Chapter 1 Introduction

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Introduction to oysters in Florida

The dominant and only reef-forming bivalve in Florida is the eastern oyster, also known as the American oyster, Crassostrea virginica (Fig. 1.1). The eastern oyster is found intertidally and in shallow subtidal depths along Florida's nearshore and inshore estuarine waters (Fig. 1.2). Eastern oysters are ecosystem engineers as well as keystone species, and the reefs they build provide a variety of critical ecosystem services to coastal communities (Grabowski et al. 2012). Oyster reefs are commercially valuable as a harvested resource and indirectly valuable for protecting shorelines against erosion (Grabowski and Peterson 2007, Scyphers et al. 2011). As filter feeders, oysters improve water quality and clarity by removing nutrients and other pollutants from the water column (Kellogg et al. 2014). The Florida State Wildlife Action Plan (FWC 2012) identifies numerous species of greatest conservation need in Florida as being linked to habitat or food sources provided by oyster reefs, including the eastern oyster itself.

Eastern oysters belong to the family Ostreidae, the true oysters. Florida contains several non-reef-forming members of this family including the mangrove oyster (*C. rhizophorae*), crested oyster (*Ostrea stentina*), threaded oyster (*Teskeyostrea weberi*), frond oyster (*Dendostrea frons*, typically found on soft corals), and possibly the commercial sponge oyster (*Ostrea permollis*), a Caribbean species. The crested oyster is difficult to distinguish from the eastern oyster without examining the inside of the shell. Florida also has oysters in the family Pteriidae (the pearl or winged oysters), including the scaly pearly oyster (*Pinctada longisquamosa*), Atlantic pearly oyster (*P. imbricata*), black-lipped pearly oyster (*P. margaritif-*



Figure 1.1. Eastern oyster (*Crassostrea virginica*) shells are easily recognizable by the purple or red-brown scar left by the adductor muscle. The morphology of the shell varies widely (Galstoff 1964). Photo credit: Kara Radabaugh.

era), Atlantic wing oyster (*Pteria colymbus*), and glassy wing oyster (*P. hirundo*). Pteriidae tree oysters, including the flat tree oyster (*Isognomon alatus*), bicolor purse-oyster (*I. bicolor*), and radial purse-oyster (*I. radiatus*), co-occur in some locations associated with mangroves and are occasionally found in small numbers on reefs of the eastern oyster. One species of hammer oyster (family Malleidae), the Caribbean hammer oyster (*Malleus candeanus*), is found only in coral reef habitats. Finally, foam oysters (family Gryphaeidae) are also found on coral and other



Figure 1.2. Oyster reef extent in the state of Florida (FWC compilation of oyster maps, FWC 2018).

marine hardbottom. Florida has two native species of foam oysters, the Atlantic (*Hyotissa mcgintyi*) and deepwater (*Neopycnodonte cochlear*), as well as one introduced species, the giant foam oyster (*H. hyotis*) (Forbes 1966, Thayer et al. 2005, Mikkelsen and Bieler 2008).

Eastern oyster life history and ecology

Eastern oysters reproduce via broadcast spawning with external fertilization, while other oysters (e.g. *Ostrea* spp.) reproduce via internal fertilization and brooding before the release of larvae. Because multiple generations of oysters settle on top of one another, numerous generations

ations of eastern oysters can contribute to a diverse mixture of genotypes during spawning (NOAA 2007). Areas with low oyster density have lower spawning biomass and consequent decreased rates of fertilization (Mann and Evans 1998). Spawning generally requires water temperatures above 20 °C (68 °F); while May–October is the peak period in Florida, reproduction may continue year-round in all but the coldest times of the year (Berrigan et al. 1991, Volety et al. 2009).

