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# Foreword

Almost everyone loves the shore. This margin between our own familiar ground and the vast ocean wilderness can both comfort and excite us. Many of us recall serenely filling our senses with surf tumbling onto a beach, only to have that peace punctuated by delight—a sudden and beautiful visage from the sea, a shadow in a wave, a leap and a splash, or a lingering presence offering detailed wonder. That nature and we share more than coincidence of space in this coastal ecosystem. We share a need for it.

This book is about a vital but underappreciated natural feature—Florida's nearshore reefs—oases of life that the authors refer to as "Islands in the Sand." "Underappreciated?" you question. Yes, vastly so. Still, we enjoy these reefs immensely. We prosper from their flora and fauna, and are treated to the landscapes they present at low tide, and through our dive mask. Our profits from nearshore reef services occupy many levels, including the all-important economic benefit measured by dollars. Yet, although we gain from these lovely, diverse, accessible patches of hard sea-bottom, we fail to appreciate the full depth of these shallow reefs. That is to say, we fall short of understanding them, of grasping the habitat's worth and significance, and of knowing outright how our actions can threaten it.

The authors of this book, who are experts across multiple fields, have prepared a detailed ecological description of Florida's coastal reefs. It is a portrayal that is both academic and easily absorbed, and is essential for coastal managers, scientists, or anyone wanting to deepen their coastal relationship. This book catalogs features of nearshore reefs—their dynamic cycles of ecological change, their function as hotspots for biodiversity, their role in the lives of rare species, and in our own lives.

Especially now, our aptitude for the mutual relationship we have with nearshore reefs is crucial to their pulse of persistence. Over eons, these reefs of the surf zone blossomed and withered to the beat of storms and natural sand movement, periodically harboring unique lives lived in haste, and marine animals in formative stages or just passing through. But as our coast has become more crowded, this habitat has suffered from our insistence on permanence within such a dynamic system. Where beach sands once came and went, we construct buildings on dangerous ground requiring defense against change. This messy and expensive coastal battle often involves pumping sand to artificially replace what the sea consumes, and as an unintended consequence of this engineering, reefs, which contributed to the original value of the real estate, are kept smothered.

The paradox of habitat affinity and habitat harm is precisely why this book is essential. The affinity is self-evident. To visit a Florida beach adorned by nearshore reef at low tide is to experience uniquely accessible nature—life-filled tide pools that tempt the curiosity of children and bring out blissful biophilia in us all. But understanding the potential harm to our nearshore reefs requires insight into how this habitat functions. To the extent that this knowledge leads to watchful stewardship and temperance of our coastal actions, we will keep our mutually beneficial relationship with coastal reefs. On this journey, this book will be our guide.

Blair Witherington, Ph.D., Floridana Beach, Florida, USA
*Florida's Living Beaches* and *Our Sea Turtles*

# Preface

The management of coastal resources is increasingly focused on ecosystem approaches that not only consider primary habitats of concern but their connectivity to adjacent systems. Amidst the cross-shelf mosaic of habitats of mainland Florida's east coast, estuaries with mangroves and seagrasses share many flows, including energy and propagules, with reefs and pelagic waters offshore. Along the highly dynamic land-ocean margin, nearshore hardbottom habitats at 0-4 m depths exist as reef patches for over a thousand documented organisms, amidst long stretches of sand. This volume is the first to describe the fundamentals of the biological, physical, ecological, and management attributes of east Florida's nearshore reefs. Since many coastal residents interact with these reefs and have many questions, we have also tried to make this book accessible to laypersons (e.g., the imagery, a Glossary for technical terms, and book structure) to make these habitats more understandable.

We introduce nearshore hardbottom habitats from southern St. Johns County to northern Miami-Dade County and foundational ecological concepts in Chap. 1. In Chap. 2, we discuss the geology and distribution of nearshore hardbottom reefs and the associated oceanographic setting in the region in which they occur. In Chap. 3 through 6, we synthesize the peer-reviewed scientific and gray literatures, and provide unpublished data based on decades of experience with these reefs among the co-authors. We describe the known species groups, their latitudinal and depth distributions, reproduction, trophic functions, and connectivity for algae and cyanobacteria (Chap. 3), invertebrates (Chap. 4), fishes (Chap. 5), and sea turtles (Chap. 6).

In Chap. 7, we integrate assemblage-scale ecological perspectives among these flora and fauna. We discuss the potential roles of disturbance and latitude in affecting abundance and distribution with respect to habitat use, and populations and energetic connectivity along the east Florida coast. In Chap. 8, the responses of these organisms to varying degrees of natural and anthropogenic disturbances are examined. We then discuss approaches for minimizing impacts to nearshore hardbottom reefs during large fill projects, with a focus on artificial reef mitigation. In Chap. 9, we summarize research findings for each major taxonomic group, nearshore hardbottom reef ecology, and management with a focus on future research opportunities across all issues.

In examining these diverse nearshore hardbottom reef issues, we hope to provide a useful reference for coastal researchers, managers, and educators, as well as anyone else interested in these habitats and their connectivity to the sea and land. We hope this book inspires increased research on these systems and improved science-based conservation of the marine biodiversity of coastal Florida and other regions with nearshore hardbottom reefs.

