CORAL REEFS

Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs

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The rapid degradation of coral reefs is one of the most serious biodiversity problems facing our generation. Mesophotic coral reefs (at depths of 30 to 150 meters) have been widely hypothesized to provide refuge from natural and anthropogenic impacts, a promise for the survival of shallow reefs. The potential role of mesophotic reefs as universal refuges is often highlighted in reef conservation research. This hypothesis rests on two assumptions: (i) that there is considerable overlap in species composition and connectivity between shallow and deep populations and (ii) that deep reefs are less susceptible to anthropogenic and natural impacts than their shallower counterparts. Here we present evidence contradicting these assumptions and argue that mesophotic reefs are distinct, impacted, and in as much need of protection as shallow coral reefs.

Coral reefs are perhaps the most threatened ecosystem on the planet, and because of their narrow optimum temperature range, they are suffering catastrophic damage caused by climate change (*1*). Because many species occur across a wide depth range, the deeper portions of coral reefs have generally been considered potential refuges for shallow organisms (*2*, *3*). As these reefs are difficult to survey, species overlap between shallow and mesophotic zones has been traditionally determined by analyzing reported depth ranges alone. This method consistently yields results that show low species turnover and high overlap between depth zones for shallow reef fishes and corals (69.9 and 77% overlap, respectively, between shallow and upper mesophotic zones in the Caribbean) (*4*, *5*), therefore lending support to the refuge hypothesis.

However, because depth ranges are based on historical records across tens to hundreds of years, they include outliers and are misleading in evaluating true community overlap. Through technical diving down to depths of 150 m, we reevaluated the potential refuge role of mesophotic ecosystems by analyzing in situ observations. Our underwater visual censuses of reef fish communities in the Pacific and the western Atlantic show high dissimilarity between shallow and mesophotic depth strata (Fig. 1) and indicate that the main driver of assemblage composition change across the depth gradient is species turnover (Fig. 2). We obtained an almost identical result in our analysis of coral diversity in relation to depth. This pattern contrasts with analyses of species overlap on the basis of depth ranges alone, which show that change in diversity across depths results mostly from a decrease in species richness (i.e., nestedness), with much higher species overlap among depths (Fig. 2). Even though we observed 27% of the shallow reef fish assemblage reaching the mesophotic zone, the majority of these species are not true depth generalists, being much more abundant in one depth strata or the other (fig. S1).

Furthermore, current exploration of Pacific and Caribbean mesophotic habitats by using closed-circuit rebreathers and submersibles still yields high rates of new species discovery (*6*–*8*), showing that many species restricted to mesophotic depths are still being revealed. Reef fish community assessments have shown that the majority of organisms reported between 30 and 150 m are restricted to those depths (*8*–*12*), a sign of strong depth specificity (*4*, *8*). Additionally, even some of the few true depth-generalist species can have their populations genetically disconnected between deep and shallow zones (*13*, *14*).

Therefore, most species display a strong preference for a specific depth zone, indicating that deep reefs do not constitute a refuge for the vast majority of shallow reef–associated organisms. Because the depth ranges of top predators (sharks, jacks, groupers, and snappers) may span shallow and deep habitats, they are often assumed to find refuge from fishers at lower depths (*15*). However, acoustic telemetry and dietary analyses show that they move across shallow and mesophotic depth zones daily and that more than half of their food is captured in shallow habitats (*16*). Thus, these predators are potentially captured even in places where mesophotic depths are sheltered from fishing.

The second assumption of the refuge hypothesis is that mesophotic coral ecosystems are less susceptible to human and natural impacts than shallow coral reefs. However, we documented both types of disturbance reaching deep reefs. For example, hurricanes and tropical storms cause extensive physical damage to shallow coral reefs, and their impacts have critical ecological consequences (*17*, *18*). Because large surface waves cause most of the damage to shallow reefs, deep reefs were believed to be less affected by hurricanes (*19*). We observed the effects of Hurricane Matthew (22 September to 9 October 2016) over the entire coral reef system (down to a depth of 135 m) just 4 days after Matthew's passage over the Bahamas. Coral reefs situated 40 miles outside of the hurricane path, both at shallow and mesophotic depths, exhibited no signs of physical destruction and sedimentation (Fig. 3B). However, within the hurricane path, upper mesophotic coral reefs were completely buried by sediment under a thick layer of suspended solids. A cloud of particulate matter and biogenic debris was observed in the water column of many sites (Fig. 3C). Lower mesophotic zones to depths of 135 m were also covered by sediment, and strong physical damage was evident, probably caused by an avalanche of coral and other debris cascading down the reef wall (Fig. 3D). Similar observations of cyclone-associated damage at mesophotic reefs have been reported for the Great Barrier Reef (*20*).

