rhodolith beds, ledges, and walls). The MCE fish species richness in Bermuda was lower but increased with depth, whereas those in Curaçao had higher species richness overall, but richness decreased with depth. As with previous studies, they also found high turnover across depths but noted a major break between 80 and 90 m.

Although some common themes are evident throughout most or all of these studies, there are also some noteworthy differences. Studies in the tropical Atlantic tended to find faunal breaks in the range of 60–80 m, whereas studies in the Red Sea, Australia, and Hawai‘i found more pronounced breaks in the range of 25–30 m, with the lowest turnover in Hawai‘i at 40–60 m. Given the broad geographic spread of these studies (tropical Atlantic, Hawai‘i, Australia, and the Red Sea), the different methods used to capture data (ROVs, rebreather divers, and BRUVs), and the different methods used to analyze those data, it’s not surprising that results are inconsistent. While there has been some suggestion that a consistent faunal break among all taxa may exist at around 60 m (Slattery and Lesser 2012; Semmler et al. 2017), this may be overly influenced by results for certain invertebrate taxa and from the Caribbean, Gulf of Mexico, and other parts of the tropical Atlantic and may not reflect broader MCE fish communities worldwide. Moreover, most of the studies cited above were confined to the upper half of the MCE depth range (i.e., 30–70 m), thereby ignoring patterns that may

occur at greater depths within MCEs. For example, Pinheiro et al. (2016) and Pyle et al. (2016a) found the greatest turnover at 80–90 m and 110–120 m, respectively.

40.3 Biogeography

Drawing from an abundance of data and relatively stable taxonomy, coral reef fishes have frequently been the subject of studies examining broad patterns of biogeography (e.g., Springer 1982; Randall 1998; Pyle 1999b; Bellwood and Wainright 2002; Floeter et al. 2008; Briggs and Bowen 2012; Cowman and Bellwood 2013). Among the most consistent and conspicuous biogeographic patterns within, the tropical Indo-Pacific region is a peak in overall species richness in the Indo-Australian Archipelago (i.e., Indonesia, the Philippines, Papua New Guinea, and southern Taiwan), with attenuating diversity eastward across the Pacific Ocean (Briggs 1974; Rosen 1988; Carpenter 1998; Myers 1999; Pyle 1999b; Bellwood and Wainright 2002; Mora et al. 2003; Carpenter and Springer 2005; Allen 2008; Allen and Erdmann 2012). Many different hypotheses have been proposed to explain this pattern and have been summarized in Bowen et al. (2013), Gaither and Rocha (2013), and Bellwood et al. (2015). In most cases, these broad biogeographic hypotheses are based on data relating to fish distributions in shallow waters (<30 m).

In addition to depth limitations, the limited location of MCE studies is a problem for broad geographic analyses of fishes known to inhabit MCEs. Studies focused on MCEs are disproportionate in their geographic distribution as demonstrated by the published literature (Fig. 40.3). Over 50% of the publications have focused on the tropical western Atlantic Ocean (including the Caribbean, Gulf of Mexico, and Brazil) and 17% in the Hawaiian Islands. Both the tropical western Atlantic Ocean and the Hawaiian Islands are areas of low diversity in comparison to the tropical Indo-Pacific region, which encompasses nearly ten times the geographic area and coral reef fish diversity.

The lack of widespread distributional data for MCEs throughout the Indo-Pacific severely limits the degree to which broad biogeographic patterns of fishes on MCEs can be made (Pyle 1999b; Pyle and Copus 2019). Though robust quantitative data at appropriate locations across the Pacific are still lacking, there are a few qualitative and/or anecdotal observations based on surveys across the Pacific that are worth noting. For example, MCEs in the Pacific are generally inhabited by a mixture of species that also occur on shallow reefs, as well as species restricted to MCEs, with no clear qualitative dominance by either group. In many cases, species primarily occupy deeper reefs but are occasionally found in shallow habitats; conversely, many species that are primarily restricted to shallow reefs are also occasionally found on MCEs. Such species should be distinguished from those species that are robustly represented in both shallow

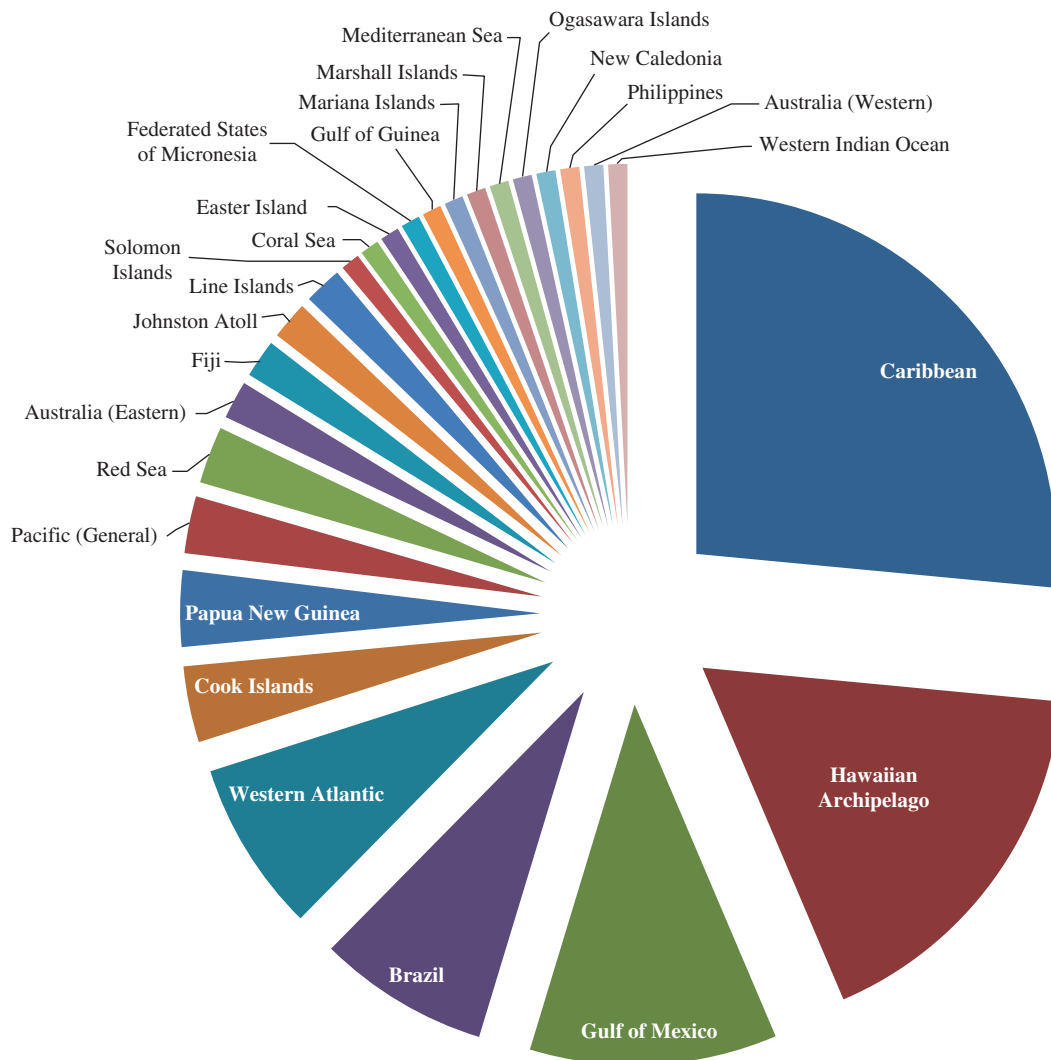


Fig. 40.3 Geographic distribution of publications ($n = 117$) focused on MCE fishes. (R.L. Pyle, unpubl. data)

habitats and MCEs. Among the species well represented across a broad depth range, many tend to be species with wide geographic ranges (e.g., *Forcipiger* spp., *Aulostomus chinensis*, *Zanclus cornutus*, *Sufflamen bursa*, *Pomacanthus imperator*, and *Pterois volitans*). By contrast, species restricted to MCE habitats tend to have narrow distributions (see Sect. 40.3.1), though there are a few exceptions (i.e., certain species of *Plectranthias*, *Pseudanthias*, and *Chromis*, which are broadly distributed throughout the Pacific). Because so little work has been done in the Indian Ocean, it is difficult to speculate on distribution patterns beyond the Pacific Ocean.

Although limited quantitative data prevent meaningful large-scale biogeographic analyses of fishes inhabiting MCEs, several studies have examined biogeographic patterns on a smaller scale, particularly in the Hawaiian Archipelago and nearby Johnston Atoll, and in the tropical western Atlantic.

