



Pulley Ridge, Gulf of Mexico, USA

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Abstract

Pulley Ridge is a limestone ridge that extends nearly 300 km along the southwestern Florida shelf in the eastern Gulf of Mexico. The southern terminus of Pulley Ridge supports a mesophotic coral ecosystem (MCE) at depths of 59–105 m and is the deepest known photosynthetic coral reef off the continental United States. The biodiversity consists of 95 species of macroalgae, 92 demosponges, 18 octocorals, 17 scleractinian corals, 9 antipatharian corals, and 86 fishes. Twenty managed fishery species occur at Pulley Ridge including red grouper, and since 2010 the lionfish population has dramatically increased. The dominant scleractinian corals are plate like corals of the family Agariciidae (*Agaricia* spp. and *Helioseris cucullata*), *Montastraea cavernosa*, *Madracis* spp., and *Oculina diffusa*. The percent cover of benthic biota averaged 49.9% over all regions of Pulley Ridge, and macroalgae were dominant (46.5% cover). Scleractinian corals averaged 1.5% cover and

sponges had 1.2% cover. In the past 10 years, the Pulley Ridge MCE had a substantial loss of scleractinian coral. The percent coral cover on the Main Ridge dropped from 12.8% in 2003 to 0.9% by 2012–2015, a 93% loss of coral. However, recent surveys show the majority of corals to be relatively healthy; only 1.21% of the colonies counted (38,368) showed signs consistent with “white syndromes” disease. The prevalence of disease on Pulley Ridge is relatively low compared to the Caribbean. The factors causing the decline of the coral communities at Pulley Ridge between 2003 and 2012 are unknown.

Keywords

Mesophotic coral ecosystems · Pulley Ridge · Coral · Lionfish · Red grouper

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4.1 Introduction

Pulley Ridge is the deepest known photosynthetic coral reef off the continental United States (Halley et al. 2003; Cross et al. 2005; Jarrett et al. 2005; Hine et al. 2008). It is a limestone ridge that extends for nearly 300 km along the west Florida shelf in the eastern Gulf of Mexico and lies about 250 km west of mainland Florida and 50 km from the nearest shallow reefs at the Dry Tortugas in the Florida Keys (Fig. 4.1). Only the southern terminus of this geological feature supports a mesophotic coral ecosystem (MCE) of photosynthetic hard corals, macroalgae, sponges, and reef fishes (Hine et al. 2008; Reed 2016; Harter et al. 2017). The Pulley Ridge MCE ranges in depth from 59 to 105 m and covers an area of approximately 1011 km². Of this, 345 km² was designated in 2005 by the National Oceanic and Atmospheric Administration (NOAA) and the Gulf of Mexico Fishery Management Council as a Habitat Area of Particular Concern (HAPC) under the Magnuson-Stevens Fishery Conservation

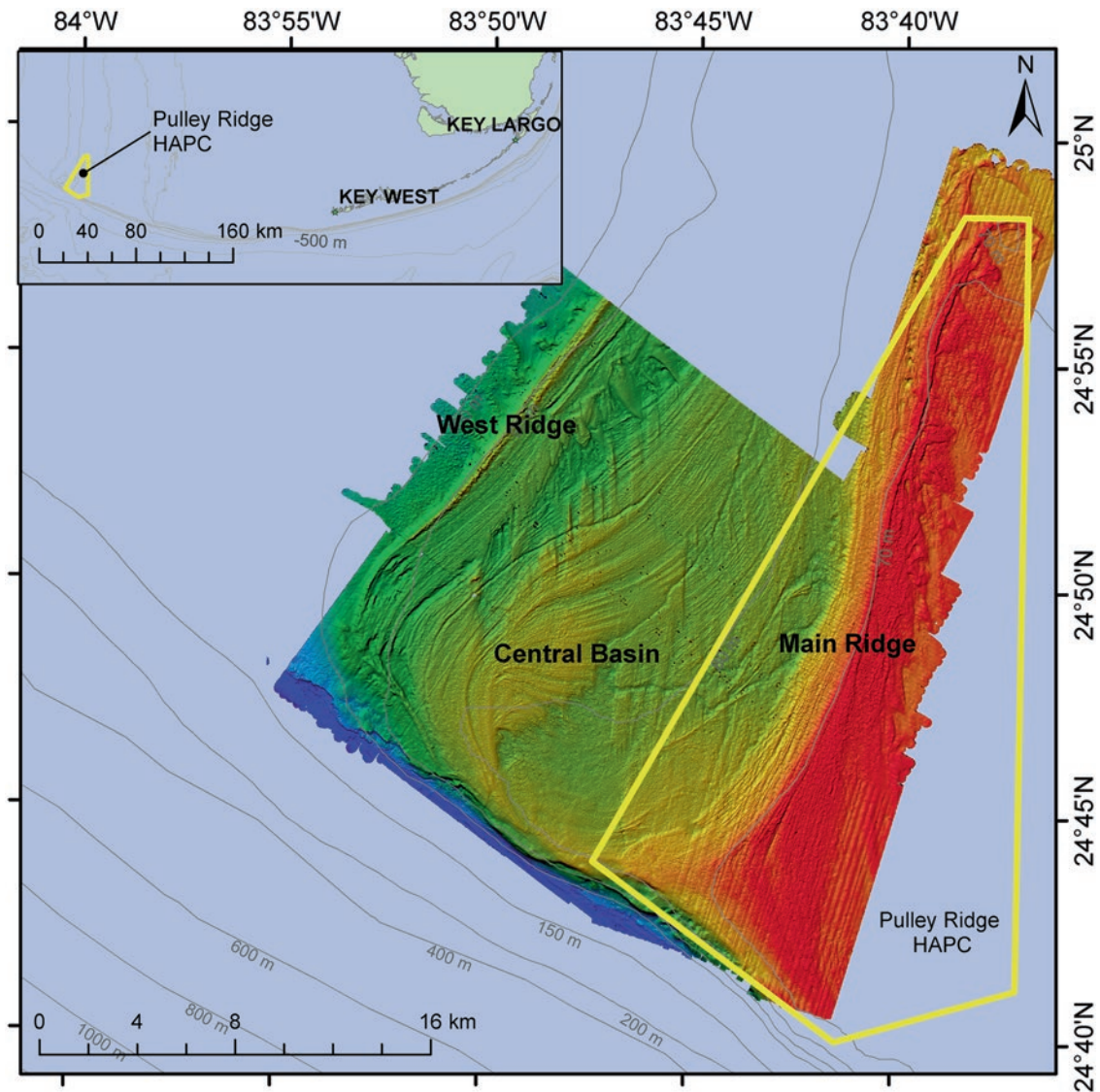


Fig. 4.1 Multibeam sonar map of the Pulley Ridge MCE off the southwest coast of Florida. Habitat regions include Main Ridge within the original Pulley Ridge Habitat Area of Particular Concern (yellow polygon), Central Basin, and West Ridge. (Multibeam: Naar 1999; NOAA 2003; Cross et al. 2005)

and Management Act to protect the coral habitat from damage by fishing operations. In 2018, the HAPC was expanded by 666 km² to encompass the entire MCE.