We also detected signs of heavy fishing, sedimentation, coral bleaching, and invasive species at mesophotic depths in the Pacific and Caribbean (Fig. 3, E to H). For example, plastic trash and fishing debris were observed in similarly high frequencies at shallow and mesophotic depths in the Philippines (table S7). The only deep reefs that consistently show little to no signs of human impacts are those distant from human population centers (Fig. 3, A and B) (*11*), and the same can be said for shallow coral reefs (*21*). Mesophotic ecosystems close to densely populated islands with a narrow shelf are particularly vulnerable to those impacts. Thus, the real refuges seem to be located in regions far from humans, regardless of depth. However, not even these can escape the impacts of climate change (*1*). Additionally, because of constant population expansion and increased demand for food and natural resources, fishing and mining impacts are beginning to reach even the most distant and isolated deep and shallow coral reefs alike (*22*, *23*).

These observations suggest that the potential for deep reefs to act in a refuge capacity is far less than we have previously hoped, as mesophotic ecosystems are home to largely distinct and independent communities and may be affected by both human and natural disturbances as much as shallow reefs are. Moreover, unlike their shallow counterparts, deep reefs are rarely the focus of conservation efforts because of the widespread belief that they are out of human reach and because they are largely unsurveyed (*5*). Many of these reefs may have already been degraded and/or eliminated by destructive fishing, mining, and sedimentation, and many species and potential natural resources may disappear before we have the chance to discover and study them. Because of the generally slower growth of reef-building

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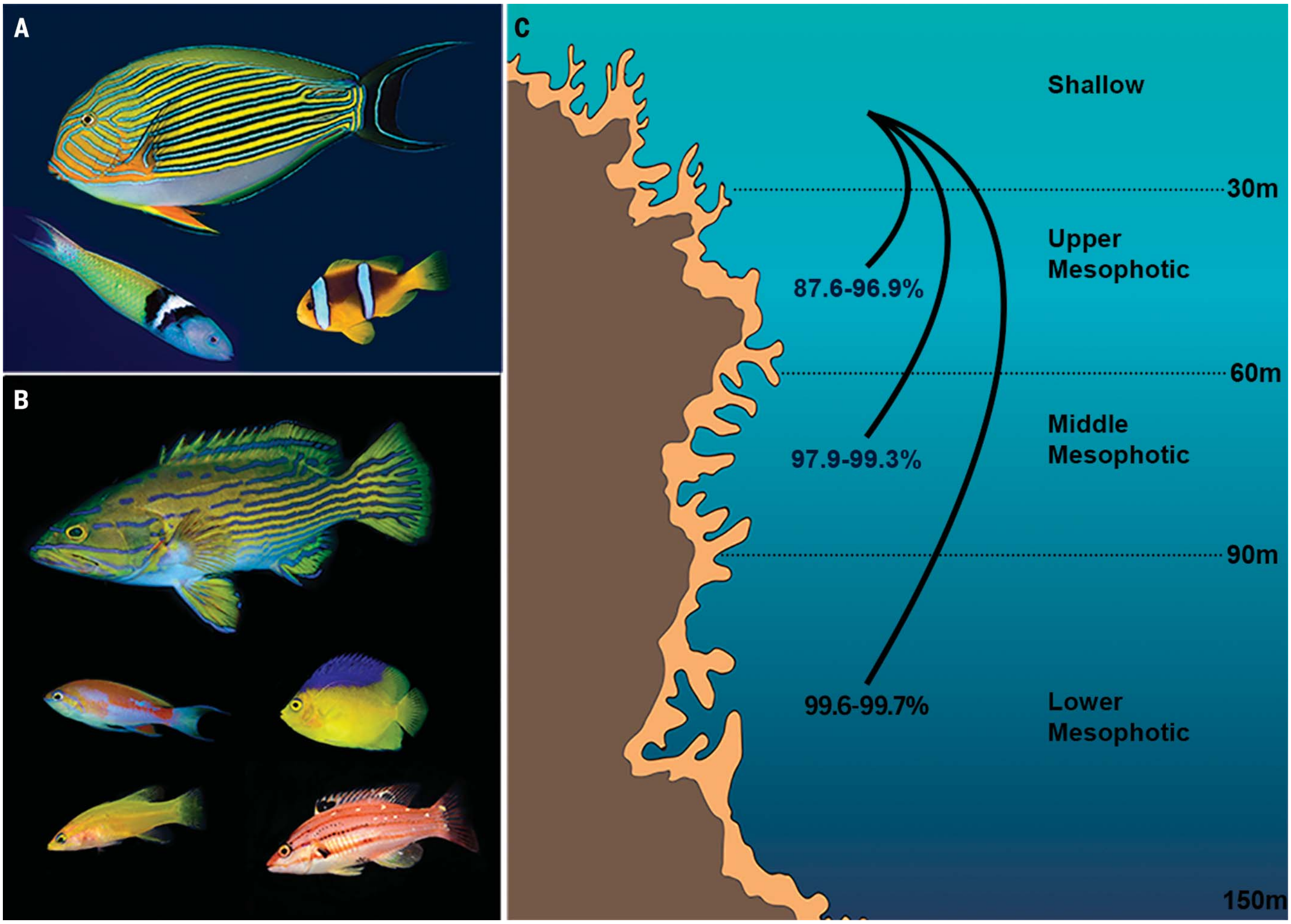