After hatching, eastern oysters spend 2–3 weeks as planktonic larvae before settling on a hard substrate (Stallworthy 1979, Kennedy 1996). During settlement, oyster larvae attach to a substrate and metamorphose

into their sessile benthic form. Successful recruitment refers to both settlement and some period of postsettlement survival (Wildlish and Kristmanson 1997, Baggett et al. 2014). Rates of settlement are generally dictated by larval density, water residence time, water quality, substrate availability, and larval mortality. In contrast, recruitment and postsettlement survival are additionally influenced by rates of predation, environmental stress, and competition with other bivalve species or conspecifics (Mann and Evans 1998, Baggett et al. 2014). Recruitment is therefore highly variable spatially and temporally (on both seasonal and annual timescales). Estuaries with high rates of flushing tend to have low but more consistent recruitment, while estuaries with low flushing have higher but more variable recruitment (Kennedy 1996). After settling, oysters can reach reproductive maturity in as little as four weeks and grow to a length of 7-8 cm (3 in) in the first 18–24 months in Florida's warm waters (NOAA 2007, FWC 2010, VanderKooy 2012). Most eastern oysters are protandrous hermaphrodites, meaning that they begin life as males and later change to primarily female reproductive organs. Some females may revert to male later in life (Thompson et al. 1996).

Spawning and larval development may be reduced in response to high temperatures or abrupt changes in temperature (Kennedy et al. 1996). While oysters are tolerant of extreme high temperatures up to 36–40 °C (97–104 °F), their tolerance decreases above 28 °C (82 °F) if the high temperatures co-occur with disease, low oxygen, or salinity extremes (Shumway 1996, Coen and Bishop 2015, Rybovich et al. 2016, Southworth et al. 2017). Tolerance of salinity extremes are similarly limited if combined with higher temperatures (Shumway 1996). Temperature and salinity influence nearly every aspect of oyster physiology, including feeding, respiration, reproduction, larval life span, growth, and survival (Shumway 1996). While eastern oysters can briefly tolerate extreme salinity ranging from 5 to 40, prolonged exposure to salinity outside their ideal range of 14 to 28 can harm both subtidal and intertidal populations (Shumway 1996, Baggett et al. 2014, Coen and Bishop 2015). Growth and reproduction decrease at low salinity, and oysters can suffer high rates of mortality over a short period under freshwater conditions (Shumway 1996, Thayer et al. 2005, Turner 2006). While oysters can physiologically tolerate high salinity for extended periods, they are more vulnerable to disease and predation as marine predators and parasites of oysters can survive and reproduce in those saline conditions (Coen and Bishop 2015, Garland and Kimbro 2015). Several estuaries in Florida are home to significant populations of oysters that survive in an average salinity range of 30–35 (Parker et al. 2013). These populations are predominantly intertidal and so have daily protection from marine predators during exposure at low tide. Oysters in these reefs must have some combination of a reproductive potential that exceeds predation and parasitism or have a genetic aptitude towards survival at high salinity (Koehn et al. 1980a).

Eastern oysters in Florida are of two relatively distinct genotypes, which can be differentiated by genetic analyses. The Atlantic coast of the United States from Maine to Cape Canaveral, on the east coast of Florida, predominantly supports the Atlantic coast genetic stock, while the southeastern Atlantic and Gulf of Mexico coasts from Florida to Texas are home to the Gulf coast genetic stock (Buroker 1983, Hare and Avise 1996, FWC 2010). Marine invertebrate species including bivalves often exist as a metapopulation, a group of spatially separated local populations with some degree of interbreeding and genetic exchange (Kritzer and Sale 2006, Bert et al. 2014). For instance, Florida bay scallops (Argopecten irradians concentricus) exhibit genetic exchange between local populations within the larger metapopulation (Bert et al. 2014). The eastern oyster is also such a species; its local populations can be relatively isolated, but interbreeding and larval export sometimes occur (Reeb and Avise 1990, Murray and Hare 2006, Varney et al. 2009, Anderson et al. 2014, Arnold et al. 2017).

Larval export and settlement in neighboring estuaries are key to the maintenance of a population's genetic diversity (Kritzer and Sale 2006). Most of Florida's estuaries once had abundant oyster reefs, but the areal extent of these reefs has declined significantly (see discussion on threats below). When the oyster population in an estuary declines, it reduces the chances that larvae will be exported from that estuary and subsequently imported by a neighboring estuary. As a result, oyster populations in each estuary function largely as an isolated local population with only occasional larval exchange (Arnold et al. 2017). Detailed genetic analyses are needed to determine the degree of larval export and genetic isolation among Florida's remaining oyster reefs, as genetic diversity is key to oyster populations surviving the variety of environmental stressors they currently face (Koehn et al. 1980b, Hilbish and Koehn 1987, Arnold et al. 2017).