4.1.1 Research History

Although evidence is anecdotal, fishermen probably fished the region of Pulley Ridge going back to the late 1800s. The ridge was named after the eminent malacologist, Thomas Pulley (1914–1985), after dredge surveys conducted there in the 1950s (Taylor 2006). In the 1960s, the Hourglass cruises explored the west Florida shelf including regions of northern Pulley Ridge (Lyons and Collard 1974). During the 1980s,

the Department of Interior’s Minerals Management Service conducted surveys of the continental margin over much of the US Gulf of Mexico for future oil and gas leasing (Holt and Bartz 1983). Of these, the Southwest Florida Shelf Ecosystems Study led by Continental Shelf Associates, Inc. assessed 55 stations including 2 on southern Pulley Ridge, where they found hard bottom substrate covered with living biota including the hard corals *Agaricia* spp. and *Madracis decactis*, the green alga *Anadyomene menziesii*, and crustose red algae (Phillips et al. 1990).

Between 1999 and 2003, the Sustainable Seas Expedition led by the US Geological Survey, NOAA, and the Office of Naval Research provided the first detailed documentation of the Main Ridge region of southern Pulley Ridge using multi-

beam and side-scan sonar bathymetry (Naar 1999; NOAA 2003), 28 video transects with the *DeepWorker* submersible and a remotely operated vehicle (ROV), and 5 dredge samples (Halley et al. 2003; Cross et al. 2004, 2005; Jarrett et al. 2005; Hine et al. 2008; Jaap 2015). According to the US Geological Survey, the coral on Pulley Ridge was “considerably healthier than coral from shallow-water reefs nearly worldwide” (USGS 2005). Beginning in 2004, NOAA Fisheries conducted a series of cruises along Pulley Ridge to determine the abundance and distribution of fishes, with emphasis on economically important species.

In 2010, the Florida Shelf-Edge Expedition (FLoSEE) was conducted by the NOAA Cooperative Institute of Ocean Exploration, Research and Technology at Harbor Branch Oceanographic Institute, Florida Atlantic University (CIOERT HBOI-FAU), to survey deep reefs along the west Florida shelf that may be impacted by the Deepwater Horizon oil spill (Reed and Rogers 2011). Seven *Johnson-Sea-Link* submersible dives were conducted on Pulley Ridge; no evidence of oil was found on the reef. In 2011, the FLoSEE II cruise revisited Pulley Ridge. Eleven *Kraken* ROV dives and 4 high-resolution multibeam maps were made (Reed 2011), including the first surveys of the West Ridge (Fig. 4.1).

From 2012 to 2015, the NOAA National Centers for Coastal Ocean Science supported the most detailed surveys yet of Pulley Ridge. The project had three objectives: to understand population connectivity of key reef species between MCEs and shallow reefs, assess community structure at Pulley Ridge and the Dry Tortugas, and determine the value of the Pulley Ridge resource. ROV photo/video surveys, conducted by CIOERT HBOI-FAU and the University of Miami, characterized 68 1-km² random blocks within and adjacent to the HAPC (Figs. 4.1 and 4.2; Harter et al. 2017; Reed et al. 2017). These were the first dives to document quantitatively the drastic coral loss within the Pulley Ridge HAPC that occurred since the 2003 surveys. An oceanographic mooring at the HAPC provided information on currents, with an acoustic Doppler current profiler (ADCP), and conductivity, temperature, and depth (CTD), which were used for physical oceanographic modeling using an extended Florida Keys Hybrid Coordinate Ocean Model (HYCOM; sensu Kourafalou and Kang 2012; Kourafalou et al. 2018) and biophysical modeling of key species (Vaz et al. 2016; Sponaugle and Cowen 2019).

4.2 Environmental Setting

Pulley Ridge is a submerged former barrier island (Fig. 4.1) with multiple ridges and recurved spits that provide elevated topography and lithified substrate for sessile biota (Hine et al. 2008). The ridge formed during the early Holocene marine transgression approximately 12,000–

14,000 years ago was submerged by sea-level rise (Locker et al. 1996). The sea-level rise during the glacial melts was punctuated by episodes of slow rise or still stands, during which beach ridges and eolian dunes had sufficient time to become cemented in non-marine environments. Based on multibeam imagery, the hard bottom on Pulley Ridge is estimated to be no thicker than 1–2 m (Hine et al. 2008).

Pulley Ridge is regularly bathed by the Loop Current, the prevailing current in the Gulf of Mexico, which brings relatively clear, warm water to this area from the Caribbean Sea. Satellite sea surface temperature and chlorophyll *a* data confirm the influence of the Loop Current on Pulley Ridge (Jarrett et al. 2005). This current separates the clear, oligotrophic, outer-shelf waters from the higher nutrient, interior-shelf waters. Loop Current water transparency is comparable to that of the Sargasso Sea. Seafloor light measurements at southern Pulley Ridge (65–70 m) were only 1–2% (5–30 $\mu\text{E m}^{-2} \text{s}^{-1}$) of available surface light (photosynthetically active radiation), which is 5% of the light typically available to shallow-water reefs (Jarrett et al. 2005). Chlorophyll *a* values measured in 1999 at southern Pulley Ridge generally ranged between 0.1 and 0.2 mg m^{-3} and did not exceed 0.3 mg m^{-3} (Jarrett et al. 2005). The reef is near the continental shelf-edge break, which allows upwelling events to provide nutrient-rich waters to Pulley Ridge (Halley et al. 2003; Cross et al. 2005; Hine et al. 2008).

From 2012 to 2015, an ADCP and CTD were moored at the HAPC at a depth of 69 m by NOAA’s Atlantic Oceanographic and Meteorological Laboratory. During this period, hourly bottom temperatures ranged from 18.5 to 28.5 °C, with the maximum and minimum observations occurring within a period of less than 3 months of each other between August and November 2013. The maximum bottom current was 62 cm s^{-1} (1.2 knots) recorded in June 2013, flowing toward the southeast, and maximum surface current was 134 cm s^{-1} (2.6 knots). These strong currents occurred during a prolonged period in 2013 when the Loop Current was flowing very near or directly over top of the Pulley Ridge (Kourafalou et al. 2018). In August 2014 and 2015, a CTD attached to the ROV recorded bottom temperatures ranging from 18.5 to 22.5 °C at depths of 58–93 m, with salinity ranging from 36.2 to 36.5 PSU and oxygen from 4.90 to 5.22 ml L^{-1} (J.K. Reed, unpubl. data).