Fig. 1. Depth distribution of diversity in coral ecosystems. (**A**) Typical shallow coral reef fishes *Acanthurus lineatus*, *Thalassoma bifasciatum*, and *Amphiprion clarkii*. (**B**) Typical mesophotic fishes *Cephalopholis polleni*, *Pseudanthias hutomoi*, *Liopropoma latifasciatum*, *Centropyge colini*, and *Bodianus leucosticticus*. Species in (A) and (B) are listed from left to right for each row. (**C**) Bray-Curtis dissimilarity between shallow reef fish communities and mesophotic depth zones.

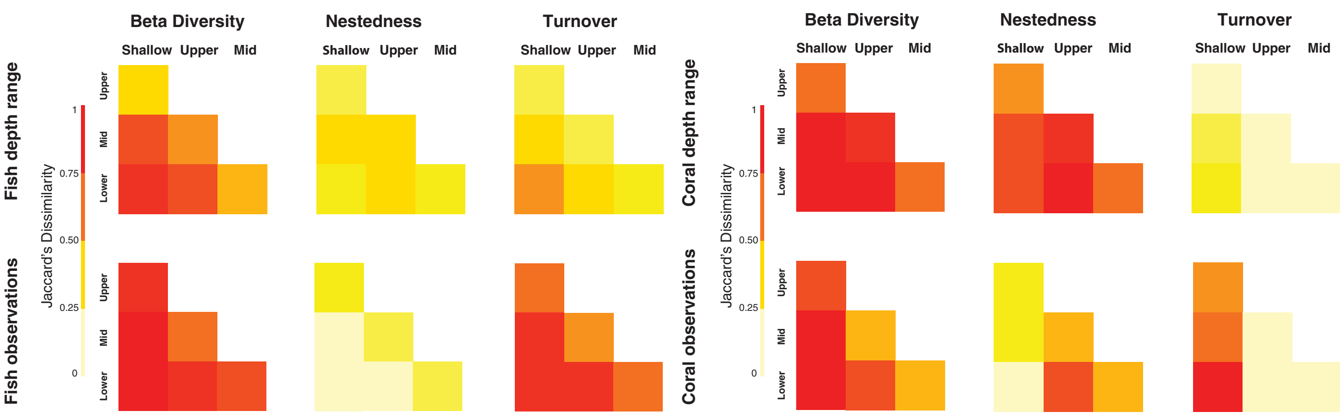

Fig. 2. Diversity analyses of fish and coral communities across depth strata. Changes in beta diversity and its two components (nestedness and turnover) are shown for fish and coral depth ranges and observations. Nestedness is the main cause of beta diversity change in depth range datasets, indicating high species overlap. Conversely, turnover is the main driver in in situ datasets, indicating low species overlap due to species replacement.