The fish assemblages of the Hawaiian Archipelago have been the subject of a great deal of study, including both shallow and deep environments (Jordan and Evermann 1905; Gosline 1957; Gosline and Brock 1960; Randall 1995, 2007; Mundy 2005; Pyle et al. 2016a). Most of the biogeographic patterns within the archipelago, particularly involving fishes on MCEs, are represented by changes in the proportional representation of endemic species and individuals in different parts of the archipelago and changes in patterns of diversity between the main Hawaiian Islands and the Northwestern Hawaiian Islands (see Sect. 40.3.1). Several studies have examined fishes both shallow and deep at nearby Johnston Atoll (Gosline 1955; Randall et al. 1985; Kosaki 1989; Kosaki et al. 1991; Wagner et al. 2014). In particular, Wagner et al. (2014) found that most of the fishes inhabiting MCE depths at Johnston Atoll were also recorded from shallower (<30 m) depths or were species known to inhabit shallower

depths in other localities. The only fish species known to be endemic to Johnston Atoll is the angelfish *Centropyge nahackyi* Kosaki 1989, a species inhabiting MCEs that has occasionally been observed or collected off the island of Hawai'i (though no breeding population likely exists in the Hawaiian Islands). In general, the fish fauna inhabiting MCEs at Johnston Atoll parallels that of the Hawaiian Islands, in much the same way that the shallow reef fauna does (Randall et al. 1985; Kosaki et al. 1991; Mundy 2005).

Pinheiro et al. (2016) suggested that depth is an important driver of variation in the community structure in parts of the tropical western Atlantic, but geography also plays a major role in the structure of isolated islands, shaping endemic species. Feitoza et al. (2005) found that MCEs of tropical northeastern Brazil are home to several subtropical shallow-water species. Several of these recorded species were previously considered to have a disjunct distribution, suggesting that the deep reefs may function as a faunal corridor between habitats in southeastern Brazil and the Caribbean (Feitoza et al. 2005). Later, analyzing commercial fisheries data, Olavo et al. (2011) corroborated this hypothesis, pointing out shelf-edge habitats as dispersion corridors for deep reef fishes along the South American continental margin.

Simon et al. (2006), studying reef fishes on MCEs of the Abrolhos Bank off the central Brazilian coast, described a transition zone between tropical and subtropical assemblages. They found a higher proportion of shallow-water species inhabiting the northern reefs, while the southern reefs presented lower temperatures and a stronger turnover of species, including new species and a higher proportion of subtropical fishes. Moreover, MCEs of Brazilian oceanic islands and seamounts are home to many endemic species (Pinheiro et al. 2015; Rosa et al. 2016). The distribution of some endemics, present in seamounts relatively close to the mainland, indicates mechanisms of ecological speciation and adaptation to oceanic environments (Pinheiro et al. 2015).

40.3.1 Endemism and Diversity Attenuation

Data from surveys of MCE fishes throughout the tropical Pacific indicates that species restricted to MCEs tend to have *smaller* geographic ranges, in general (Pyle 2000). This pattern of smaller geographic ranges corresponds to *higher* rates of geographic endemism (on average) compared to shallow reef species (e.g., see Fig. 40.4). This increased endemism among fishes on MCEs resulted in 50% more total new species being discovered in Papua New Guinea and Palau combined, than if distribution patterns on MCEs were consistent with what are known on shallow reefs (Pyle 2005). This trend has held for data on MCE fishes in Fiji as well (Pyle 2019b).

The pattern of increased representation of endemic species on MCEs has been corroborated within the Hawaiian

Archipelago (including Johnston Atoll). Kane et al. (2014) found 46% of the species inhabiting MCEs in the Northwestern Hawaiian Islands were Hawaiian endemics (compared with only 30% endemic representation among shallow reef species), with the levels of endemism increasing up the chain to the northwest. At Kure Atoll, the farthest atoll in the Northwestern Hawaiian Islands, 100% of the fishes observed during quantitative transects were Hawaiian endemics (Fig. 40.5; Kosaki et al. 2016).

This pattern of endemism was corroborated by Fukunaga et al. (2017a, b) and further separated into three regions: a southeastern region primarily characterized by the presence of the introduced species *Lutjanus kasmira*, a northwestern region where fish assemblages are largely composed of endemic species, and a middle region with levels of endemism comparable to the southeastern region, but not dominated by *L. kasmira*. The observed patterns may be explained (at least in part) by differences in temperature across the latitudinal gradient of the archipelago (Fukunaga et al. 2017a, b). In particular, temperature may play a role in explaining why many species restricted to MCEs within the Hawaiian Archipelago occur at much greater depths in the Main Hawaiian Islands to the southeast than they do in the Northwestern Hawaiian Islands (e.g., see Table 40.2 and Fig. 40.6). Indeed, temperature may not only shape different depth distributions at different geographic locations but also establish biodiversity shifts across depth within individual locations.

Similar examples have been documented in Brazil, where *Centropyge aurantonotus* occurs at 45–200 m and *Chromis jubauna* at 60–80 m in tropical northeast Brazil, compared to 12–50 m and 10–40 m, respectively, in temperate southeast Brazil. Simon et al. (2016) found an assemblage composed of 12% Brazilian endemics at Abrolhos Bank, with some exclusive to MCEs. Similarly, half of the endemic species of Trindade Island (off Brazil) are also found on MCEs at several seamounts, some close to the mainland (Pinheiro et al. 2015), and a higher proportion and abundance of endemics were found on MCEs of Bermuda compared to other islands of the Greater Caribbean (Pinheiro et al. 2016).

Our observations across the Pacific suggest that major faunal shifts in fish species assemblages correspond to major thermoclines at different depths. For example, in many areas of Micronesia, substantial thermoclines have been documented at various depths across the MCE range. Although exact depths can vary substantially both seasonally and due to internal waves (Wolanski et al. 2004; Pomar et al. 2012), substantial temperature transitions occur at roughly 30 m (shifting from the high to low 20 s °C), 90 m (from low 20 s to high teens °C), and 120 m (from high to low teens °C), and these depths correspond approximately to apparent upper and lower depth boundaries for certain species (R.L. Pyle, pers. obs.). More accurate survey data correlated to actual water temperatures across depths is needed to quantify and elucidate these qualitative patterns.



Fig. 40.4 Examples of endemic fish species from MCEs. (a) *Liopropoma aurora* (Jordan and Evermann 1903) (Hawaiian Islands), (b) *Prognathodes obliquus* (Lubbock and Edwards 1980) (St. Paul's Rocks), (c) *Tosanoides obama* Pyle, Kosaki and Greene 2016b (Northwestern Hawaiian Islands), (d) *Chromis cadenati* Whitley 1951 (West Africa), (e) *Pseudanthias hawaiiensis* (Randall 1979) (Hawaiian Islands), (f) *Cirrhilabrus jordani* Snyder 1904 (Hawaiian Islands), (g) *Xanthichthys greenei* Pyle and Earle 2013 (Line Islands), (h) *Neoniphon pencei* Copus, Pyle and Earle 2015b (Cook Islands), (i) *Centropyge nahackyi* Kosaki 1989 (Johnston Atoll), (j) *Chromis struhsakeri* Randall and Swerdloff 1973 (Hawaiian Islands) (Photo credits: R.L. Pyle (a, c, e, f), L.A. Rocha (b, d), B.D. Greene (g), J.L. Earle (h), R.K. Kosaki (i), and R.K. Whitton (j); composite image by R.L. Pyle, can be reused under the CC BY license)



Fig. 40.5 Every fish species in this photograph taken at a depth of 90 m off Kure Atoll in the Northwestern Hawaiian Islands is endemic to the Hawaiian Archipelago. Species depicted include (in order of abundance): *Pseudanthias thompsoni*, *Caprodon unicolor*, *Chromis struhsakeri*, *Chaetodon miliaris*, *Bodianus albotaeniatus*, *B. sanguineus*, *B. bathycapros*, *Odontanthias fuscipinnis*, and *Genicanthus personatus*. (Photo credit: R. L. Pyle, can be reused under the CC BY license)

Table 40.2 Species known to occur at greater depths within the Main Hawaiian Islands (MHI) compared with the Northwestern Hawaiian Islands (NWHI)

Species	MHI	NWHI
	Depth range (m)	Depth range (m)
<i>Genicanthus personatus</i> Randall 1975	70–150	9–70
<i>Odontanthias fuscipinnis</i> (Jenkins 1901)	90–260	50–100
<i>Prognathodes basabei</i> Pyle and Kosaki 2016	106–187	50–90
<i>Bodianus sanguineus</i> (Jordan and Evermann 1903)	88–152	50–91
<i>Bodianus bathycapros</i> Gomon 2006	147–219	76–90
<i>Suezichthys tripunctatus</i> Randall and Kotthaus 1977	119–272	85–100
<i>Caprodon unicolor</i> Katayama 1975	140–192	35–91
<i>Evistias acutirostris</i> (Temminck and Schlegel 1844)	44–141	15–80
<i>Epinephelus quernus</i> Seale 1901	120–350	15–100

See also Fig. 40.6

Another qualitative but important observation we have made during our surveys across the Pacific has been that the diversity of MCE fishes within the Indo-Australian Archipelago and tropical western Pacific (e.g., Palau, Fiji, Vanuatu, and Solomon Islands) is roughly comparable to the

diversity of species in more central and eastern parts of the Pacific (e.g., Samoa, Line Islands, Cook Islands, and Society Islands; Pyle 2005). This observation is one of the bases for the formulation of the “habitat persistence” hypothesis (HPH; Pyle et al. [In Press](#)).