4.3 Habitat Description

Based on the geomorphology of the multibeam maps (Fig. 4.1), Pulley Ridge was divided into three regions: Main Ridge, Central Basin, and West Ridge for the 2012–2015

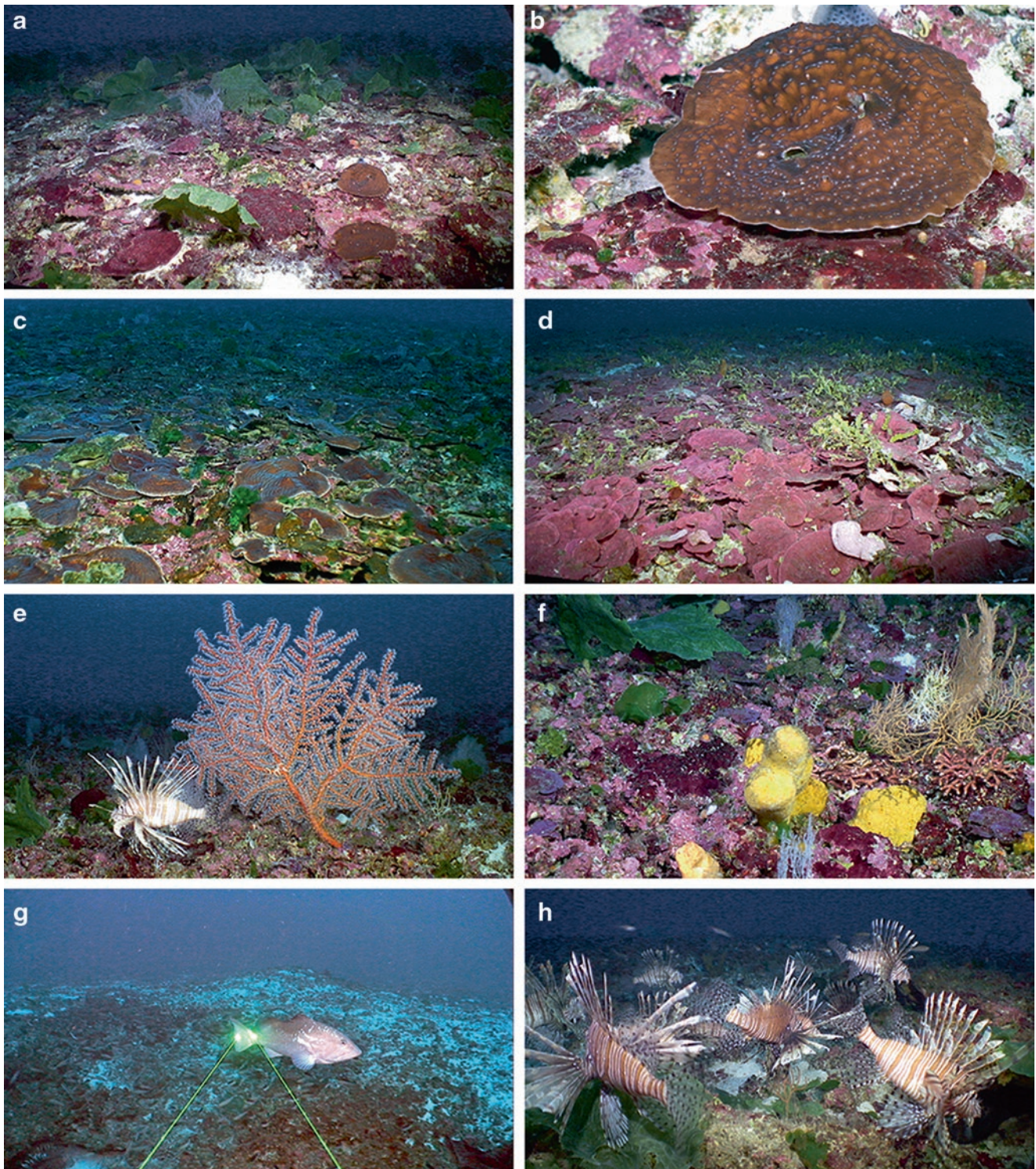


Fig. 4.2 Flora and Fauna of Pulley Ridge. (a) Main Ridge: green algae *Anadyomene menziesii*, crustose coralline red algae, and corals *Helioseris cucullata* and *Antipathes* sp., depth 74 m. (b) *H. cucullata*, close up of Fig. a. (c) Central Basin: field of *Agaricia* spp. coral, depth 80 m. (d) Central Basin: crustose coralline red algae and the green algae *Halimeda copiosa*, depth 80 m. (e) West Ridge: octocoral *Swiftia exserta* with lionfish, depth 79 m. (f) West Ridge: diverse biota of various demosponges, crustose coralline algae, octocorals, branching *Madracis brueggemanni*, and leafy green algae *A. menziesii*, depth 81 m. (g) Central Basin: red grouper by its pit (laser = 10 cm), depth 80 m. (h) West Ridge: school of lionfish in red grouper pit, depth 84 m. (Photos: NOAA Coral Ecosystem Connectivity Expeditions)

research cruises. The Main Ridge is the shallowest area ranging from 59 m on top of the ridge to 75 m at the base, the Central Basin is from 72 to 83 m in depth, and the West Ridge is the deepest at 76–105 m (Reed et al. 2017). All three regions of southern Pulley Ridge (Main Ridge, Central Basin, and West Ridge) are MCE habitat and generally consist of low rugosity, low relief (< 0.5 m), rock/coral pavement, and rubble substrate. However, red grouper (*Epinephelus morio*) pits are common throughout the region and provide habitat of relatively higher rugosity and moderate slope (10–30°). The grouper pits range from 8 to 15 m in diameter and 1–2 m deep

(Harter et al. 2017; Reed et al. 2017). These pits are one of the main contributors to habitat structure and fish diversity at Pulley Ridge. Red grouper modify their habitat by excavating sediment to expose rocky depressions (or pits) on the seafloor. These excavations increase the architectural complexity of the habitat, attracting many reef-associated species and providing shelter for juveniles of some economically important fish species and increasing biodiversity (Coleman et al. 2010). Up to 340 pits km² are visible in the multibeam maps, which extrapolates to an estimated 136,000 red grouper pits within the Pulley Ridge HAPC (Figs. 4.2 and 4.3).