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# Contents

# Author Biography

**Daniel A. McCarthy, PhD** is a professor in the Department of Biology and Marine Science and the Marine Science Research Institute, Jacksonville University. He is a marine benthic ecologist with over 25 years of field and laboratory research experience. His research has focused on the ecology and restoration of estuarine and coastal reef systems. He obtained his Bachelor of Science at Jacksonville University, Master of Science at Florida State University, and Ph.D. at King's College, University of London. He served as a postdoctoral fellow with the Smithsonian Institution for 3 years before coming to Jacksonville University.

**Kenyon C. Lindeman, PhD** is a professor in the Department of Ocean Engineering and Marine Sciences, Florida Institute of Technology. His work focuses on nearshore habitats, fishery management, marine protected areas, and coastal climate adaptation. He has worked as a research scientist with NOAA, the University of Miami, and several conservation science nonprofit organizations. Over 70 research publications include articles in over 20 peer-reviewed journals and 4 coauthored or coedited books. He received a Bachelor of Science at FIT, Master of Science at the University of Puerto Rico, and PhD at the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

**David B. Snyder, MS** is a senior scientist at CSA Ocean Sciences Inc., Stuart, Florida. He is a fish ecologist and marine biologist with more than 35 years of experience. He has participated in marine environmental assessments worldwide and has sampled fishes from a variety of habitats ranging from the continental slope to freshwater streams. Such efforts have included multiple surveys of fishes and epibiota associated with nearshore reefs subject to impact from dredge and fill projects off the eastern and western Florida coasts. He obtained his Bachelor of Science from the University of Florida and his Master of Science from Florida Atlantic University.

**Karen G. Holloway-Adkins, PhD** is a senior scientist and executive director of East Coast Biologists, Inc. (a non-profit for scientific research and education) in Indialantic, Florida. She has over 28 years of experience in the field of marine biology and sea turtle ecology with research that is focused on inwater developmental habitat and the ecological role of sea turtles in marine ecosystems. She worked 18+ years as a biologist monitoring protected species and habitat at NASA's John F. Kennedy Space Center. She received her Bachelor and Master of Science degrees in Biology from the University of Central Florida and her Doctoral degree from Florida Atlantic University. She currently serves as courtesy affiliate faculty within the Biology Department at both universities.

# Part I
# Nearshore Hardbottom Reefs Within the East Florida Seascape

# Chapter 1
# Introduction

## 1.1 Nearshore Hardbottom Reefs of East Florida

Nearshore hardbottom reefs (NHRs) are a relatively little-known component of the diverse marine habitat mosaic along Florida's east coast. Also known as nearshore hardbottom, coquina, or worm rock, these shallow reefs occur across the coast between deeper offshore reefs, and estuarine mangroves and seagrass meadows, straddling the marine surf zone in some areas of east Florida's coastline. These reefs were not created by corals but are large rock outcroppings of the Anastasia Limestone and Miami Limestone geological formations in most cases (Fig. 1.1).

The Anastasia Limestone formation is composed of sand and mollusk shells (particularly the small coquina clam, *Donax*) and was formed during the late Pleistocene geological period. It occurs along most of Florida's central east coast, southward to approximately Hillsboro Inlet in Broward County where it intergrades in complex manners with nearshore ridges of mixed Holocene origin (e.g., Banks et al. 2007) and also abuts the Miami Limestone formation. More information on these limestone formations and their marine outcroppings that form the rigid foundation for these NHRs is in Chap. 2. The reefs are surrounded by sediments that are continuously redistributed by waves and tides, which bury and uncover reef habitat within and among seasons. This book seeks to compile the most current information on this complex and lesser-known coastal habitat system.

Nearshore hardbottom that is not created by living corals has many geological sources and forms around the Greater Caribbean, from the coquina and worm reefs of NHRs of mainland east Florida, to the ironshore of the Bahamas and Cayman Islands, to the razor sharp *dientes de perro* (dog teeth) of northern Cuba, including much of Havana's shore. NHRs are commonly called rocky reefs or rocky intertidal shores in many regions globally. Although the nearshore reefs of mainland east Florida span an approximately 450 kilometer (km) stretch of coastline, little summary information is available on this discontinuous reef system at the current northern limits of the subtropical northwest Atlantic.