Oysters grow best in regions where water currents move settled particulates. These currents provide water exchange for feeding and keep oysters from being smothered in sediment, their own feces, or pseudofeces (incorporated particulates expelled by the oyster with mucus that did not pass through the digestive tract) (Lenihan 1999, Levinton et al. 2001). Oysters filter feed on phytoplank-

ton, small zooplankton, bacteria, suspended particulate organic matter, and dissolved organic matter in the water column (Langdon and Newell 1996, Dame et al. 2001). Oysters remove excess organic matter and fine sediments from the water; this filter feeding increases water clarity and improves light conditions for seagrass and other benthic photosynthesizers (Booth and Heck 2009, Peterson and Heck 2001a, 2001b). Additional benefits may occur when the complex structure of oyster reefs entrains sediments by physical processes; these benefits include improved water quality and stabilized reef structure resulting from the filling of pore spaces between shells (Walles et al. 2015). Additionally, algae and associated organisms often form a complex film that encrusts oyster shells and serves as an important food source for invertebrates that live within the microhabitats of oyster reefs.

Oyster reefs and shell budgets

Over many decades, multiple generations of oysters settle upon one another, constructing complex calcium carbonate reefs. Reef accretion depends on the rate of shell deposition relative to rate of shell loss; the balance between the two can be quantified as a shell budget (Powell et al. 2006). Natural shell deposition occurs through the growth and calcification of oysters. Large, longlived oysters are particularly important contributors of shell material (Waldbusser et al. 2013). Oyster growth encourages further reef building as shell presence leads to increased settlement of calcifying organisms. For this reason, occasional die-offs can even increase the rate of carbonate addition to the reef (Kidwell and Jablonski 1983). Shell mass can be lost as a result of bioerosion (from boring sponges, worms, and mollusks), chemical degradation, dissolution, subsidence, burial, erosion, and habitat loss due to harvesting or dredging (Powell et al. 2006, Waldbusser et al. 2011, Rodriguez et al. 2014). Oyster reefs with a balanced shell budget can maintain their intertidal position or depth in the water column in response to changes in water depth as sea level rises. Yet many oyster reefs in Florida and the eastern United States have negative shell budgets; this shell loss results from a complex set of factors (see discussion on threats, below).

Oyster reefs are found in the majority of bays and lagoons in Florida (Fig. 1.2). Local oyster distribution is limited to locations with hard substrates for attachment, such as hardbottom, mangroves (Fig. 1.3), seawalls, pilings, or shell accumulations (FWC 2010, Drexler et al. 2014). Fringing intertidal oyster reefs occur on the edges of shallow embankments in and around estuaries and lagoons, where they stabilize shorelines and prevent erosion



Figure 1.3. Oysters growing intertidally on red mangrove (*Rhizophora mangle*) prop roots. Photo credit: Kara Radabaugh.



Figure 1.4. Oyster reefs are home to numerous other invertebrates, including predators of oysters such as the crown conch (*Melongena corona*) and reef associates such as the West Indian false cerith (*Batillaria minima*). Photo credit: Kara Radabaugh.

(Scyphers et al. 2011, Hanke et al. 2017). Subtidal reefs are generally found in water less than 4–5 m (13–16 ft) deep (MacKenzie 1996, NOAA 2007). The physical structure of the reef and its associated fauna provide a complex refuge and feeding habitat for many invertebrates including mollusks, echinoderms, fish, crustaceans, flatworms, boring sponges, polychaetes, mammals, and birds (Fig. 1.4; ASMFC 2007, Coen et al. 2007, zu Ermgassen et al. 2016). Over 30 species of greatest conservation need in Florida are linked to habitat or food sources provided by oyster

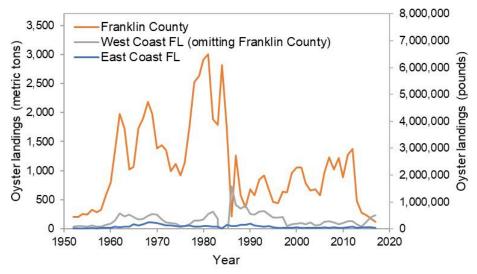


Figure 1.5. Oyster harvest in Franklin County (Apalachicola Bay), the remainder of the west coast of Florida, and the east coast of Florida from 1951 to 2017. Oyster landings data before 1986 were collected under a voluntary reporting system. Data sources: 1951–1983, Florida Commercial Marine Fish Landings (see Appendix A); 1984–1985, Berrigan (1990); 1986–2017, FWC (2018).

reefs, including the American Oystercatcher (*Haemato-pus palliates*), the Short-billed Dowitcher (*Limnodromus griseus*), the Marbled Godwit (*Limosa fedoa*), the diamond-backed terrapin (*Malaclemys terrapin*), the peppermint shrimp (*Lysmata wurdemanni*), and the banded tulip snail (*Fasciolaria lilium*) (FWC 2012).