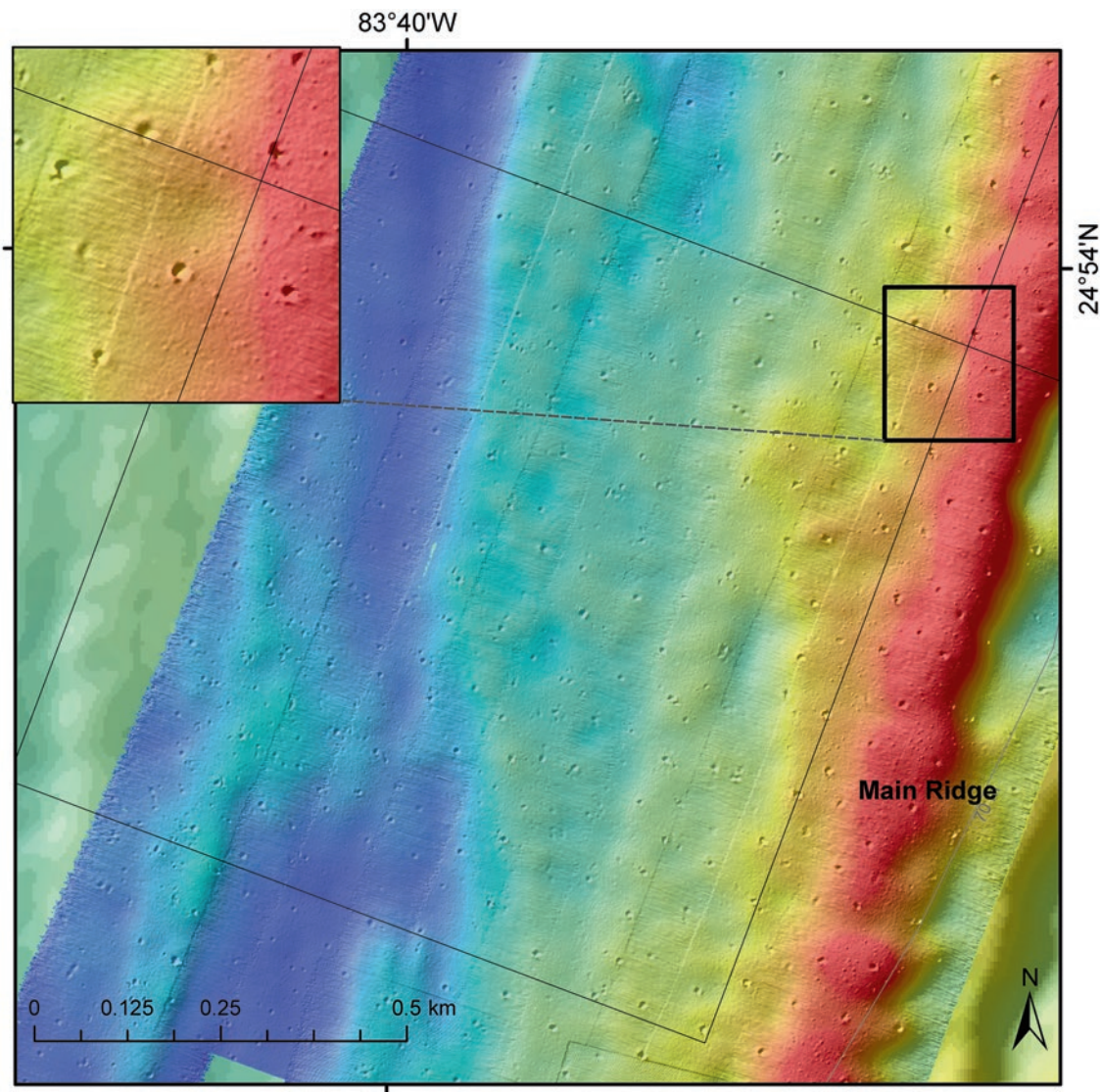


Fig. 4.3 Multibeam of Pulley Ridge showing dense red grouper pits (8–15 m in diameter) in a 1 km² block (light black square) along the Main Ridge. Dark square = inset showing detail of pits. (Multibeam from Reed 2011)

4.4 Biodiversity

A total of 86 fish and 234 benthic macrobiota species have been documented at Pulley Ridge (Fig. 4.2; Reed et al. 2017). The benthic species consist of 95 macroalgae, 92 demosponges, 18 gorgonian octocorals, 17 scleractinian corals, and 9 antipatharians (Table 4.1).

4.4.1 Macroalgae

Macroalgae are the most species-rich benthic macrobiota on Pulley Ridge. Although taxonomic analyses are still in progress, a total of 60 species of Rhodophyta, 25 Chlorophyta, and 10 Phaeophyta have been identified. The most common red algae are crustose corallines, which are predominant in the Central Basin and West Ridge (i.e., the deeper regions of Pulley Ridge). Other common red algae are foliose species of *Halymenia* and *Kallymenia* and crustose species of *Peyssonnelia*. In contrast, green algae are predominant on the Main Ridge, which is the shallowest region. The leafy green alga *Anadyomene menziesii*, which is endemic to Pulley Ridge, is the most common species (Fig. 4.4). The 17 m depth differential, from 59 m on top of the Main Ridge to 76 m on top of the West Ridge, results in the observed spatial changes of the dominant species from green algae to red algae due to reduced light availability. Other common green algae include *Codium* spp., *Caulerpa racemosa*, *Caulerpa sertularioides*, *Halimeda* spp., *Valonia ventricosa*, and *Verdigellas peltata*. The brown algae are less common and dominated by *Dictyota* spp., *Lobophora variegata*, *Sargassum* sp., and *Padina* sp.

4.4.2 Anthozoans

Anthozoans at Pulley Ridge consist of 17 species of Scleractinia (hard corals), 18 Octocorallia (gorgonians), 9 Antipatharia (black corals), and 4 Alcyonacea (soft corals) (Table 4.1; Reed et al. 2017).

Scleractinian Corals The dominant colonial scleractinian corals are the plate like colonies of the family Agariciidae (*Agaricia* spp. and *Helioseris cucullata*), *Montastraea cavernosa*, several species of *Madracis*, and *Oculina diffusa*. At these depths *M. cavernosa* also forms platelike colonies, whereas in shallower water, they are commonly conical to mound shaped (Baker et al. 2016). There are spatial differences within Pulley Ridge in the distribution of these taxa. The depth range for the agariciid corals is from 59 to 105 m. The distribution of *M. cavernosa* ranges from 62 to 68 m. Coral cover is greatest in the Central

Basin outside of the HAPC (Reed et al. 2017). Except for a few sporadic occurrences, *M. cavernosa* is only found on the Main Ridge. The agariciid plate corals are present in every region of Pulley Ridge but are most dominant on the Main Ridge and Central Basin. *Madracis brueggemanni* and *Madracis formosa* are the most abundant corals on the West Ridge but are also common on the Central Basin and Main Ridge.

Non-scleractinian Corals The dominant Octocorallia (gorgonians) are Primnoidae, Ellisellidae, Plexauridae, *Nicella* spp., *Hypnogorgia pendula*, and *Carijoa riisei* (Reed et al. 2017). The Antipatharia (black corals) include *Antipathes atlantica*, *A. furcata*, *Elatopathes abietina*, *Tanacetipathes* spp., and *Stichopathes luekeni* (Table 4.1). Octocorals and Antipatharia are most common at the West Ridge (Fig. 4.4). Other common Anthozoans include Alcyonacea (*Chironophthya caribaea* and *Nidalia* sp.), Actiniaria (*Condylactis gigantea*), Stylasteridae, Zoanthidae, Corallimorpharia, and Hydroida (Reed et al. 2017).