40.3.2 Habitat Persistence Hypothesis

The HPH is based on two qualitative observations concerning MCE fish species patterns: increased rates of endemism and absence of an eastward diversity gradient across the Pacific (Pyle et al. [In Press](#)). The original framework for this hypothesis was included in Kosaki et al. (1991), and expanded upon by Pyle (2005), and stipulates that shallow reef habitats persist across glacial cycles in regions with sloped bathymetry (e.g., continental regions and large islands) but are extirpated in regions with steep bathymetry (e.g., coral atolls) during low sea-level stands, in contrast to MCE habitats, which persist in all regions. The primary biogeographic implication of the HPH is that the observed biodiversity attenuation on shallow reefs may be due to cyclic recolonization of oceanic islands from areas with shallow-habitat persistence across glacial sea-level cycles (10^5 – 10^6 years), rather than hypothesized processes operating over



Fig. 40.6 Examples of fish species that occur deeper in more tropical waters and shallower in cooler waters (see also Table 40.2). (a) *Prognathodes basabei* Pyle and Kosaki 2016, (b) *Odontanthias fuscipinnis* (Jenkins 1901), (c) *Caprodon unicolor* Katayama 1975, (d) *Epinephelus quernus* Seale 1901, (e) *Genicanthus personatus* Randall 1975, (f) *Bodianus bathycapros* Gomon 2006, (g) *B. sanguineus* (Jordan and Evermann 1903), (h) *Suezichthys tripunctatus* Randall and Kotthaus 1977, (i) *Evisτίας acutirostris* (Temminck and Schlegel 1844), (j) *Chromis struhsakeri* Randall and Swardloff 1973. Images (e, g, j) have been inverted horizontally. (Photo credits: R.L. Pyle, can be reused under the CC BY license)

speciation time scales. The HPH posits seven specific testable predictions, including (1) higher rates of endemism on MCEs and areas of sloping bathymetry, (2) more “species complexes” among species inhabiting MCEs, (3) stronger population genetic structure among MCE species, (4) lower than average genetic diversity among shallow reef species in areas of steep bathymetry, (5) stronger genetic signals of recent population expansions among shallow reef species, (6) reduced eastward attenuation of diversity for MCE species, and (7) shallow reef species diversity attenuation with increasing distance from areas with shallow-habitat persistence. Testing these predictions will require extensive exploration and quantitative documentation of MCEs throughout all tropical regions, but particularly within the Indo-Pacific region. Additionally, the HPH may apply to other groups of marine organisms in addition to fishes and may serve as a framework for future studies.

40.3.3 Genetic Connectivity

Most studies investigating the genetic connectivity of reef fishes have focused on shallow reefs (<30 m) and connectivity across geographic scales (i.e., horizontal connectivity). However, many of the shallow coral reef fish species for which genetic connectivity studies have been conducted are also known to inhabit MCEs. For example, a parameterized search using Web of Science™ (Clarivate Analytics 2017) was conducted for publications containing population genetic diversity data from tropical marine habitats (sensu Keyse et al. 2014). These parameters resulted in 1377 publications, the titles and abstracts of which were assessed and discarded if the focal species was not a coral reef fish species (as defined in the Sect. 40.4). This additional filtering yielded 118 publications and a list of 115 species of fishes for which genetic connectivity has been studied. Based on depth data from the Global Biodiversity Information Facility (GBIF) database (described in the Sect. 40.4), of the 115 species, 106 (92%) were either specifically collected on shallow coral reefs (<30 m) or the depth could not be confidently determined within the methods of the respective publication. The remaining nine species (8%) were specifically reported as collected from MCEs (or deeper). However, 78 (68%) of the fish species in the shallow connectivity studies have depth ranges that extend to depths of 30–90 m and 26 (23%) extend to 90–150 m. For many species of coral reef fishes that occupy both shallow coral reefs and MCEs, horizontal connectivity patterns are known; however, little is known of the extent to which subpopulations on MCEs are connected to those on shallow coral reefs (i.e., vertical connectivity). However one study, Tenggardjaja et al. (2014), found that the endemic Threespot Chromis (*Chromis verater*) has a single continuous population across shallow and adjacent MCEs in

the Hawaiian Archipelago. Similar to *C. verater*, most fishes with broad depth ranges may also exhibit highly connected populations between MCEs and shallow coral reefs, but this has yet to be tested, and caution in making broad generalizations should be exercised until more vertical connectivity studies have been completed. It is yet to be determined whether future research will reveal whether connectivity patterns of MCEs are similar to shallow coral reefs for species spanning both depth zones.

There have been a few connectivity studies on fishes with depth distributions that only occur within MCEs, or in some cases the shallowest extent of their depth range includes MCEs. However, the species that have been examined are restricted to those that are commercially important and can be collected with hook and line. For example, both the southern red snapper (*Lutjanus purpureus*) in Brazil and the northern red snapper (*L. campechanus*) in the Caribbean reveal no genetic structure between species on shallow reefs and MCEs throughout the western Atlantic (Gomes et al. 2012). Similarly, no genetic structure was found for the crimson jobfish (*Pristipomoides filamentosus*) across its broad Indo-Pacific range, except for an isolated population in Hawai‘i (Gaither et al. 2011). Analyses of this same species, along with two additional snappers (*Etelis coruscans* and *E. marshi*) across the Hawaiian Archipelago also revealed high genetic connectivity (Gaither et al. 2011; Andrews et al. 2014). In contrast, Ovenden et al. (2004) found statistically significant population structure over a small geographical scale in the goldband snapper (*Pristipomoides multidentis*). Based on these few studies, species occurring on MCEs appear to be highly dispersive, but additional studies with a much broader range of taxa are needed before any generalizations can be made.

40.4 Analysis and Information Gaps

To analyze general patterns of fish biodiversity within MCEs, as compared with shallow reefs, occurrence records (i.e., records representing the occurrence of a particular species at a particular place and time) were assessed from two databases, GBIF (gbif.org) and the Explorer’s Log (explorers-log.com).

The GBIF database has aggregated over 788 million organism occurrence records from over 35,000 datasets worldwide. A search for records with depths between 0 and 200 m yielded just over 24 million records (GBIF 2017). These records were further filtered to include only records within latitude limits of 35° N and 35° S, with a depth greater than 0 m, and identified to a taxon among 74 families of fishes known to inhabit coral reefs. This yielded 801,653 occurrence records representing a total of 7710 species (Table 40.3).

Table 40.3 A summary of occurrence records for 74 families of coral reef fishes from GBIF and Explorer's Log databases

Family	GBIF			Explorer's log		
	Species	Records	Depth	Species	Records	Depth
Acanthuridae	84	21,254	1–200	60	1803	1–152
Anomalopidae	6	26	1–200	1	2	6
Antennariidae	47	2521	1–200	9	214	2–110
Aploactinidae	36	531	1–200	0	0	–
Apogonidae	335	25,333	1–200	72	542	1–113
Aulostomidae	4	854	1–200	1	106	2–97
Balistidae	38	8528	1–200	23	782	1–120
Batrachoididae	69	12,594	1–200	0	0	–
Blenniidae	350	14,025	1–200	45	400	1–100
Bothidae	145	9218	1–200	14	100	2–187
Caesionidae	24	2020	1–187	15	149	2–98
Callionymidae	145	7320	1–200	16	85	2–110
Caracanthidae	1	1	15	2	10	2–25
Carapidae	25	545	1–200	4	6	6–68
Centriscidae	13	1184	1–200	2	12	2–15
Chaenopsidae	79	2051	1–155	0	0	–
Chaetodontidae	128	15,682	1–200	73	2168	1–190
Cheilodactylidae	27	4281	1–200	1	6	6–17
Chlopsidae	19	1251	1–200	0	0	–
Cirrhitidae	33	2206	1–180	18	467	1–104
Congridae	145	4241	1–200	16	117	1–181
Creediidae	17	404	1–200	3	12	2–9
Diodontidae	22	4751	1–200	6	144	1–108
Ephippidae	15	5805	1–171	5	52	2–76
Fistulariidae	5	2864	1–200	1	45	2–72
Gobiesocidae	115	1669	1–195	2	10	3–12
Gobiidae	1120	77,852	1–200	101	671	1–112
Grammatidae	13	425	1–189	0	0	–
Haemulidae	123	39,879	1–200	11	124	1–65
Holocentridae	81	9529	1–200	41	1098	1–174
Kuhliidae	11	255	1–185	4	30	1–11
Kyphosidae	51	2670	1–200	13	144	1–42
Labridae	497	62,935	1–200	203	3408	1–190
Labrisomidae	114	6405	1–200	0	0	–
Lethrinidae	38	7647	1–200	17	230	1–95
Lutjanidae	108	31,825	1–200	39	563	1–197
Malacanthidae	38	1041	1–200	11	153	4–110
Microdesmidae	65	2058	1–200	14	280	1–100
Monacanthidae	104	16,482	1–200	26	402	1–131
Monocentridae	4	247	1–200	1	2	40
Moringuidae	13	870	1–200	1	1	31
Mullidae	81	16,238	1–200	22	773	1–114
Muraenidae	173	10,073	1–200	43	718	1–183
Nemipteridae	63	15,719	1–200	16	73	2–86
Ophichthidae	208	3536	1–200	18	78	1–165
Ophidiidae	124	6013	1–200	2	30	5–119
Opistognathidae	80	2972	1–183	2	7	8–26
Oplegnathidae	8	1683	1–200	2	73	2–65
Ostraciidae	23	4761	1–200	8	228	1–101
Pegasidae	6	584	1–184	2	18	7–84
Pempheridae	41	1498	1–172	8	58	1–27
Pentacerotidae	14	2283	3–200	2	16	44–141
Pholidichthyidae	3	42	1–59	1	10	8–54