Oyster harvesting in Florida

Oysters have high intrinsic economic value and have been both harvested as a food source and mined for shell (Coen et al. 2007, Grabowski et al. 2012). About 98% of Florida's oyster harvests come from the Gulf coast, and 90% of the state's historical harvests originated from Apalachicola Bay in Franklin County (Fig. 1.5; FWC 2010, VanderKooy 2012). Oysters are abundant along the Atlantic coast of Florida, though they are nearly all in intertidal reefs and harvesting is less common. Statewide harvests have varied significantly since 1950 (Fig. 1.5), largely as a result of varying salinity and the impacts of hurricanes on Apalachicola Bay (Berrigan et al. 1991, FWC 2010). In 2012–2013, a dramatic decline occurred in the oyster fishery in Apalachicola Bay due to a combination of low river flow, increased predation and disease, and removal of substrate by fishing; all these factors led to high mortality and low recruitment (Camp et al. 2015, Pine et al. 2015, Fisch and Pine 2016). Historical catch data and the fishery collapse in Apalachicola Bay are discussed in detail in Chapter 3 of this report.

Oyster decline has been even more dramatic on the mid-Atlantic coast of the United States, where commercial harvests have decreased to only 1–2% of previously recorded landings as a result of overharvesting and mortality from parasites (Beck et al. 2011). Oyster populations on the mid-Atlantic coast are now considered to be in poor condition or functionally extinct (Beck et al. 2011). Before the 2012 collapse in Apalachicola Bay, landings and oyster populations in the Gulf of Mexico were more stable than in the mid-Atlantic (NOAA 2007, Beck et al. 2011).

The Florida Shellfish Commission was established in 1913 to enact shellfish harvesting laws and implement a leasing program. Since that time, responsibility for shellfish harvesting regulations has passed through several state agencies (Arnold and Berrigan 2002). Data on historical commercial fishery yields from 1950 through 1983 were generated by a variety of agencies (see Appendix A). Commercial harvest records from 1984 to present are available from the Florida Fish and Wildlife Conservation Commission (FWC). Commercial landings from all Florida fisheries, including oysters, are available in a report generator that can sort landings by coast, region, or county at https://myfwc.com/research/saltwater/fishstats/ commercial-fisheries/landings-in-florida/ (FWC 2018). Prior to 1986, data on trips and oyster landings were collected voluntarily; the FWC has since recorded this information via a mandatory reporting system (Camp et al. 2015). The FWC establishes limits and seasons for both commercial and recreational harvest. Current regulations

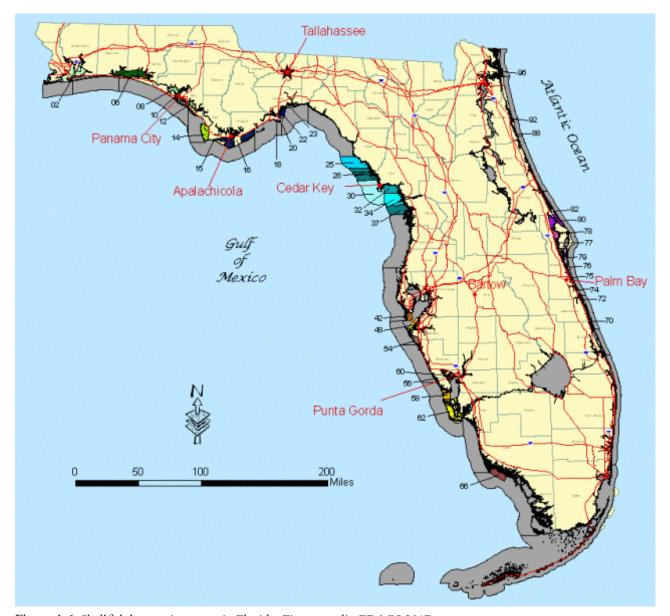


Figure 1.6. Shellfish harvesting areas in Florida. Figure credit: FDACS 2017.

for the commercial or recreational harvest of oysters may be found at http://myfwc.com/fishing/saltwater. States surrounding the Gulf of Mexico require a market size of at least 7.6 cm (3.0 in) shell height for oysters harvested from public reefs, but in Florida this size limit does not apply to private oyster leaseholders (VanderKooy 2012). Commercial oyster landings in Florida are reported as pounds of oyster meats. Conversion factors for commercial landings of oysters and other marine species may be found at https://myfwc.com/media/9085/sumfact.pdf.