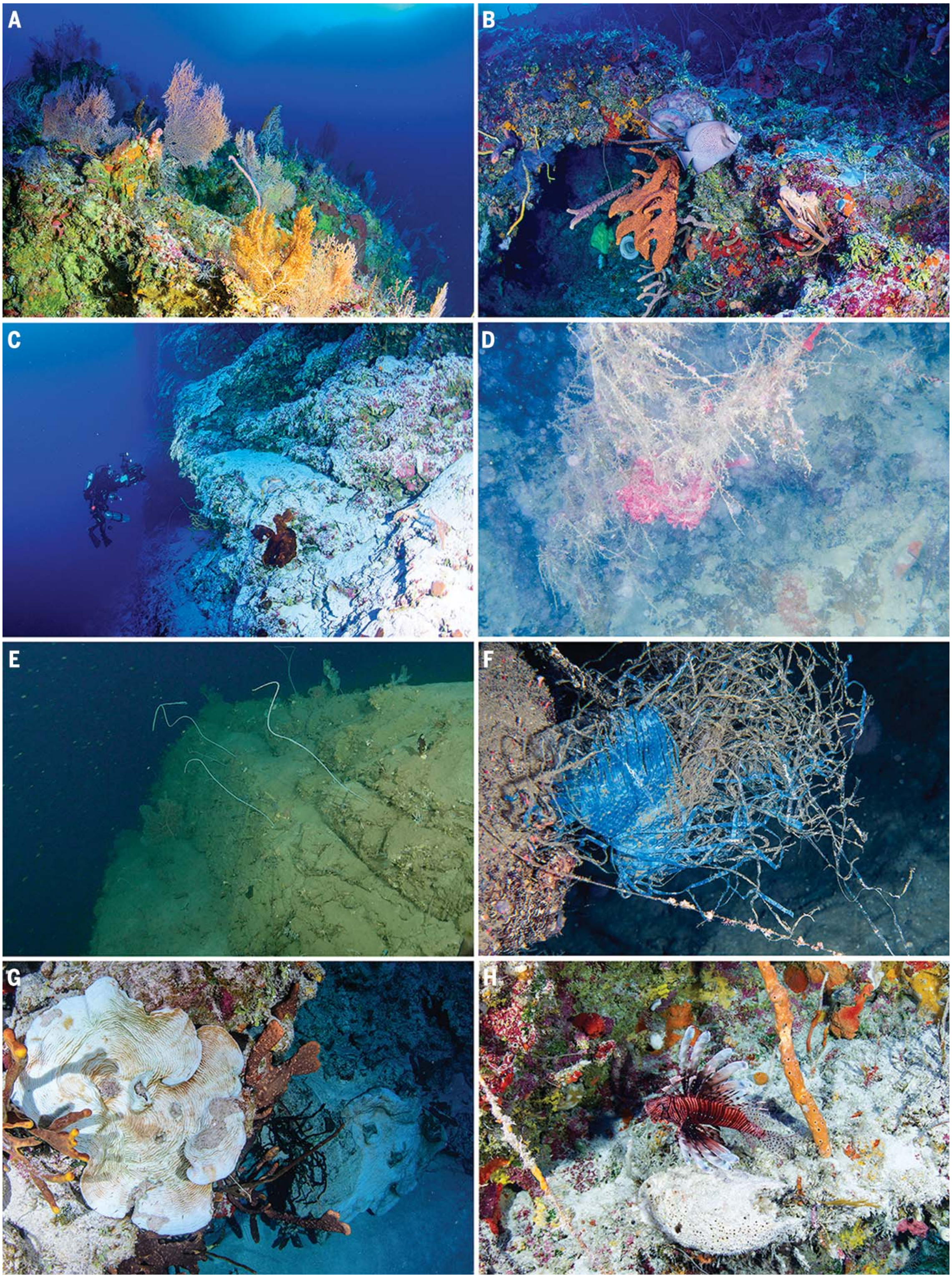

Fig. 3. Mesophotic coral ecosystems across the world. (**A**) Ecosystem in good condition at 110-m depth at Ant Atoll, Pohnpei, Micronesia. (**B**) Ecosystem in good condition at 80-m depth at Cay Sal, Bahamas. (**C**) Slope at 120-m depth covered with sand deposited by Hurricane Matthew in Cat Cay, Bahamas. (**D**) Suspended sediment stirred by Hurricane Matthew at 75-m depth in Egg Cay, Bahamas. (**E**) Terrigenous sediment covering a mesophotic slope at 130-m depth in Anilao, Philippines. (**F**) Fishing lines and plastic pollution at 150-m depth in Bauan, Philippines. (**G**) Bleached *Agaricia lamarcki* at 85-m depth in Rum Cay, Bahamas. (**H**) Invasive lionfish (*Pterois volitans*) at 115-m depth in Grand Cayman.

invertebrates at depth (*24*), recovery of these regions may depend on long-term management of disturbed areas. Thus, measures to protect deeper ecosystems should be prioritized in environmental policy for global marine conservation. Shallow coral reef conservation efforts should not rely on mesophotic ecosystems as a refuge.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6399/281/suppl/DC1
Materials and Methods
Fig. S1
Tables S1 to S7
References (*25*–*31*)

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Deep coral reefs are different

Coral reefs are under intense pressure from anthropogenically induced climate warming and habitat destruction. It has been suggested that coral reefs in deeper waters may provide a refuge less affected by human development and climate change. Rocha *et al.*, however, show that shallow and deep reefs are biologically different. Furthermore, deep (or mesophotic) reefs are also suffering from human impacts. Thus, deep reefs do not represent a potential refuge for other reef ecosystems. Indeed, they too are threatened and need protection.

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