(continued)

Table 40.3 (continued)

Family	GBIF			Explorer's log		
	Species	Records	Depth	Species	Records	Depth
Pinguipedidae	76	2631	1–200	13	193	2–187
Platycephalidae	83	21,561	1–200	6	20	5–18
Plesiopidae	46	1017	1–90	3	10	3–98
Pomacanthidae	86	13,601	1–200	49	1454	1–130
Pomacentridae	391	56,135	1–200	169	2674	1–190
Priacanthidae	20	4424	1–200	8	104	2–195
Pseudochromidae	144	4452	1–140	16	80	5–105
Samaridae	18	590	1–200	3	38	9–106
Scaridae	95	37,280	1–200	47	803	1–161
Scorpaenidae	201	12,775	1–200	45	664	1–200
Serranidae	496	38,093	1–200	121	1751	1–185
Siganidae	26	2457	1–170	18	117	2–31
Soleidae	136	4105	1–200	9	61	3–15
Solenostomidae	7	131	1–200	3	32	5–61
Sparidae	122	58,429	1–200	0	0	–
Symphysanodontidae	9	119	28–200	2	12	75–181
Syngnathidae	242	19,140	1–200	26	153	1–126
Synodontidae	71	16,912	1–200	18	304	1–183
Tetraodontidae	151	25,667	1–200	34	554	1–183
Tripterygiidae	157	4897	1–125	4	16	3–21
Zanclidae	2	556	1–150	1	95	2–86
Totals	7710	80,1653		1592	25,555	

Numbers of species represent totals and are not unique to each dataset. Depth values are ranges from minimum to maximum, in meters. Occurrence records identified to the rank of genus or higher are aggregated as a single species but likely represent more than one species

The Explorer's Log database (2017) contains over 78,000 occurrence records based on over 65,000 media files (still images and videos), over 28,000 literature records, and over 13,000 visual observations, primarily from coral reefs. Applying the same filter criteria, this database yielded 25,555 occurrence records representing a total of 1592 species among 67 of the selected 74 families (Table 40.3).

These 74 families were selected because the majority of species within them live in close association with tropical coral reef habitats. A few of the included families contain species that inhabit non-reef habitats, such as estuaries, soft-bottom coastal habitats, temperate latitudes, abyssal depths, and, in some cases, freshwater streams and rivers (e.g., Gobiidae). At least 33 additional actinopterygian fish families contain some species that live on or near coral reefs but for various reasons are not included among the target families for this analysis. Some of these families (e.g., Aploactinidae, Chanidae, Dactylopteridae, Gerreidae, Leiognathidae, Mugilidae, Scatophagidae, Toxotidae, Trichonotidae, and Uranoscopidae) live in tropical coastal waters in the same geographic regions where coral reefs are found but include relatively few species that directly inhabit coral reef environments. Other families (e.g., Atherinidae, Belonidae, Clupeidae, Engraulidae, Hemiramphidae, and Sphyrnidae) include a number of species that frequently or

occasionally live over coral reefs but in most cases do not usually associate with the reef habitat directly. Other families with a few species that inhabit coral reefs were excluded because most of the species within the family are typically associated with pelagic (Echeneidae, Scombridae), deep (Berycidae, Callanthiidae, Epigonidae, Symphysanodontidae), freshwater (Plotosidae), or other non-reef habitats (Ammodytidae, Eleotridae, Sciaenidae). The Carangidae (jacks) represent a difficult case, as several species in this family are extremely important predators on reef environments. However, they were excluded from these analyses because many species in this family are not directly associated with coral reef environments. Several families of Elasmobranchii (sharks and rays) might also be regarded as primarily composed of reef-associated species but were excluded, as was the family Latimeriidae (which includes two species of living coelacanths).

Both the GBIF and the Explorer's Log databases share certain limitations in terms of what kinds of analyses may be reliably performed. Foremost among these limitations is sampling bias, in that data collecting effort is not evenly distributed across all depths. Because many of these records have been accumulated through collections and observations by SCUBA divers, there is a tremendous overrepresentation from shallow reefs (<30 m) and a corresponding underrepre-

sensation from MCEs (≥ 30 m). There are no cases, where the sampling bias is likely to favor MCEs. In cases where taxa have been recorded from MCEs, but not shallow reefs, there is high confidence that such species genuinely are restricted to MCE depths. By contrast, species recorded only from shallow reefs (but not MCEs) may also occur within MCEs but simply have not yet been documented due to sampling bias. The number of species inhabiting MCEs that have yet to be discovered and described is almost certainly greater than what remains to be discovered on shallow reefs (Pyle 2019b).

Another limitation is the presumption that the fishes are from coral reef habitats. The combined factors of latitude limits, taxonomic family, and recorded depth strongly imply, but do not guarantee, that the records are from MCEs. Not all habitats within the latitude limits are coral reef environments nor are all species among the 74 families restricted to coral reefs. Thus, there are some records from depths shallower than 30 m that were not from coral reefs and some records from depths between 30 and 150 m that were not from MCEs. However, based on a careful review of 100 randomized records from each database, we have confirmed that the number of records from environments other than coral reefs is inconsequential to the general patterns. Additionally, taxonomic identifications in the GBIF database are not always up-to-date or reliable. However, similar to the inclusion of some non-coral reef fishes in the analysis, the impact is minimal to the general patterns. Nevertheless, the results should be considered general in nature, representing very broad patterns.

40.4.1 Taxonomic Composition

The 74 families from the GBIF and Explorer's Log databases included a total of 7724 unique species among 1269 genera (Table 40.3). All families except Symphysanodontidae have at least one representative species recorded from shallow reefs.² Similarly, only the family Caracanthidae (max depth: 25 m) has not been recorded from MCEs. Species from 260 genera among 36 families are only recorded from shallow reefs, and species from 88 genera among 30 families are known only from MCEs. An additional 11 genera (with a single species each) within the families Ophidiidae (*Bathyonus pectoralis*, *Benthocometes robustus*, *Homostolus acer*, and *Xyelacyba myersi*), Ophichthidae (*Benthenchelys cartieri* and *Kertomichthys blastorhinos*), Congridae (*Blachea xenobranchialis* and *Macrocephenchelys brevirostris*), Labrisomidae (*Haptoclinus dropi*), Gobiidae (*Apocryptes* sp.), and Serranidae (*Anatolanthias apiomycter*) are restricted

to depths in excess of 150 m (but included in the datasets because they have been recorded in less than 200 m).

Figure 40.7 summarizes the number of species in seven depth distribution categories (i.e., 0–30 m, 0–150 m, 0–150 m only, 30–150 only, 30–200 m, 150–200 m, and 0–200 m). A total of 3794 species have been recorded from both shallow reefs and MCEs. Of these, 3112 have not been recorded deeper than 150 m, while the remaining 682 species also have records from 150 to 200 m in depths. There are more species recorded only from shallow reefs (2866) than are recorded only deeper than 30 m (1606 species total, 658 of which are restricted to depths of 30–150 m). Part of the disparity in number of shallow-only (0–30 m) species compared with MCE-only species (30–150) is due to sampling bias.³

The top 20 most speciose families among the 74 listed in Table 40.3 make up 71% of the total fish species (Fig. 40.8). In most cases, more species are recorded from shallow reefs than from MCEs. Exceptions include Serranidae, Scorpaenidae, Congridae, Bothidae, and Ophidiidae. In the first two families, the difference in number of species is relatively small (12% and 15% more species in MCEs, respectively). While the difference is somewhat greater for the latter three families, (25%, 40%, and 35%, respectively), based on what is known about the biology and habitat preferences of these species, the difference in all five families may reflect actual biodiversity differences rather than sampling biases. Table 40.4 shows all 18 families having more species in MCEs than on shallow reefs. For some of the additional families (e.g., Malacanthidae, Pingupedidae, and Symphysanodontidae), the increased presence on MCEs is expected. In other cases, such as Bothidae and Samaridae, there may be less sampling bias against MCEs because they live on sediment bottoms, which are more effectively sampled with trawls than rocky reefs.