D. A. McCarthy et al., *Islands in the Sand*,
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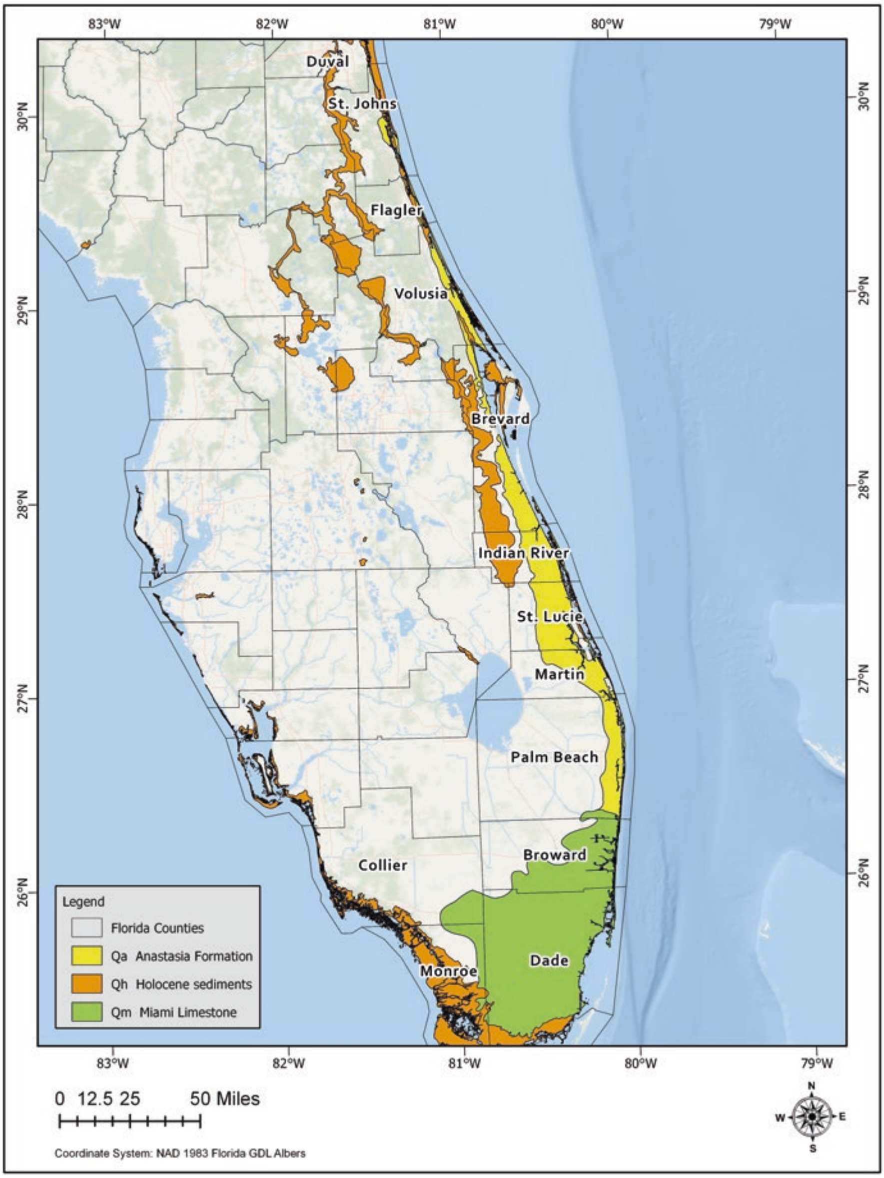


**Fig. 1.1** East Florida counties with Anastasia Limestone in yellow and Miami Limestone in green. Text has more detail on the complex interface of these two limestone formations. (Modified from Scott et al. 2001)

The study area of this book encompasses the nearshore rock outcroppings from the Anastasia and Miami Limestone formations or mixed relict Holocene ridges that can occur in coastal waters from southern St. Johns and Flagler counties in northeast Florida (approx. 29°42 N latitude) to Broward and northern Miami-Dade counties in southeast Florida (approx. 25°46 N latitude). In these regions, hardbottom reefs are the only natural hard-structure habitats at depths of 0–4 meters (m) available to nearshore organisms (Fig. 1.2). Currently, most of these structures are within shallow coastal waters and display a variety of forms from flat expanses with little relief, to vertical mounds that are emergent at low tide, to deeper structures that are less subject to tide and wave effects.

Overall, these habitats are patchily distributed from northeast to southeast Florida, usually occupying a relatively low percent of the longshore distance of most of the ten county shorelines in the region. One exception is Indian River County where large amounts of shallow hardbottom can be routinely present in nearshore areas (Fig. 1.3; see Chap. 2). These high-relief nearshore reef systems (at a latitude of 27.5° N) are known locally for some of the largest spiny lobsters in Florida and as habitat for juvenile through adult life stages of recreationally and commercially valuable reef fishes.

Throughout east Florida, the structural complexity of nearshore reef (based commonly on weathering of limestone bedrock) varies latitudinally and with water depth (Figs. 1.4 and 1.5). It is often enhanced by framework-building organisms such as tube-building polychaete worms (Gram 1965; Kirtley and Tanner 1968; Pandolfi et al. 1998; McCarthy 2001), other invertebrates (e.g., sponges, anthozoans, bryozoans), and macroalgae (Goldberg 1973; Gore et al. 1978; Nelson 1989; Nelson and Demetriades 1992; CSA International, Inc. 2009) (Fig. 1.5).

Situated among broad expanses of bare sand bottom, hardbottom reefs can serve a wide variety of ecological functions for many common tropical and subtropical reef fish and invertebrate species. These functions include settlement and nursery areas, the only feeding and spawning sites available, and shelter for hundreds of species of resident crabs, worms, shrimp and fishes, as well as a number of other animals and plants that occur in close proximity (Fig. 1.6). These functions also translate into important ecosystem services for humans as identified in the Millennium Ecosystem Assessment (MEA 2005). Nearshore reefs explicitly support recreational services (including fishing, snorkeling, surfing, and photography) and educational opportunities, under the cultural category of the MEA guidance for ecosystem services.