4.4.3 Sponges

Sponges are the most species-rich of all macrofauna, with 92 taxa identified to date. The actual species numbers are likely to increase as taxonomic analyses are in progress. The most common taxa include *Agelas clathrodes*, *A. conifera*, *A. flabelliformis*, *Aiolochoiria crassa*, *Amphimedon compressa*, *Aplysina lacunosa*, *Aplysina archeri*, *Auletta* sp., *Axinella corrugata*, *Callyspongia vaginalis*, *Erylus* sp., *Geodia gibberosa*, *G. neptuni*, *Ircinia campana*, *I. felix*, *I. strobilina*, *Niphates erecta*, *Oceanapia* sp., *Placospongia* sp., *Polymastia* sp., *Scopalina ruetzleri*, *Siphonodictyon coraliphagum*, *Spongisorites siliquaria*, *Verongula rigida*, *Xestospongia muta*, and numerous unidentified demosponges (Reed et al. 2017). Sponges are relatively common across Pulley Ridge but are most abundant on the West Ridge (Fig. 4.4). Hemispherical colonies (> 100 cm diameter) of *Spongisorites siliquaria* are one of the largest sponges found at Pulley Ridge. This unusual species is densely populated with the corkscrew-shaped gastropod *Siliquaria* sp. embedded inside the sponge with only the end of its shell exposed on the surface for filter feeding.

4.4.4 Fishes

A total of 86 fish taxa have been documented at Pulley Ridge (Harter et al. 2017; Reed et al. 2017). The most abundant fishes are school bass (*Schultzea beta*), striped grunt (*Haemulon striatum*), yellowtail reef fish (*Chromis enchry-*

Table 4.1 Anthozoa (Scleractinia, Antipatharia, and Alcyonacea) of Pulley Ridge identified from ROV photographic surveys (2012–2015) and museum specimens (USNHM)

Subclass	Order	Suborder	Family	Species	
Hexacorallia	Scleractinia			Scleractinia-unidentified colonial	
				Scleractinia-unidentified solitary cup	
			Agariciidae	<i>Agaricia fragilis</i> Dana, 1848	
				<i>Agaricia grahamae</i> Wells, 1973	
				<i>Agaricia lamarcki</i> Milne Edwards & Haime, 1851	
				<i>Agaricia undata</i> (Ellis & Solander, 1786)	
				<i>Agaricia</i> sp.	
				<i>Helioseris cucullata</i> (Ellis & Solander, 1786)	
			Montastraeidae	<i>Montastraea cavernosa</i> (Linnaeus, 1767)	
			Mussidae	<i>Scolymia cubensis</i> (Milne Edwards & Haime, 1848)	
				<i>Scolymia</i> sp.	
			Oculinidae	<i>Oculina diffusa</i> Lamarck, 1816	
			Pocilloporidae	<i>Madracis brueggemanni</i> (Ridley, 1881)	
				<i>Madracis decactis</i> (Lyman, 1859)	
				<i>Madracis formosa</i> Wells, 1973	
			<i>Madracis myriaster</i> (Milne Edwards & Haime, 1850)		
			<i>Madracis</i> sp.		
	Antipatharia				Antipatharia-unidentified
			Antipathidae	<i>Antipathes atlantica</i> Gray, 1857	
				<i>Antipathes caribbeana</i> Opresko, 1996	
				<i>Antipathes furcata</i> Gray, 1857	
				<i>Stichopathes luetkeni</i> Brook, 1889	
			Aphanipathidae	<i>Aphanipathes pedata</i> (Gray, 1857)	
				<i>Elatopathes abietina</i> (Pourtalès, 1874)	
			Myriopathidae	<i>Tanacetipathes</i> sp.	
				<i>Tanacetipathes tanacetum</i> (Pourtalès, 1880)	
	Octocorallia	Alcyonacea			Alcyonacea-unidentified
			Alcyoniina	Alcyoniina-unidentified	
				Nidaliidae	<i>Chironephthya caribaea</i> (Deichmann, 1936)
					<i>Nidalia occidentalis</i> Gray, 1835
					<i>Nidalia</i> sp.
			Calcaxonia	Ellisellidae	<i>Ellisella barbadensis</i> (Duchassaing & Michelotti, 1864)
					<i>Ellisella</i> sp.
					Ellisellidae-unidentified
					<i>Nicella goreau</i> Bayer, 1973
					<i>Nicella</i> sp.
			Isididae	Isididae-unidentified	
			Primnoidae	Primnoidae-unidentified	
		Holaxonia	Gorgoniidae	<i>Leptogorgia</i> sp.	
				<i>Pseudopterogorgia</i> sp.	
			Plexauridae	<i>Bebryce</i> sp.	
				<i>Hypnogorgia pendula</i> Duchassaing & Michelotti, 1864	
				Plexauridae-unidentified	
				<i>Swiftia exserta</i> (Ellis & Solander, 1786)	
				<i>Thesea</i> sp.	
		Scleraxonia	Spongiodermidae	<i>Diodogorgia</i> sp.	
			<i>Titanideum</i> sp.		
	Stolonifera	Clavulariidae	<i>Carijoa riisei</i> (Duchassaing & Michelotti, 1860)		