By contrast, the general trend of fewer species on MCEs compared with shallow depths is consistent (Fig. 40.8). In most cases, the number of species recorded from MCEs is somewhat lower than for shallow reefs. However, several families have conspicuously fewer species recorded from MCEs. For example, whereas over 93% of goby species (Gobiidae) have been recorded from shallow reefs, fewer than 37% have been recorded from MCEs. Although it's possible that this is due to more than twice as many species occurring on shallow reefs, recent descriptions of new gobies (Tornabene et al. 2016b; Tornabene and Baldwin 2017; Winterbottom 2017) suggest the discrepancies for this family might be more reflective of sampling bias. Gobies are small and cryptic, not easily collected with remote sampling

²A single specimen of *Symphysanodon berryi* is indicated in the GBIF database as being at a depth of 0–57 m in the Gulf of Mexico [MCZ 81819], but the actual recorded depth on the label for that specimen (a larva) is 47–57 m, so it is indeed from MCE depths.

³Another consideration is that the MCE depth zone is four times broader than the shallow depth zone. Even correcting for sampling bias, it is unlikely that four times as many species occur on MCEs than on shallow reefs, so it is likely that diversity per available habitat area is higher on shallow reefs than on MCEs.

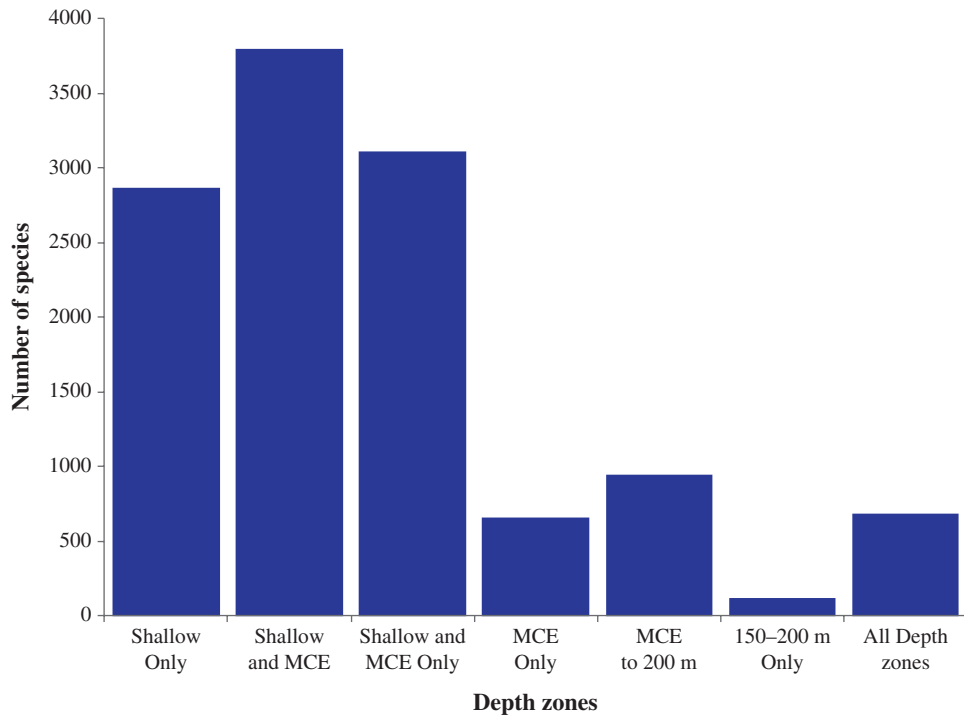


Fig. 40.7 Number of species present in seven different depth zones, those recorded from: (1) shallow reefs only (<30 m), (2) both shallow reefs and MCEs (0–150 m), (3) both shallow reefs and MCEs only (0 to ≤150 m), (4) from MCEs only (30–150 m), (5) MCEs and greater depths (30–200 m), (6) deeper than MCEs only (150–200 m), and (7) all depths (0–200 m). (Data from GBIF 2017; Explorer’s Log 2017)

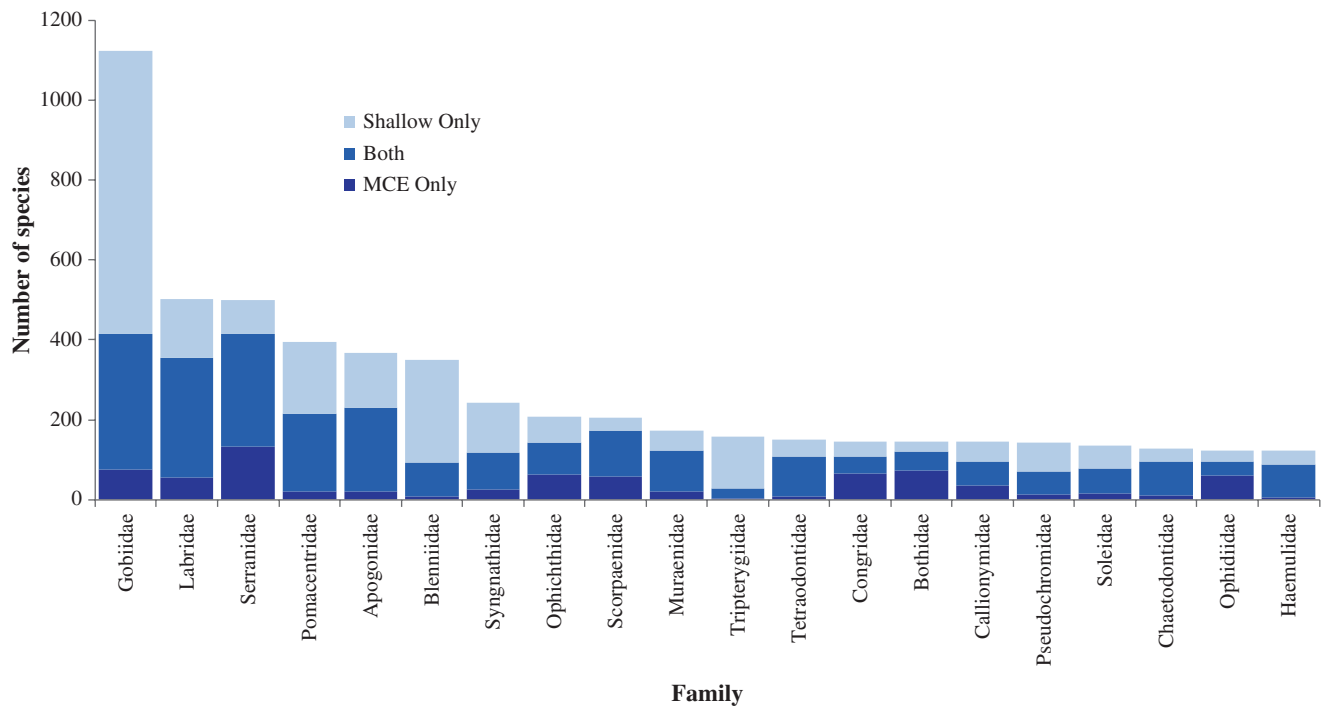


Fig. 40.8 The 20 most speciose families of coral reef fishes, comparing total species (0–150 m), species inhabiting shallow depths (0–30 m), and species inhabiting MCEs (30–150 m). (Data from GBIF 2017; Explorer’s Log 2017)

Table 40.4 Families with more species on MCEs than on shallow reefs

Family	Total species	Shallow species	MCE species	% Difference
Serranidae	499	365	415	12%
Scorpaenidae	204	146	172	15%
Congridae	146	81	108	25%
Bothidae	145	73	121	40%
Ophidiidae	123	62	96	35%
Platycephalidae	83	65	75	13%
Pinguipedidae	76	42	59	29%
Synodontidae	71	53	67	21%
Malacanthidae	37	16	37	57%
Carapidae	25	16	20	20%
Diodontidae	21	19	20	5%
Priacanthidae	19	14	17	18%
Samaridae	17	2	17	88%
Pentacerotidae	13	7	9	22%
Centriscidae	12	10	11	9%
Grammatidae	12	6	10	40%
Symphysanodontidae	8	1	7	86%
Pegasidae	5	4	5	20%

methods, and often overlooked even by technical divers. Without rotenone or other chemical-based collecting methods, goby specimens are not as readily obtained as other larger and more conspicuous coral reef fish species. A more comprehensive investigation of this family in the Caribbean region reported that 60% of 95 Caribbean goby species occur at depths >30 m (Tornabene et al. 2016a), suggesting that species in this family may well be under-sampled on MCEs worldwide. While this may also be true for other disproportionately underrepresented families on MCEs (Blenniidae and Trypterigiidae), in that members of both families are also small and generally cryptic, species in both of these families appear to be genuinely less represented within MCEs based on both their biology and results from targeted rotenone collections (Pyle 2019b).