Warm temperate to subtropical beaches and nearshore reefs from St. Johns to Miami-Dade counties along east Florida are major economic factors influencing sun-and-sand tourism and coastal real estate markets. The beaches are subject to many challenges to long-term sustainable management. Continuous pressure for more coastal development is degrading many coastal resources and threats to environmental and socio-economic systems are amplified by sea level rise (Hernández-Delgado and Rosado-Matías 2017; Kulp and Strauss 2017).

Over 6 million people share limited land and water resources within the narrow and low-elevation corridor between Miami-Dade and Palm Beach counties alone (Broward County Planning and Development Management Division 2019), with a continued push of coastal growth northward. Many NHR habitats in this region have been buried by large beach restoration projects that involve the placement of hundreds of thousands of cubic yards of fill (sediments from off-site sources). These

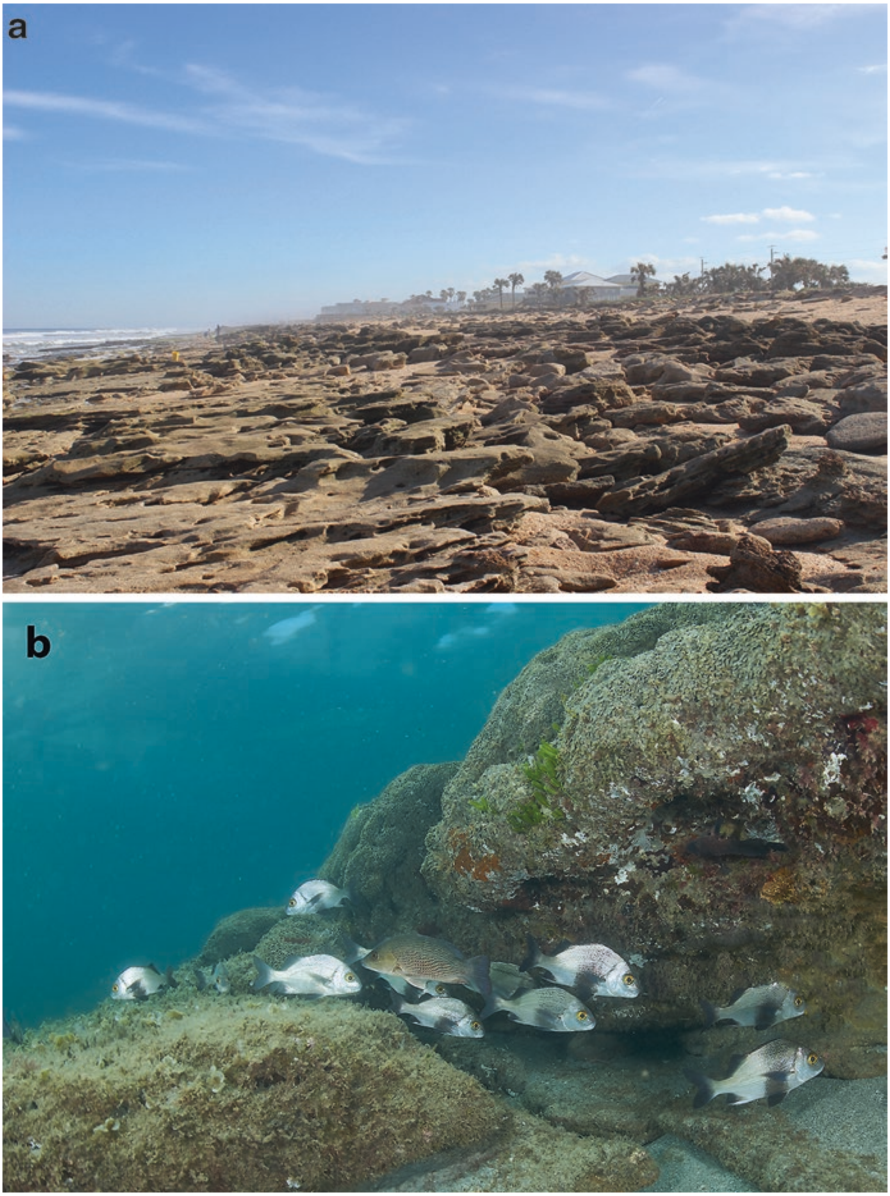


**Fig. 1.2** Nearshore hardbottom outcroppings along the Florida coast. (**a**) South of Marineland, Flagler County, Florida. (**b**) Coral Cove Park, Palm Beach County, with reef fishes, worm rock, tunicates, bryozoans, sponges, and macroalgae. (Sources: D. McCarthy; D.B. Snyder)

**Fig. 1.3** Examples of nearshore reef systems in Indian River County, Florida. (**a**) Substantial hardbottom systems throughout the county are used by divers, Wabasso area. (**b**) Large spiny lobsters are captured on hardbottom reefs at nearshore and intermediate depths. (Sources: Sebastian Inlet Tax District, VeroBeachReefs.com)