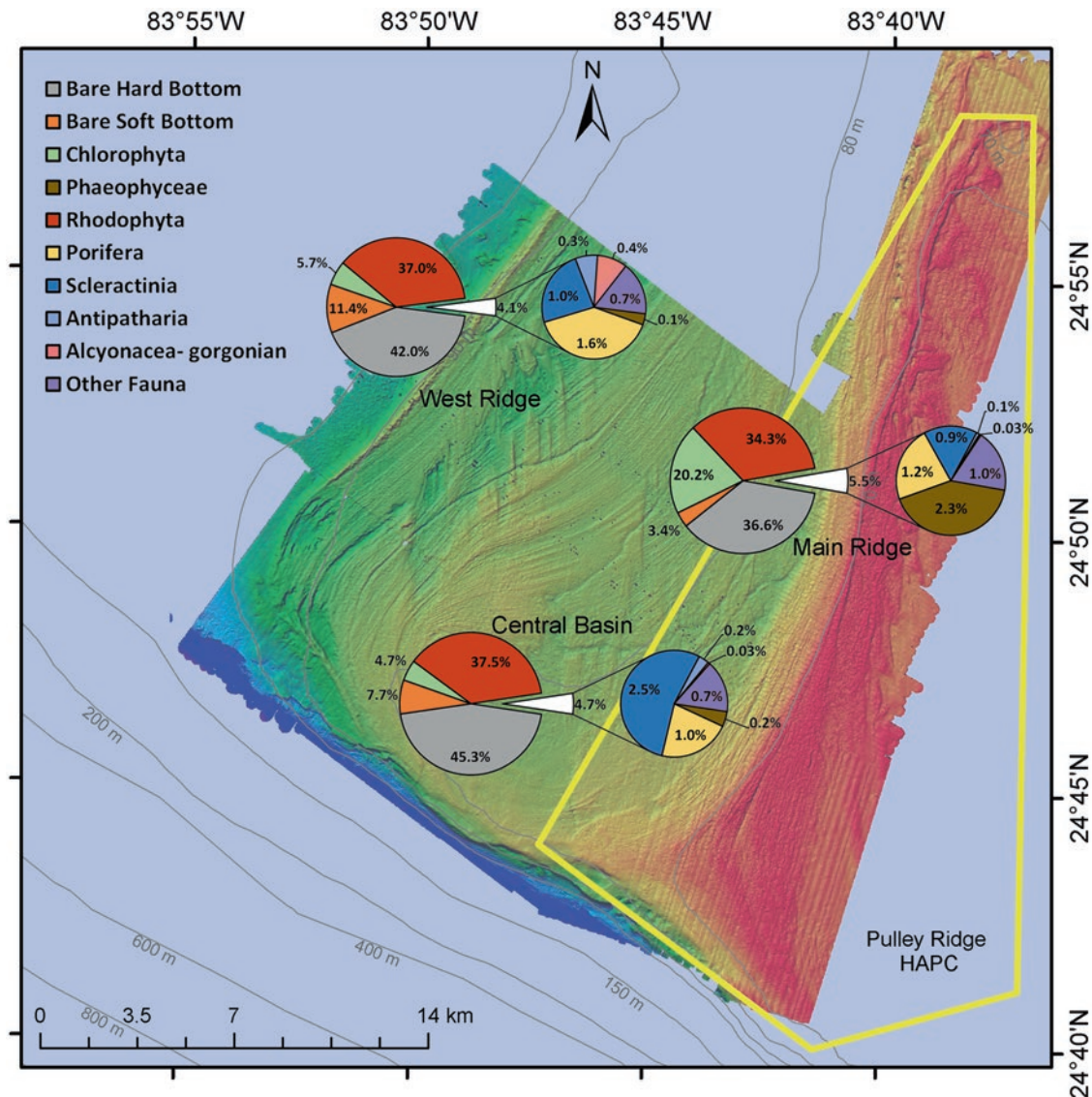


Fig. 4.4 Percent cover (CPCe Point Count) of major benthic macrobiota on the Main Ridge, Central Basin, and West Ridge from ROV surveys at Pulley Ridge during 2012 to 2015. (Reed et al. 2017)

ura), purple reef fish (*Chromis scotti*), chalk bass (*Serranus tortugarum*), reef butterflyfish (*Chaetodon sedentarius*), roughtongue bass (*Pronotoqrammus martinicensis*), cherubfish (*Centropyge argi*), cardinalfish (*Apogon* sp.), sunshinefish (*Chromis insolata*), and an unidentified *Chromis* sp. Several schooling species are abundant at night. These include schools of vermilion snapper (*Rhomboplites aurorubens*) and mackerel scad (*Decapterus macarellus*), as well as mixed schools of bonnetmouths (Inermiidae) and school bass (*Schultzzea beta*). A total of 20 managed fishery species occur at Pulley Ridge. The most abundant are almaco jack (*Seriola rivoliana*), vermilion snapper (*Rhomboplites aurorubens*), and red grouper. Fish diversity was significantly higher on the Main Ridge compared to all other Pulley Ridge regions.

Red grouper pits provide the only significant three-dimensional habitat at Pulley Ridge, and 66 of the 86 fish species found at Pulley Ridge were observed in the grouper pits (Harter et al. 2017). Of these, 16 are managed species. The red grouper and scamp (*Mycteroperca phenax*) are the most abundant economically important species associated with the pits. Occupied pits only have one red grouper. Schooling species, such as bonnetmouths and the striped grunt (*Haemulon striatum*), and small benthic fish, such as cardinalfish, damselfish, and anthiids, are the most common species associated with the grouper pits (Harter et al. 2017).

The Indo-Pacific lionfish (*Pterois* spp.) are abundant at Pulley Ridge. During the 2012–2015 surveys, 1814 lionfish were counted, and most were associated with active red

grouper pits. In 2012 lionfish were observed in 72.5% of the pits and 86.5% in 2015 (Harter et al. 2017). The maximum number of lionfish observed in a single pit was 74, and the average abundance was 6.10 individuals pit⁻¹.

4.4.5 Other Biotic Components

Other common sessile macroinvertebrates at Pulley Ridge include Bryozoa, such as a branching species of *Schizoporella* and an unidentified white fan, and ascidian tunicates dominated by Didemnidae and *Eudistoma* sp. Mobile invertebrates include Annelida such as *Filograna* sp., the fireworm *Hermodice carunculata*, and numerous Sabellidae and Serpulidae. Mollusks are present but not common. Arthropods include various brachyuran crabs, hermit crabs, arrow crabs *Stenorhynchus seticornis*, and Pycnogonida. Echinoderms are fairly common and include the crinoids *Analcidometra armata* and *Davidaster discoideus*, which are commonly seen on the green alga *Anadyomene menziesii*. Urchins include *Arbacia punctulata*, *Centrostephanus longispinus*, *Echinus* sp., *Eucidaris tribuloides*, and *Stylocidaris affinis*. Brittle stars such as *Asteroschema* sp. and *Gorgonocephalus* sp. are common along with starfish including *Narcissia trigonaria*.

4.5 Ecology

Using Coral Point Count (CPCe; Kohler and Gill 2006) from the ROV surveys in 2012–2015 (Reed et al. 2017), the percent cover of benthic biota averaged 49.9% over all regions of Pulley Ridge and ranged from 60.0% at the Main Ridge to 46.7% at the West Ridge (Table 4.2; Fig. 4.4). The dominant benthic macrobiota on Pulley Ridge were macroalgae (46.5% cover; Table 4.2), which were primarily red algae (34.5% cover), dominated by crustose coralline algae (28.5% cover). Green algae had 10.6% cover and were dominated by the leafy green alga *Anadyomene menziesii* (8.11% overall, maximum 34.55% in a single 1-km² block; Reed et al. 2017). Sponges were similar in percent cover across the three regions of Pulley Ridge (average 1.2% cover) but were greatest on the West Ridge (1.6%).

Scleractinian corals averaged 1.5% cover overall. Plate corals of the family Agariciidae (*Agaricia* spp. and *H. cucul-*

lata) were the dominant taxa (0.9% cover) followed by *Madracis* spp. (0.5%) and *M. cavernosa* (0.01%). Coral cover was highest in the Central Basin outside of the HAPC (average 2.5%, maximum 6.7% in a single 1-km² block). The Main Ridge within the HAPC averaged 0.9% (maximum 7.4% in a single block). Gorgonians averaged 0.1% cover but had their greatest cover on the West Ridge (average 0.4% cover). Black corals averaged 0.1% overall and were also greatest on the West Ridge (average 0.3% cover; Fig. 4.4).