40.4.2 Historical Patterns

Based on data from GBIF and Explorer's Log databases, the pattern of when species were first recorded (going back to the 1870s) for six depth zones (0–180 m) shows a prominent “spike” in the 1900s (Fig. 40.9a: for all depth zones, but particularly the shallowest) and is consistent with similar patterns noted for fishes in general (Pyle 1995: Fig. 12.4; Eschmeyer et al. 2010: Fig. 1). For example, during the period from about 1890 to 1920, many American marine expeditions were conducted (e.g., to the Hawaiian Islands, Alaska, Bering Sea, and Galapagos), and deep-sea exploration increased in several other countries. Additionally many monographs on groups of fishes and geographical areas were published by David Starr Jordan and his collaborators (Eschmeyer et al. 2010). The second, even larger spike

(Fig 40.9a), from around 1950 to 1980 is likely driven by the advent of SCUBA (Pyle 1995; Eschmeyer et al. 2010). In general, from the 1980s to the 2010s, there is a decline in newly recorded species from most depth zones after the 1980s. There is a similar decline for Pacific coral reef fishes, and a precipitous drop in species descriptions has occurred in the current decade (even when accounting for it being incomplete). However, the decline in new species descriptions is likely a reflection of reduced available funding for alpha-level taxonomic research, rather than a drop in new species discoveries (Pyle 1995). There was an increase of newly recorded species within the depths of 30–120 m during the 2000s. At least half of the more than 32,000 occurrence records contributing to these parts of the datasets are attributed to efforts specifically targeting MCEs, including programs utilizing BRUVS (Cappo et al. 2012; Harvey et al. 2013) and mixed-gas technical diving (Pyle 2019a, b).

40.4.3 Depth Distribution

The records in each database were clustered into 10-m depth zones. In addition to number of occurrence records and number of distinct species within each depth zone, a count of the number of observation/collection days across each zone was used as a very rough approximation of effort. The distribution of this effort across the different depths is shown in Table 40.5 and Fig. 40.10. Although the approximate effort represented in both databases varied considerably across depths as predicted (with far more effort concentrated in the shallower depth zones), surprisingly the Species per Unit Effort (SPUE; number of species per observation/collection day) was remarkably consistent. In Fig. 40.10, the proportional distri-

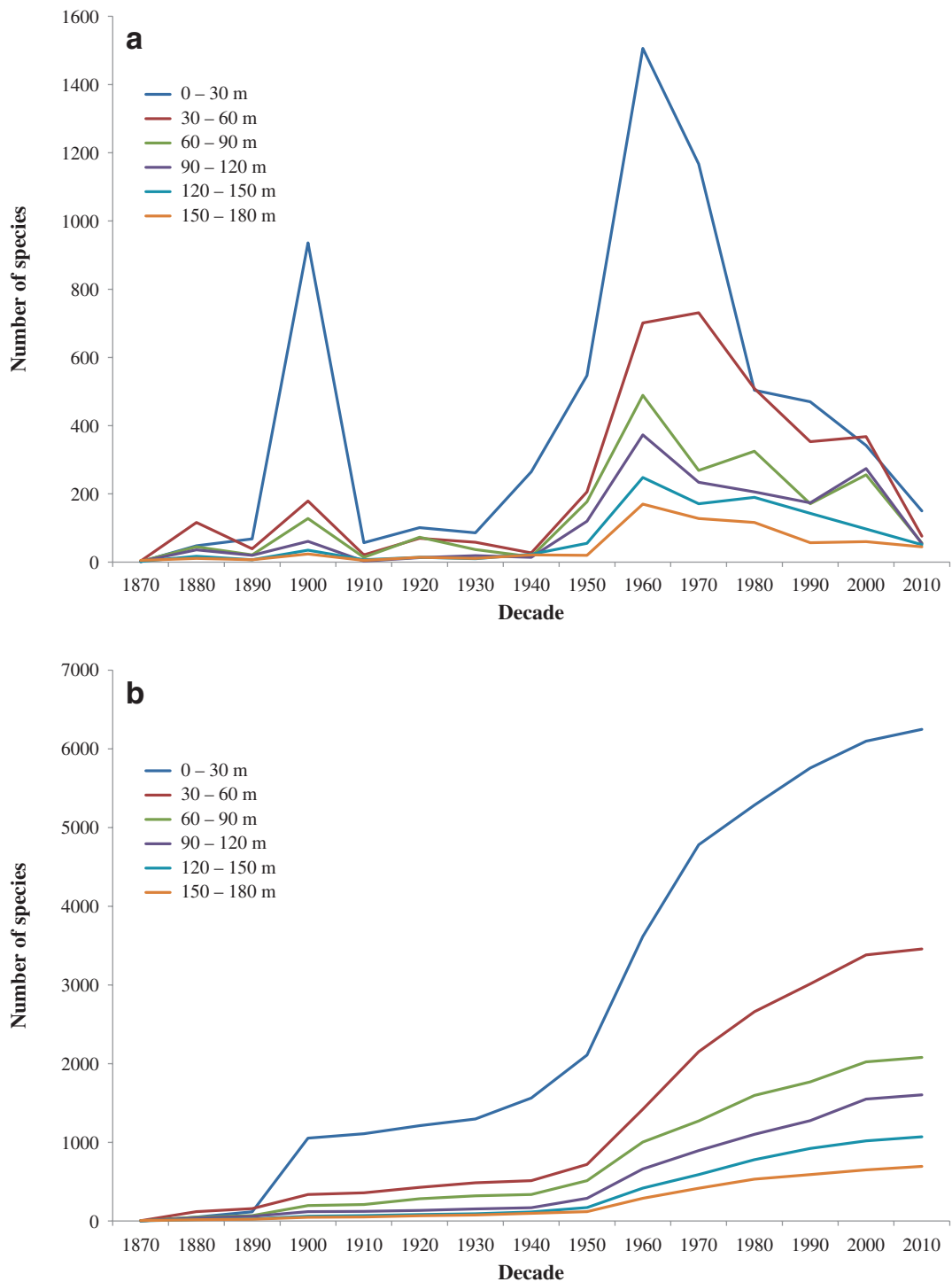


Fig. 40.9 Number of species recorded for the first time (a) and cumulative number of species (b) recorded within 30-m-depth zones from the 1870s to the 2010s. (Data from GBIF 2017; Explorer's Log 2017)

tribution of effort across depth zones was largely consistent for both databases, except that the GBIF database included an unusually large sampling effort in the shallowest depth zone (0–10 m) and the Explorer's Log database in depths less than 20 m. Also, the sampling effort in the Explorer's Log data-

base drops abruptly at depths below 180 m (with only 2–4 sampling days for each zone, so were not included in the graph). The only other discrepancy is a disproportionately low sampling effort in the 40–50 m depth zone in the Explorer's Log database. The most likely explanation for this

Table 40.5 A summary of approximate sampling effort as represented by number of days sampled and as the percentage of total sampling effort, as well as the total number of species and the calculated number of species per sampling day (SPUE or Species per Unit Effort)

Depth zone (m)	GBIF				Explorer's log			
	Days	%	Species	SPUE	Days	%	Species	SPUE
0–10	12,537	30.7%	5607	0.45	852	32.5%	1126	1.32
10–20	5806	14.2%	4647	0.80	718	27.4%	1115	1.55
20–30	4177	10.2%	3912	0.94	295	11.2%	547	1.85
30–40	2949	7.2%	2983	1.01	175	6.7%	352	2.01
40–50	2330	5.7%	2223	0.95	88	3.4%	228	2.59
50–60	2023	5.0%	1950	0.96	107	4.1%	242	2.26
60–70	1748	4.3%	1668	0.95	100	3.8%	264	2.64
70–80	1372	3.4%	1358	0.99	74	2.8%	189	2.55
80–90	984	2.4%	1124	1.14	78	3.0%	177	2.27
90–100	1126	2.8%	1263	1.12	54	2.1%	165	3.06
100–110	864	2.1%	884	1.02	35	1.3%	101	2.89
110–120	626	1.5%	765	1.22	14	0.53%	40	2.86
120–130	645	1.58%	753	1.17	10	0.38%	26	2.60
130–140	546	1.34%	525	0.96	4	0.15%	15	3.75
140–150	604	1.6%	621	1.03	3	0.11%	10	3.33
150–160	486	1.2%	398	0.82	3	0.11%	8	2.67
160–170	506	1.2%	412	0.81	4	0.15%	10	2.50
170–180	516	1.3%	428	0.83	4	0.15%	7	1.75
180–190	527	1.3%	496	0.94	3	0.11%	18	6.00
190–200	475	1.2%	533	1.12	2	0.08%	5	2.50