**Fig. 1.4** Tide pools along nearshore hardbottom reefs, Coral Cove County Park, south Jupiter Island, northern Palm Beach County, Florida. (Source: D.B. Snyder)

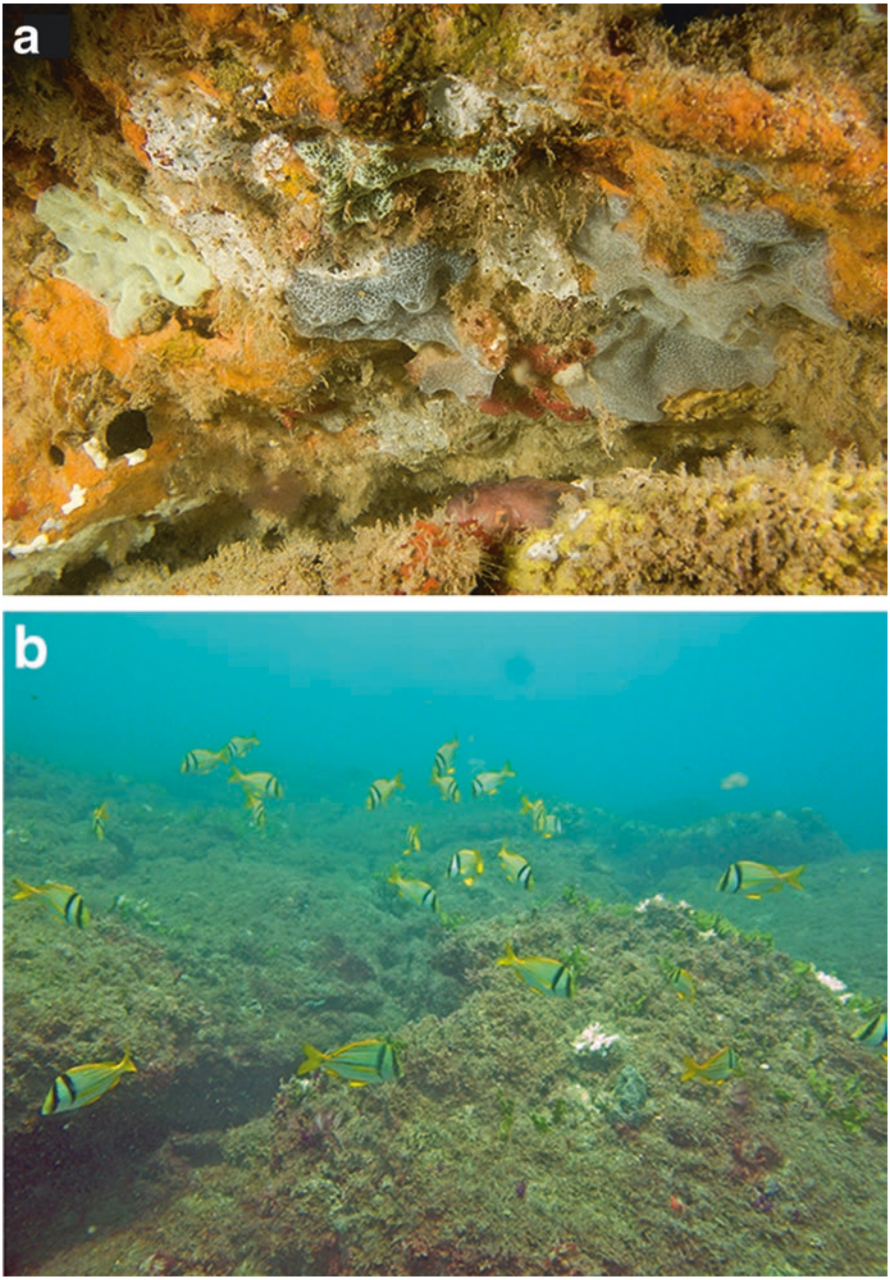


**Fig. 1.5** Macro- and micro-scale complexity created by sessile epibiota on shallow Florida reefs. (**a**) Microhabitat complexity under a nearshore reef ledge with over ten species of sponges, tunicates, hydrozoans, macroalgae, and fish, MacArthur Beach State Park, Palm Beach County, Florida. (**b**) Nearshore hardbottom reef at the St. Lucie Reef (Peck's Lake) in Martin County, Florida. (Sources: D.B. Snyder, D. McCarthy)

**Fig. 1.6** Juvenile stage of the green sea turtle (*Chelonia mydas*) feeding on algae on a nearshore hardbottom reef, Boca Raton, Palm Beach County, Florida. (Source: K. Jones)

projects involve complex policies to administratively permit the burial and mitigation of the reefs (Lindeman and Ruppert 2011; FDEP (Florida Department of Environmental Protection) 2014; Kosmynin et al. 2016). These issues reflect a pressing need for a comprehensive survey of these nearshore reefs and functions to effectively employ ecosystem-based management for their conservation.