From the 2012 to 2015 ROV dives, a total of 8072 images were analyzed for coral colony density, and 51,814 living scleractinian corals were counted. Overall, the density of all scleractinians was 6.8 colonies m⁻²; plate coral density (*Agaricia* spp. and *H. cucullata*) was greatest at 4.9 colonies m⁻², *M. cavernosa* was 0.002 colonies m⁻², and *Madracis* spp. were 1.7 colonies m⁻². The southern Central Basin region had the greatest hard coral density overall (15.8 colonies m⁻²), followed by the Main Ridge (6.2 colonies m⁻²) and West Ridge (3.1 colonies m⁻²).

Comparisons of the scleractinian coral cover at Pulley Ridge over time showed a substantial loss of coral in the past 10 years (Hine et al. 2008; Reed et al. 2017). In 2003, Pulley Ridge was dominated by crustose coralline algae, leafy green algae (*A. menziesii*), and scleractinian corals (*Agaricia fragilis*, *A. undata*, *A. lamarcki*, *Helioseris* [syn. *Leptoseris*] *cucullata*, *M. cavernosa*, *Oculina* sp., and *Madracis* spp.). *Agaricia* spp. were the dominant scleractinian coral with colonies up to 50 cm in diameter and with up to 60% cover of live coral (Hine et al. 2008). By 2012–2015, the mean percent coral cover on the Main Ridge had dropped from 12.8% in 2003 to 0.9%, a 93% loss of coral. In 1981, the only previous quantitative survey at Pulley Ridge documented 9.0% coral cover for one 1-km² block on the Main Ridge (Phillips et al. 1990). The region of highest coral cover on Pulley Ridge by 2012–2015 was clearly the Central Basin (Table 4.2), which previous studies did not sample.

The question remains regarding how stable over time is the Pulley Ridge MCE? If the system incurs a catastrophic loss of biota, is it able to revive and survive? Few studies have looked at the long-term stability and resilience of MCEs; however, MCEs are vulnerable to impacts from climate change, bottom trawling, invasive species, and pollution (Andradi-Brown et al. 2016). We now have evidence of a catastrophic coral loss on Pulley Ridge MCE over the past 10 years. Pulley Ridge MCE is showing resilience in that

Table 4.2 Percent cover (CPCe Point Count) of benthic macrobiota identified from ROV surveys at Pulley Ridge during 2012 to 2015 R/V *Walton Smith* cruises (Reed et al. 2017)

Location	Scleractinia (%)	Octocorallia (%)	Antipatharia (%)	Porifera (%)	Algae (%)
Pulley Ridge	1.5	0.1	0.1	1.2	46.5
Main Ridge	0.9	0.03	0.1	1.2	57.2
Central Basin	2.5	0.03	0.2	1.0	42.8
West Ridge	1.0	0.4	0.3	1.6	42.9

during this die-off, there appears to have been a concurrent major coral settlement at least in the Central Basin where 68% of the corals are relatively new recruits (< 5 cm diameter). It is possible that trawling could have facilitated asexual fragmentation of the coral colonies (Dahl 2013), but it is also viable that the new recruits are a result of sexual reproduction.

The “deep reef refugia” hypothesis (Glynn 1996; Bongaerts et al. 2010) suggests that MCEs may provide increased resilience for shallow reef species through the export of larvae. To assess the ecological importance of MCEs as refugia, the vertical and horizontal connectivity of MCEs to shallow-water reefs must be confirmed. Is there evidence of physical or ecological connectivity between Pulley Ridge MCE and the Florida Keys’ shallow reefs? The circulation over Pulley Ridge and the Florida Keys is influenced by both local and remote forcing, as well as the Loop and Florida Currents and their associated eddies (Kourafalou and Kang 2012). The Loop and Florida Currents are often in close proximity to Pulley Ridge and facilitate physical connectivity with the downstream reefs of the Dry Tortugas and the Florida Keys. Biophysical modeling of larval dispersal for the bicolor damselfish (*Stegastes partitus*) indicates that Pulley Ridge MCE has sporadic one-way connectivity from Pulley Ridge to the shallow-water reefs of the Dry Tortugas and the Florida Keys (Vaz et al. 2016). Potential connectivity between Pulley Ridge and the downstream shallow and mesophotic reefs of the Florida Keys is species-dependent (Sponaugle and Cowen 2019).

At Pulley Ridge, red grouper and lionfish are the two top-level predators that inhabit the grouper pits and exhibit high site fidelity. Fish species composition associated with the grouper pits was significantly different depending on the predator species (Harter et al. 2017). Various small damselfish species (sunshinest, purple reef fish, and yellowtail reef fish) and cardinalfish (*Apogon* spp.), as well as several other fish species, including scamp, striped grunt, and school bass, had higher abundances in grouper pits with lionfish, suggesting there was not a negative lionfish effect. Instead, pits with lionfish had both greater species diversity and species richness and higher abundances of some fish species. Lionfish may therefore actively select areas where species richness and prey density are highest. Areas where lionfish are found may reflect not only favorable habitat for lionfish but also for native fishes. These pits are essentially the only feature on Pulley Ridge with enough structural complexity to provide suitable habitat for both large predators and small reef fish. If fishes are actively recruiting to these pits in high abundance, it is conceivable that an effect from lionfish may not be observed. An alternative explanation for the lack of a lionfish effect could be the short length of time since lionfish

have colonized the region (i.e., first observed by the FLoSEE cruise in 2010, n = 6 lionfish).

4.6 Threats and Conservation Issues

4.6.1 Coral Bleaching/Disease

Most corals seen on Pulley Ridge appear to be relatively healthy, although a small percentage showed signs of recent disease or bleaching (Table 4.3; Fig. 4.5). From the ROV surveys in 2012–2015, 1.21% of the total colonies of *Agariciidae* and *M. cavernosa* counted (38,368) showed signs of disease, consistent with “white syndromes” disease (Weil and Hooten 2008), which are characterized by irregular patches of recently dead, white skeleton, often extending from the outer rim. Specimens with white syndromes were collected from Pulley Ridge, and the interfaces between the healthy tissue and the diseased tissue were examined by microscopy and bacterial community profiling. No specific pathogens could be identified. The prevalence of disease on Pulley Ridge in 2012–2015 is lower than that reported in the Caribbean (Ruiz-Moreno et al. 2012). Bleaching was apparent in 0.88% of the colonies. Bottom temperature records at Pulley Ridge are limited and averaged 22.3 °C. During 2012–2015, bottom temperatures at Pulley Ridge were neither warm nor cold enough to cause bleaching. Cold-water upwelling events along the west Florida shelf are not unusual as the Loop Current meanders along the Florida shelf-edge. It is possible that a strong, long lasting cold-water upwelling event could impact coral health.

4.6.2 Invasive Species

During the 2012–2015 surveys, 1814 lionfish were counted. Several studies have revealed deleterious effects of the invasion of lionfish on abundances and species richness of native fishes through predation and competition in shallow water (Albins and Hixon 2008). However, other studies including one at Pulley Ridge (Harter et al. 2017) reported no negative effect from the invasion of lionfish (Elise et al. 2014).