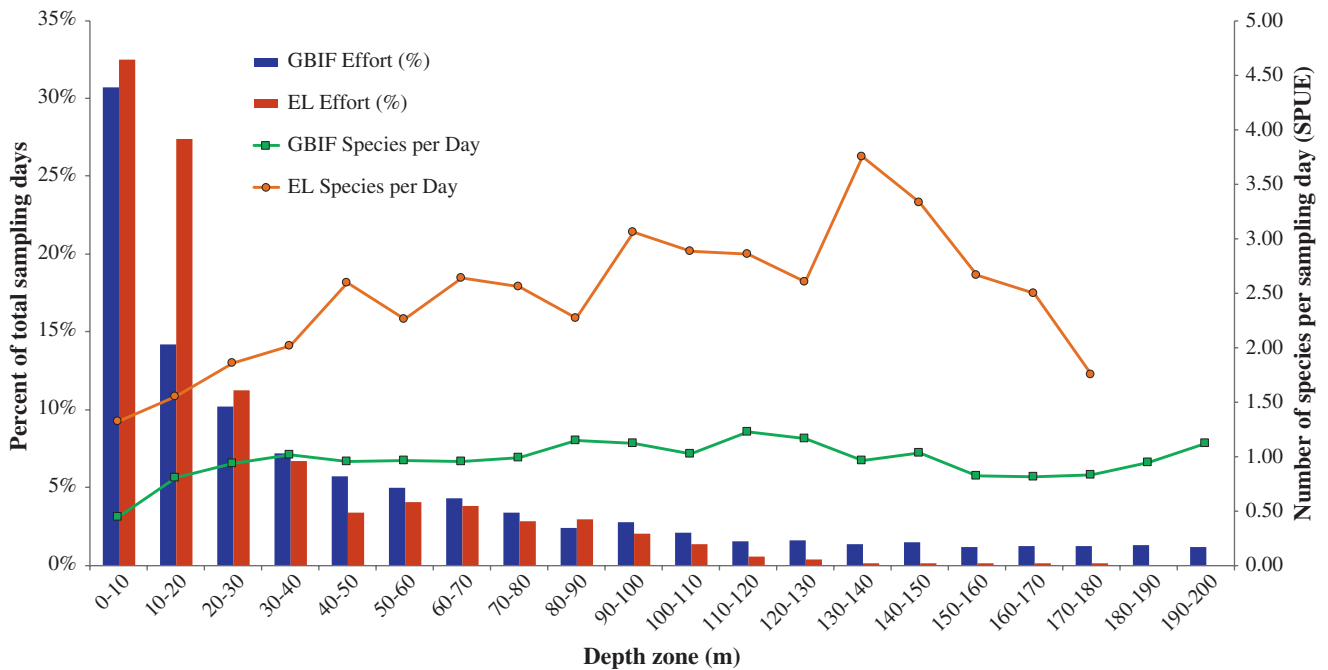


Fig. 40.10 Distribution of sampling effort across 10-m depth zones for both the GBIF and Explorer's Log databases. Bars represent percent of total sampling days within each depth zone, and lines represent the "Species per Unit Effort" (SPUE), defined as the total number of species divided by the total number of sampling days within each depth zone

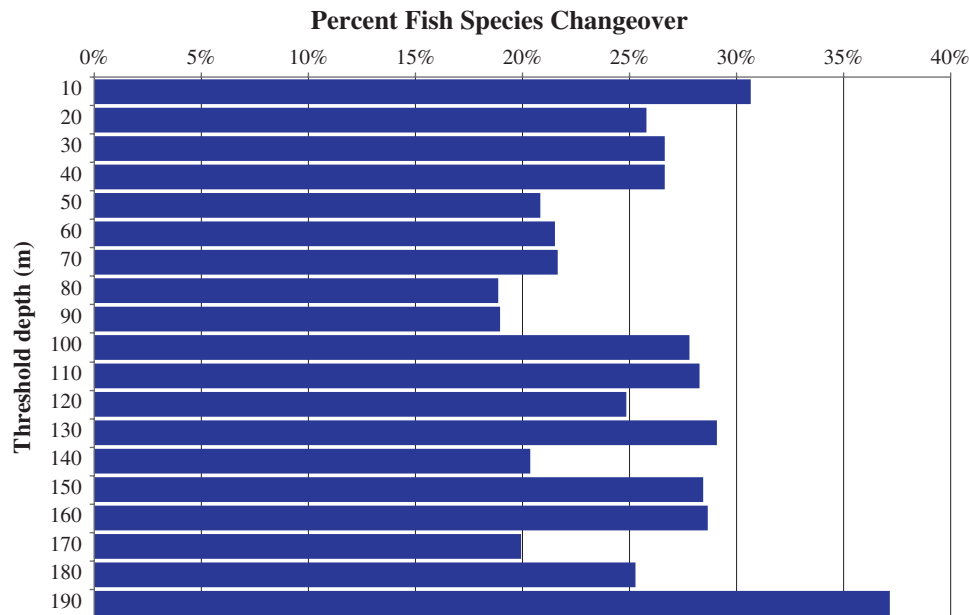


Fig. 40.11 Species composition turnover across different depth threshold values. Bars represent the combined number of species with a maximum depth within 10 m above the threshold depth and species with a minimum depth within 10 m below the threshold depth, expressed as a percentage of the total number of species within ± 10 m of the threshold depth. (Data from GBIF 2017; Explorer’s Log 2017)

pattern is that Explorer’s Log data are derived mostly from diving activities and that depth zone is shallower than most targeted dives but deeper than where divers spend meaningful time for decompression purposes (or conducting shallow dives). As a consequence, this depth zone represents the least amount of time spent during most dives (shallow or deep) and therefore has disproportionately fewer occurrence records.

The SPUE values for the GBIF database were surprisingly consistent (~ 1 species per sampling day, $\pm \sim 0.2$) across all but the shallowest of depth zones (0.45 species per sampling day). The discrepancy for the shallowest depth zone may suggest that the total number of species is approaching “saturation,” such that additional sampling days fail to yield additional species. The remarkable consistency of total SPUE (sampling days) across all but the shallowest of depth zones might suggest that total species diversity is more or less consistent across depths, which is not consistent with other studies that have measured species richness across depth gradients more directly (e.g., Pyle et al. 2016a; Pyle 2019b). There are several reasons why the data presented here may not reliably represent actual species richness across depths. Total days of sampling is a very crude measure of sampling effort, due to the fact that a single day spent collecting in shallow water may yield far more specimens and species than a single day in deeper environments (Pyle 2019a). While this bias may suggest that proportional species richness in deep habitats may actually be higher, a contrary bias is that deep-targeted sampling may be more intensely focused on documenting new records and new spe-

cies compared to more routine shallow reef sampling. Results should be interpreted as provisional until substantiated with more precisely directed research.

Although sampling biases in these databases do not lend themselves to more robust methods of β -diversity analyses (e.g., Koleff et al. 2003; Brokovich et al. 2008), a very rough estimation of species turnover can be made following the technique described in Pyle et al. (2016a: supplementary material).⁴ Results of this analysis (Fig. 40.11) are similar to those presented in Pyle et al. (2016a) for Hawai’i fishes in that both show relatively high turnover in shallow depths (20–30 m in Hawai’i; 10–40 m in this dataset) and relatively low turnover at greater depths of 40–60 m in Hawai’i and 50–90 m in this dataset. The main difference is that this dataset shows a proportionally larger overall turnover at the shallowest and deepest depth intervals. Although this is only a very crude measure of β diversity (in addition to the stated limitations of

⁴At each 10-m threshold depth interval, the number of species with a reported maximum depth within 10 m above the threshold depth were added to the number of species with a reported minimum depth within 10 m below the threshold depth (representing the total number of species participating in a turnover within ± 10 m of the threshold depth), and the summed value was divided by the total number of species that occur within ± 10 m of the threshold depth, to yield a percentage of species that participate in a turnover at each depth zone. Larger values indicate a more substantial break; smaller values indicate a less substantial break. Percentage of total species within a depth zone was used instead of absolute numbers of species to avoid artificially biasing the amount of change due to differences in α diversity at different depths.

the datasets), these results may suggest that the general faunal break at around 60 m is unwarranted for fishes.

40.5 Future Directions

Some of the earliest studies to specifically examine MCEs (Brock and Chamberlain 1968; Strasburg et al. 1968) included fishes among their priorities and results. Over 400 studies involving MCE fishes have been published since 1968 (Fig. 40.12). The general pattern of publications for fishes mirrors that of MCEs in general. Three quarters of all studies on MCE fishes during the past 50 years have been published within the past 6 years and are consistent with the pattern of publications for MCEs as a whole (Turner et al. 2017).

While this is certainly a promising trend, as is the case for all aspects of MCE research, the extent of what we do not know vastly exceeds that which we have learned. A search for “coral reef fish” on Google Scholar returns more than 300,000 publications (as of 2017). Within the 6-year period from 2012 to 2017 alone, the number of publications focused on MCE fishes was only 0.5% ($n = 300$) of the total

($n = 60,760$). The disparity between how much research is focused on MCE fishes compared to shallow reef fishes is dramatic when considering that MCEs represent 80% of the overall depth range of coral reef habitat (Pyle and Copus 2019).

Even if the trend for increasing research focused on fishes within MCEs (and MCEs in general) continues, it will still fall far short of what is needed to properly document the diversity of MCE fishes, especially given the threats coral reef habitats face in the decades to come. Therefore, priorities for future research must be sharpened. Based on the general patterns presented herein, we have identified two main priorities for MCE fish research: discovering and documenting the extent of fish diversity on MCEs and transitioning from qualitative to more quantitative hypothesis-driven research.