Although comparatively little is published in peer-reviewed scientific journals about NHRs of mainland east Florida, much information is available from research, industry, and permitting literature that include fields such as organismal and population biology, community ecology, coastal geology, physical oceanography, and fishery science. Therefore, we examined relevant peer-reviewed journals and texts as well as unpublished (or gray) literature to hierarchically structure and compare the primary biotic assemblages for these reefs. This synthesis of information consists of three sections. Part 1 (Chaps. 1 and 2) contains an introduction to east Florida nearshore reefs, their oceanographic setting, geologic sources, and distribution across mainland counties. Part 2 (Chaps. 3, 4, 5, and 6) contains assemblage-scale chapters on macroalgae and cyanobacteria, invertebrates, fishes, and sea turtles; reviewing known nearshore reef diversity and functions. Part 3 (Chaps. 7, 8, and 9) synthesizes the information from prior chapters to address integrative ecology, stress/disturbance characterization, management alternatives, and future research needs and opportunities. We have also included a Glossary of terms at the end of the book.

## 1.2 Nearshore, Intermediate, and Offshore Hardbottom Reefs

Scientists generally examine patterns of change in species composition along environmental gradients to help understand the role of factors (e.g., depth, sedimentation, predation, disturbance) on ecological community structure and function (e.g., Nekola and White 1999; Worm and Tittensor 2018). In many cases, distinguishing between NHRs and deeper habitats can be complicated, with patterns also varying by latitude along the east Florida coast (CSA International, Inc. 2009; Walker 2012; Walker and Gilliam 2013). Individual taxa can respond to dozens of physical and biological gradients independently, such that biotic assemblages may not conform to strict rules based on depth zonation. However, important reef tract characteristics do vary with broad depth categories in east Florida (Gilmore Jr. et al. 1981; CSA International, Inc. 2009; Walker 2012; Walker and Gilliam 2013; CSA Ocean Sciences Inc. 2014; Gilliam et al. 2018). Our primary focus here is on comparative analyses of invertebrates, fishes, macroalgae, and marine turtles (Part 2) among NHRs of 0–4 m depths although we also discuss connectivity with the deeper intermediate hardbottom reefs at 4–10 m (IHR), and offshore hardbottom reefs deeper than 10 m (OHR). Figure 1.7 shows examples of an IHR and OHR. We emphasize that depth "boundaries" between NHRs, IHRs, and OHRs are artificial benchmarks to allow comparison among highly variable abiotic and biotic gradients; they are not self-contained zones.

The use of the 0–4 m depth range for NHRs of east Florida's mainland is based on assemblage differences by depth ranges previously reported (CSA International, Inc. 2009; CSA Ocean Sciences Inc. 2014). Shallow reefs in many sites along the coast are often not present below 4 m until reef lines re-emerge at greater depths. Within the 0–4 m depth range, quantitative differences have been observed in both epibiota coverage and macroalgae biomass between the shallowest and deepest depths of NHRs (CSA Ocean Sciences Inc. 2014). It can be useful to refer to an intertidal (0–1 m) and a subtidal area (1–4 m) (CSA Ocean Sciences Inc. 2014). This approach allows for a finer scale assessment of assemblages considering observed microhabitat variability that can occur at very small spatial scales. Both areas are populated by disturbance-adapted organisms, and distributional patterns vary due to the dynamics of the physical environment. The 0–4 m depth range is also most susceptible to burial by sediments placed in efforts to widen eroded beaches.

Complex physical and biological assemblage relationships exist between intermediate and offshore depth ranges for hardbottom (Fig. 1.7), with most available studies concentrated on the southern part of the east Florida coast (Goldberg 1973; Moyer et al. 2003; Banks et al. 2008; Walker 2012; Walker and Gilliam 2013; Stathakopoulos and Riegl 2015). Light penetration, water temperature, sedimentation, and circulation vary considerably in shallower hardbottom areas and greatly influence the structure and dynamics of invertebrate assemblages (Rogers 1990; Banks et al. 2008; Harborne et al. 2017). Species composition and abundance at settlement for common reef fishes also varies across nearshore and mid shelf depths (e.g., Jordan et al. 2012).

Palm Beach through Monroe counties have the most highly studied coral reef areas along the mainland east Florida coast (Lighty 1977; Moyer et al. 2003; Banks et al. 2007; Walker 2012). Onshore to offshore, several studies from southeast Florida counties refer to the nearshore ridge complex (3–5 m), and inner (~ 8 m), middle (~ 15 m) and outer reefs (~ 16 m) (Moyer et al. 2003; Banks et al. 2008; Walker 2012; Cumming 2017). The hardbottom habitats across the reef lines are colonized by characteristic northern Caribbean, tropical reef fauna and flora, and