Table 4.3 Percentage of total population of plate corals (*Agaricia* spp. and *Helioseris cucullata*) and *M. cavernosa* showing signs of white syndromes disease and bleaching (based on total counts of all individual corals) (Reed et al. 2017)

Region	Bleaching (%)	White syndromes (%)
Main Ridge	2.10	3.16
Central Basin	0.73	0.99
West Ridge	0.73	0.42
Grand Total	0.88	1.21

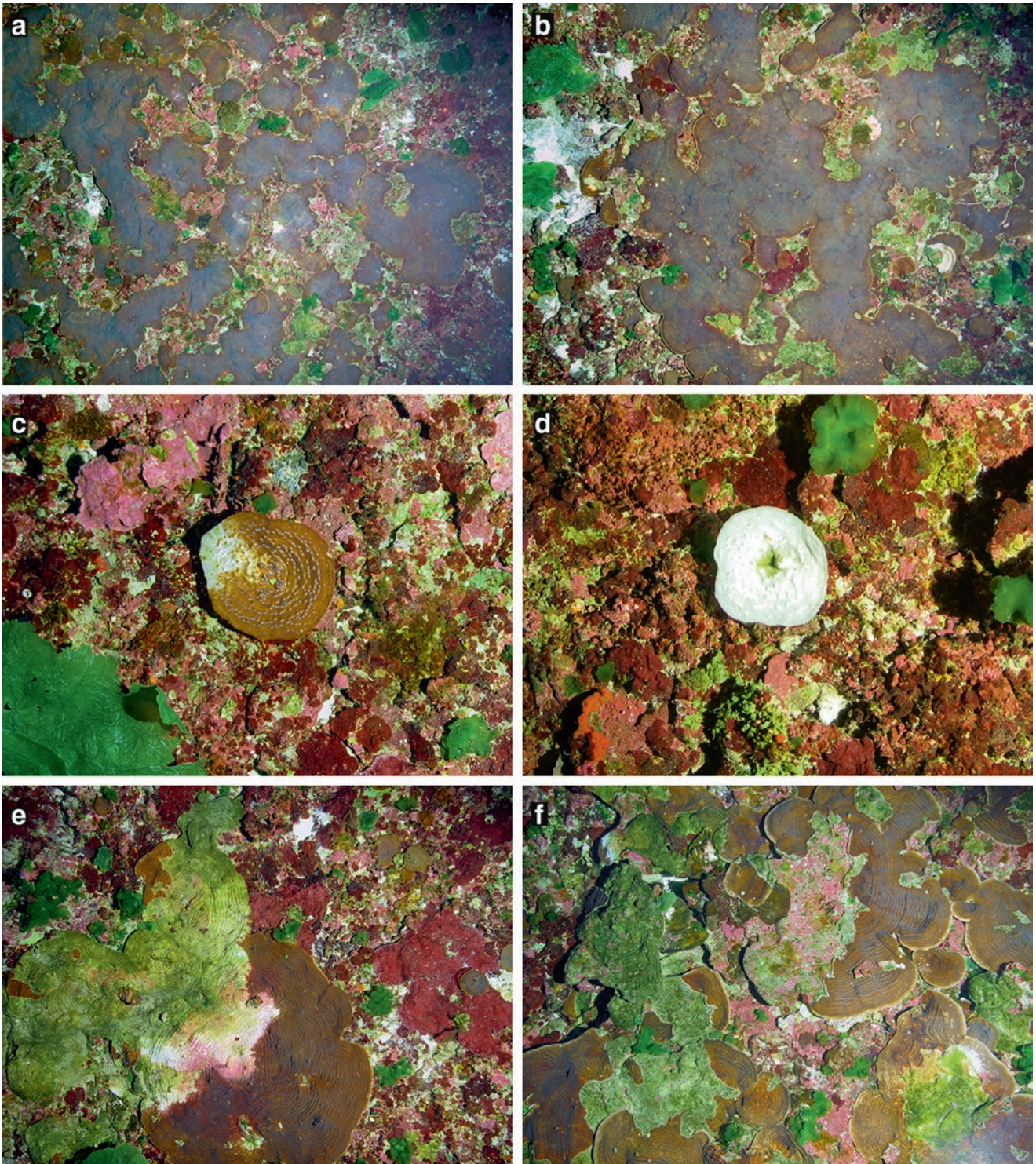


Fig. 4.5 Agariciidae corals from the Central Basin of Pulley Ridge showing various stages of mortality. (a) Colonies of *Agaricia grahamae* that are either remnants of a super colony or are coalescing individual colonies (green lasers near center = 10 cm; field of view = 3.0 m across), depth 75 m. (b) Large *A. grahamae* (207 cm in diameter), with white patches of recent dead, depth 75 m. (c) to (f) Series of coral images showing various stages of mortality on Pulley Ridge: (c) *Helioseris cucullata* partially diseased or dying, depth 77 m. (d) *H. cucullata* 100% recent mortality with no algal growth and no signs of tissue, depth 77 m. (e) Large plates of *Agaricia* sp. (> 1 m diameter) showing recent mortality (white skeleton) and old mortality (with green algae and crustose coralline algae), depth 78 m. (f) Large plates of *Agaricia* sp. with parts showing signs of old mortality, with recognizable coralline ridges, depth 78 m. (Photos: NOAA Coral Ecosystem Connectivity Expeditions)

4.6.3 Mississippi River Runoff

Satellite ocean color imagery of chlorophyll *a* plumes shows the clear influence on Pulley Ridge from the Mississippi River, over 375 nmi away (NOAA CoastWatch 2015). These plumes associated with Mississippi River water entrainment in the Loop Current periodically reach the west Florida shelf and Pulley Ridge (Le Hénaff and Kourafalou 2016). Surface seawater salinities in the eastern Gulf of Mexico are generally oceanic (34–37 psu); however, when the Mississippi River outflow becomes entrained in the Loop Current, this discharge can affect salinity and turbidity, light transmission through the water column, as well as transport-associated pollutants.

4.6.4 Fisheries

The Pulley Ridge HAPC regulations prohibit bottom tending gear such as bottom trawls, bottom longlines, buoy gears, pots, and/or traps and bottom anchoring by fishing vessels (NOAA 2013). However, hook and line fishing for grouper is allowed. This may explain why differences in the abundance of red grouper were not observed inside versus outside the HAPC (Harter et al. 2017). Overexploitation of red grouper could have negative effects on biodiversity at Pulley Ridge. Grouper pits inhabited by red grouper were observed to have greater species diversity and fish abundances compared with the levels observed at pits not inhabited by a red grouper. Increased fish abundance and diversity are attributable to the pits with a red grouper being actively maintained, with the resident grouper of a pit using its fins and mouth to keep the pit scoured down to the rock ledges (Harter et al. 2017). Once a pit loses the adult red grouper (due to fishing, natural mortality, or other factors), the pit begins to fill in with sediment. The presence of fishes in grouper pits is significant for fishery management because a change in pit activity and numbers may impact the presence and abundance of economically important fish.

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