40.5.1 Discover and Document the Extent of Fish Diversity on MCEs

The most important task for future research involves a much more coordinated and concentrated effort to discover and document the true extent of MCE fish diversity. Discovering

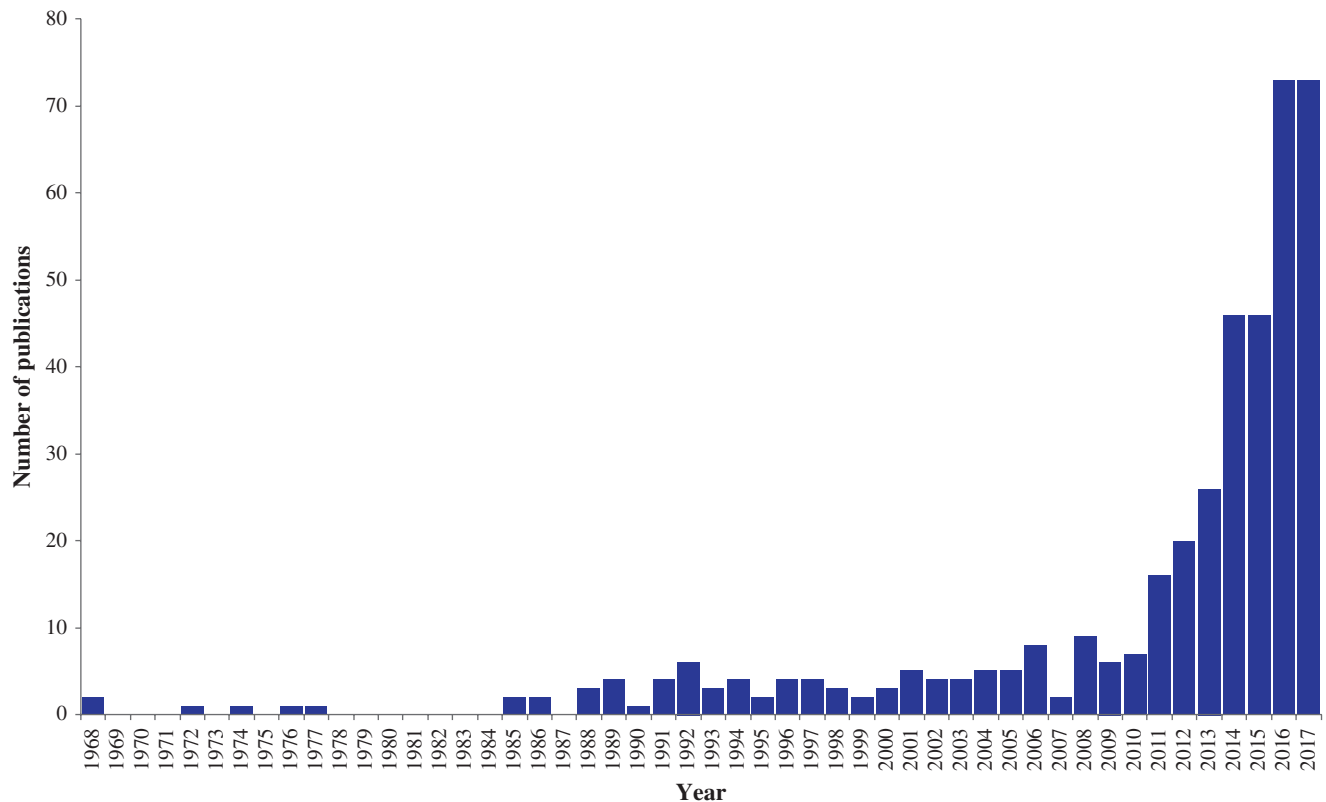


Fig. 40.12 Total number of publications involving MCE fishes by year (R.L. Pyle, unpubl. data)

new species is an obvious component of this but only a first step. It is equally important to reliably document (i.e., via collected specimens or photo/video documentation) the presence of known species at different depths in MCEs worldwide. This effort should prioritize the gathering of quantitative transect data, as well as more thorough collection efforts that allow for the documentation of cryptic species (e.g., rotenone stations). Given the overall disparity between where MCE research on fishes has been focused geographically (Fig. 40.3) and where the bulk of MCE fish biodiversity resides (i.e., the understudied Indo-West Pacific region), research priorities should focus more intensively on reconciling that disparity. Specifically, this means more focused effort on exploring, sampling, and otherwise documenting MCE biodiversity throughout much of the tropical insular Pacific, many parts of the Indo-Australian Archipelago, and the entire Indian Ocean, which will require an increase in implementation of available technologies and a collaborative environment of data and sample sharing within the MCE research community.

- *Identify candidate MCE habitats.* Perhaps the most important step in documenting MCEs is to better understand where they are. To establish priorities for targeted research, one of the most important steps that can be achieved is better bathymetric mapping from multi-beam sonar technologies. Based on this bathymetry data, preliminary habitat assessments can be achieved fairly easily with drop cameras and towed camera systems.
- *Use a variety of technologies.* All available exploration technologies should be involved with this effort, including submersibles, ROVs, AUVs, BRUVS, non-baited, time-lapse or interval videos, technical divers, and other remote imaging or sampling methods. Each of these technologies comes with its own strengths, weaknesses, and biases, but collectively they will allow better characterization of MCE habitats than any one technology. In particular, projects should integrate and coordinate different technologies to more effectively maximize research efforts. Several projects (e.g., Pyle 2019a; Pyle et al. 2016a) have had great success with coordinating submersibles and technical divers, leveraging the complementary strengths of each method. Similarly, ROV and AUV technologies could be used as a very effective tool for surveying and mapping large MCE areas and in identifying specific target sites where technical divers can focus on collecting and quantitatively assessing fish species, which divers can do in far greater detail and with better efficiency than other technologies. Studies involving BRUVS could benefit from using ROVs or technical divers to “ground truth” the species present,

which would allow for more accurate taxonomic identifications. These are just a few examples of how different technologies can be used together in ways that allow for more effective and efficient MCE exploration.

- *Improve the sharing of information and samples.* In addition to better coordination of technologies during field research, the ichthyological research community would greatly benefit from improved sharing of data. The more than 800,000 species occurrence records downloaded from GBIF and analyzed herein are valuable for understanding large-scale patterns of MCE fish biodiversity but are extremely limited. Not only do they suffer from sampling bias, they are also heavily skewed toward collected specimens preserved in museums. GBIF accepts image-based and observation-based occurrence records, as well as specimen records, so databases that specialize in documenting non-vouchered occurrence records (such as Explorer’s Log) should regularly contribute updated content to GBIF. Even individual research projects should ensure that their observational and image-based data (which can be easily represented as species occurrence records) end up being published to GBIF (certain journals, such as the *Biodiversity Data Journal* and *ZooKeys* already perform this service on behalf of authors). This kind of sharing is not limited to data. Specimens and their associated tissue samples (and resulting DNA sequences) should be more broadly shared, and researchers should more effectively coordinate to capitalize on existing projects in specific geographic regions. Certainly, individual researchers will wish to publish their results first before exposing raw data, but after primary studies have been published, it is extremely important to ensure raw data and collected samples are shared and archived in such a way that they can be used for larger-scale studies.

40.5.2 Transition from Qualitative to More Quantitative, Hypothesis-Driven Research

The second main priority for MCE fish research involves more focused, hypothesis-driven research. While much still needs to be accomplished in terms of basic exploration and documentation, our broader understanding of MCE fishes has matured to the point where more in-depth research is warranted. An excellent example of this is Tornabene et al. (2016a), who investigated evolutionary depth transitions in the family Gobiidae to infer the timing of shallow-to-deep habitat transitions. They reported at least four transitions across depth believed to have occurred in two broad time

periods (Miocene and Pliocene-Pleistocene). They also found at least three evolutionary lineages that invaded deep habitats and subsequently speciated. Another excellent example is the work being done by the National Oceanic and Atmospheric Administration (NOAA) funded researchers in the Northwestern Hawaiian Islands (e.g., Kane et al. 2014; Fukunaga et al. 2016, 2017). Thanks to consistent methods of conducting quantitative surveys of MCE fishes on an annual basis, in the context of a robust dataset available from similar studies on shallow reefs and extensive high-resolution bathymetric data, they are able to start examining more precise patterns of tropic partitioning, biogeography, and endemism across a substantial geographic region and also monitor changes over time as both natural cycles and responses to long-term environmental trends (such as ocean warming and acidification).

These more in-depth, hypothesis-driven research projects should be conducted in geographic regions with optimal logistical support. Most of the basic biological processes they investigate can be extrapolated to other MCEs in more remote and difficult to access regions.

The gap between what has been done and what needs to be done in terms of understanding the diversity of fishes on MCEs is large, and filling that gap requires more effective coordination of research plans and result sharing. A key component to successful MCE documentation involves the need for more funding. As the global awareness of the existence and importance of MCEs increases through high-profile publications (e.g., Baker et al. 2016; Weiss 2017), funding for MCE research should increase. Also, as more institutions support MCE research, the trend toward both more funding and more diversified research projects should continue to improve.

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