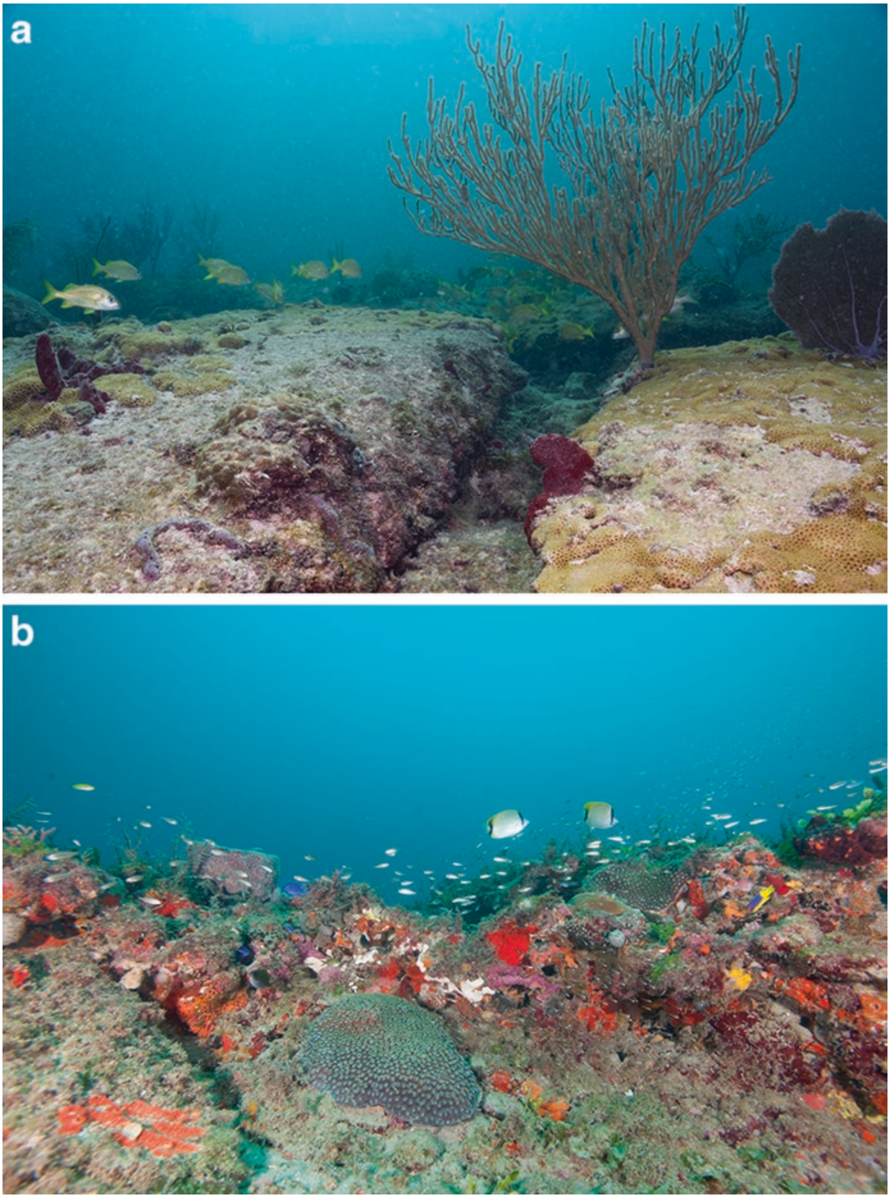


**Fig. 1.7** Examples of: (**a**) intermediate hardbottom (8 m depth), Dania, Broward County (**b**) offshore hardbottom with coral structure near Jupiter, Palm Beach County (20 m depth). (Source: D. B. Snyder)

are necessary for coral colonization and growth (Goldberg 1973; Banks et al. 2008). Moyer et al. (2003) found differences in benthic communities between the inner, middle, and outer reefs (e.g., densities of octocorals and sponges were lower on the inner reef, presumably in response to greater physical variability in shallower waters).

The majority of NHRs of east Florida are within 200 m of the mean high-water mark with little hardbottom in intermediate depths. However, there are notable exceptions in which hardbottom structure is continuous across the shelf through NHR, IHR, and OHR depths. Locations include Riomar Reef in Indian River County, Bathtub Reef and St. Lucie Reef (Peck's Lake) in Martin County, Breakers Reef in Palm Beach County, and some areas of Broward County. More details on the distribution and latitudinal variation of these nearshore reefs is provided in Chap. 2.

## 1.3 Ecological Concepts and Terms

Documentation of how nearshore reefs function as habitat for a diverse set of organisms was guided by fundamental ecological concepts regarding distributions, abundances, and diversities of very different, co-occurring species. To accomplish this, we documented not only the identities of taxa present, but also how these taxa organize into assemblages, how their life histories are adapted for these shallow habitats, and how they respond to or recover from disturbances in these nearshore areas with high wind and wave energy. Our ecological perspectives include the importance of non-equilibrium conditions in shallow ecological systems. This is because resource managers and others often need to consider a general lack of equilibrium when managing ecosystems (e.g., Shrader-Frechette and McCoy 1995; Sale 2011; Selkoe et al. 2015).

To interpret local diversity or assemblage structure, we focused on ecological patterns among species to better understand the distribution and abundance of organisms. This reflects a perspective similar to that advanced by Andrewartha et al. (1954, 1984) and others including Walter and Hengeveld (2014). These autecological approaches mesh well with theories that incorporate spatial and temporal dynamics into understanding of assemblages (e.g., Pickett and White 1985; Petraitis 2013; Menge et al. 2017; Pittman 2017). NHR environments can vary considerably over space and time, and support a broad range of species with distinct environmental adaptations. These invertebrate and algae species interact in manners that can also induce regime shifts in assemblage composition (O'Brien and Scheibling 2018). To constrain ambiguity introduced by sometimes variable terminologies, many technical terms are defined in the Glossary within the context in which they are applied.