The Florida Department of Agriculture and Consumer Services (FDACS) divides Florida into shellfish management areas (Fig. 1.6) and issues leases for the cultivation of oysters. Shellfish management areas are classified into sections that are deemed approved, conditionally

approved, conditionally restricted, restricted, or prohibited for shellfish harvest. As filter feeders, oysters may accumulate harmful substances including heavy metals, toxins from harmful algal blooms (HABs), pathogenic bacteria such as *Vibrio parahaemolyticus*, and viruses like Norovirus. Therefore, bays in Florida in which oysters are commercially harvested for human consumption are monitored for bacteria, red tide, and other pollutants by FDACS and FWC. FDACS can issue closures of shellfish harvest areas when oysters are not safe for consumption. The regional status of shellfish harvesting areas in Florida is available at http://shellfish.floridaaquaculture.com/seas/seas_statusmap.htm.

Oyster shells have been dredged or mined in Florida for use in road construction, in decorative projects such



Figure 1.7. Bagged cultch is used to provide a substrate for oyster settlement. Photo credit: GTMNERR.

as driveways and walkways, or as material for oyster settlement (known as cultch) for oyster restoration efforts (Whitfield 1975). Extensive shell deposits across Florida can be found in middens from centuries of harvesting by indigenous populations (Dame 2009, Saunders and Russo 2011). Oyster shells were mined extensively in Florida from shell middens as well as from submerged and intertidal oyster reefs. Before 1947, companies could dredge shell from live oyster reefs that were deemed unproductive, so long as an artificial reef was constructed as replacement. But productive reefs were sometimes targeted for dredging, and restored extent often fell short of the original reefs (Whitfield 1975). Extensive shell dredging operations led to a decline in suitable oyster habitat in several estuaries due to a lack of suitable hard substrate and excess sedimentation (Whitfield 1975).

Because oysters provide essential ecosystem services and are so important economically, a great deal of effort is being exerted to enhance or restore oyster reefs. Restoration objectives may focus on increasing harvest potential or improving the value of the ecosystem services provided by oyster reefs. Oyster settlement is encouraged in many areas of Florida through the provision of cultch such as bagged or unconsolidated natural or fossil shell (Fig. 1.7; Brumbaugh et al. 2006, Walters et al. 2017). Management practices for fisheries often include replacing harvested substrate with cultch. As shell and fossil shell become more expensive or difficult to find, some oyster restoration projects, especially large commercial reefs, have switched to various types of rock, especially limestone. A variety of other alternative substrates can also be used in oyster reef restoration (concrete, porcelain, sandstone, granite, clam shell, engineered options, etc.; Goelz 2017). The Oyster Restoration Workgroup website, available at http://www.oyster-restoration.org, presents an array of resources regarding site selection, materials, gear, implementation, monitoring, and reports of oyster restoration projects.

Threats to oyster reefs

Globally, oyster reef habitat has declined by more than 85%, and remaining habitats are often in poor condition (Beck et al. 2011). In the United States, oyster spatial extent has decreased by as much as 64%, and oyster biomass has



Figure 1.8. A lightning whelk (*Sinistrofulgur sinistrum*) consuming oysters on a reef in Tampa Bay, Florida. Photo credit: Christine Russo.

declined by 88% (zu Ermgassen et al. 2012). Worldwide, declines are due primarily to unsustainable harvesting practices in combination with disease, pollution, sedimentation, and competition with nonnative species (Beck et al. 2009, Beck et al. 2011, Gillies et al. 2015). The loss of this keystone species can alter the trophic structure of an estuary. For example, in the Chesapeake Bay, dramatic declines in oyster populations have been linked to increased occurrences of hypoxia and shifting food chain dominance from benthic to pelagic organisms (Ulanowicz and Tuttle 1992, Thayer et al. 2005, Breitburg and Fulford 2006).