### 1.3.1 Equilibrium and Scale

Ecological communities of nearshore reefs do not typically exhibit equilibrium conditions either spatially or temporally when examined over long time-scales. The lack of equilibrium conditions exhibited by many biotic components (e.g., Chaps. 7 and 9) has important implications for assessing impacts of stressors on these ecological systems, as well as assessing the success of mitigation approaches (Parker and Wiens 2005; Perring et al. 2015; Rohr et al. 2018). The assumption of equilibrium conditions does not accurately portray the individual and community-level dynamics among many faunal and floral groups when assessing impacts and the results of mitigation to offset impacts (Parker and Wiens 2005; Giron-Nava et al. 2017).

In non-equilibrium systems like that of NHRs, disturbance can be considered an inherent property of the ecosystem and equilibria can be artefacts of observation, not major properties of the system (Wallington et al. 2005). Unfortunately, many of these ideas have not been translated into regulatory arenas (Sale 2011). Shrader-Frechette and McCoy (1995) summarized key conceptual issues and emphasized the importance of case study approaches, contending that problem-solving would be most effective when ecological knowledge (natural history) as well as ecological theory was applied (Boström et al. 2011). Extreme events (e.g., Gaines and Denny 1993) often influence the outer boundaries of what may be observed in an assemblage, with NHRs as prominent examples in coastal east Florida.

The assessment of equilibrium of biota encountered on or in the vicinity of nearshore reefs is inherently based on the scale of observation. The perceived structure of all levels of ecological hierarchies depends upon the spatial and temporal scales at which they are examined. Clearly, smaller scales (m) will exhibit higher variability than larger scales (km). Consideration of spatial scale is paramount to an understanding of assemblage patch dynamics, particularly in disturbance-mediated environments (Levin and Paine 1974; Pickett and White 1985; Wiens 1989; Kotliar and Wiens 1990; Wu and Loucks 1995; O'Connor and Byrnes 2013; Menge et al. 2015; Witman et al. 2015; Jackson et al. 2017; Schneider 2017) such as east Florida's coast.

### 1.3.2 Foundation Species and Associated Concepts

Prominent species have been used to characterize assemblages for many decades in theoretical and applied ecology, and the concepts of focal or indicator species have been discussed in detail (Zacharias and Roff 2001; Siddig et al. 2016). For example, a keystone species is commonly treated as any predator or functional group which exerts a strong effect over the food-web structure of the associated community (Paine 1966, 1969). We also use the term 'foundation' species (Dayton 1972) to include any species that has a strong (often increasing) effect on local species richness, distribution, and abundance by either creating habitat, modifying the environment, or affecting species interactions or resource availability (Altieri and van de Koppel 2014).

Foundation species that create substantial habitat features are often referred to as habitat or ecosystem engineers which can increase available shelter to enhance species richness and abundance as well as reduce abiotic stress (e.g., Wright and Gribben 2017; Pocklington et al. 2019). A foundation species in many nearshore hardbottom areas is the sabellariid reef-building worm *Phragmatopoma lapidosa* (see Chaps. 4 and 7).

Simberloff (1998) reviewed a variety of approaches that use representative or analytically valuable species with terms including indicator, flagship, and umbrella species. Specific distinctions among these terms can be considered tenuous, commonly because of imprecise metrics of performance and unclear objectives (Simberloff 1998), though various reviews and many studies still usefully employ these terms to varying degrees (e.g., Zacharias and Roff 2001; Siddig et al. 2016).

### *1.3.3 Ecological Functions and Ecosystem Services*

The conceptual underpinnings and terminology associated with the concept of ecological functions are highly variable and encompass many metrics (Wilson 1999; Hooper et al. 2002; Törnroos et al. 2015; Bellwood et al. 2019). At least four broad meanings for the term function were identified by Jax (2005): (1) processes of changes of state (e.g., organismal feeding); (2) the merging of multiple processes in a whole system context (e.g., system functioning); (3) ecological roles within systems (e.g., functional groups such as producers or consumers); and (4) particular services of the system to society (e.g., ecosystem services for humans such as photosynthesis or maintenance of biological diversity).

In terms of marine organisms and assemblages on NHRs, we primarily focus on ecological functions that are related to: (1) habitat structure and shelter use (e.g. nesting and spawning sites, settlement and juvenile habitat use, ecosystem engineering), and (2) trophic dynamics (e.g., autotrophy, herbivory, carnivory, cleaning symbiosis, planktivory and suspension feeding, detritivory and omnivory). This approach considers important feeding interactions and also non-trophic interactions as emphasized in recent research (Kéfi et al. 2015; Pérez-Matus et al. 2017). In addition, we also recognize the functional connectivity among coastal systems and uses by adjacent human populations.

The examination of ecological functions and human societies has a considerable history and humans receive services from ecosystems in at least four major categories (Hooper et al. 2002; MEA 2005; Folke et al. 2005; Bodin et al. 2014; Armitage et al. 2017). In terms of the regulating services category, NHRs as in Figs. 1.3, 1.4, 1.5 and 1.6 are important in the original positioning of barrier island and beach