Although Florida oyster populations were considered to be more stable than those in many other regions (Beck et al. 2011, zu Ermgassen et al. 2012), the State still classifies reefs as being in relatively poor and declining condition with a very high level of habitat threat (FWC 2012). It is estimated that 80-90% of oyster reefs have been lost in several Florida estuaries (Meeder et al. 2001, Schmid et al. 2006, Estevez 2010, Boswell et al. 2012, Kaufman 2017). Although Apalachicola Bay historically dominated state harvests, it suffered serious declines in 2012-2013 and has not recovered (Fig. 1.5; Pine et al. 2015). The most critical stressors identified in Florida's State Wildlife Action Plan include altered hydrologic regimes, altered water quality, and habitat disturbance (FWC 2012). These and other threats are described in further detail below.

Altered hydrology and salinity: Altered hydrology as a result of stormwater management, canalization, freshwater withdrawal, and coastal development is the most significant threat to bivalve habitats in Florida (FWC 2012, Camp et al. 2015). Altered hydrology and low flushing can lead to extreme salinity events, increased sedimentation, low oxygen levels, and increased temperature. Channelization reduces sheetwater flow through coastal wetlands and concentrates freshwater runoff, reducing salinity around outflows beyond levels optimal for oyster growth and reproduction (Thayer et al. 2005, Turner 2006). Conversely, freshwater withdrawal, diverted stormwater runoff, and drought conditions can increase estuarine salinity, making oysters more vulnerable to predation and disease (Coen and Bishop 2015). Rapidly changing or seasonally variable salinity can also have detrimental effects on fish and invertebrate communities associated with oyster reefs (Tolley et al. 2006) but may provide relief from predation and disease. A large number of oyster reefs in Florida are stressed by salinity extremes brought about by altered hydrology, particularly in south Florida, Apalachicola Bay, and the Big Bend (Tolley et al. 2005, Parker et al. 2013, Camp et al. 2015, Frederick et al. 2016). The locations of oyster reefs have even shifted inshore or upriver in the Big Bend and the Everglades, following the lower salinity regimes (Volety et al. 2009, Seavey et al. 2011).



Figure 1.9. Boring-sponge infestation on an oyster shell. Photo credit: Linda Walters.

Predation: Rates of predation and density of predators (native and nonnative) on oyster reefs are influenced by a variety of physical factors including salinity, temperature, and dissolved oxygen (Eggleston 1990, White and Wilson 1996, Tolley et al. 2005, Garland and Kimbro 2015). High salinity allows for the survival of marine predators, making oysters vulnerable to high rates of predation. Predators of eastern oysters include crown conchs (Melongena corona), oyster drills (Stramonita haemastoma and Urosalpinx cinerea), mud crabs (Panopeus herbstii), black drum (Pogonias cromis), and occasionally lightning whelks (Sinistrofulgur sinistrum) (Fig. 1.8; Tolley et al. 2005). Predation occurs statewide, but high mortality due to predation has especially been noted in Apalachicola Bay and the Big Bend following periods of increased salinity (Camp et al. 2015, Frederick et al. 2016).

Development: Oysters are subject to direct habitat loss as a result of coastal development, shoreline hardening, and dredging, but they are also indirectly vulnerable to diminished water quality and increased pollutants and sedimentation associated with coastal development (Frazel 2009). Hardened shorelines interrupt the transition area from upland to benthic habitat. While seawalls often provide a substrate for oyster settlement, the surface area is often smaller than that of the intertidal habitat they replace. Reflected wave energy from seawalls can also undermine potential adjacent oyster habitat. Oyster habitat has been lost to development across Florida, most notably

in areas of high population density such as Tampa Bay, Sarasota Bay, Charlotte Harbor, Naples Bay, and much of southeast Florida.

Substrate loss: The physical removal of oyster reefs and associated shell through harvesting, mining, construction, or dredging reduces the overall reef footprint and available substrate for settlement of new oysters. While reefs naturally lose substrate through degradation and dissolution, ocean acidification also presents challenges for all calcifying marine and estuarine organisms and is expected to lower rates of calcification and survival while increasing shell degradation (Hofmann 2010, Waldbusser et al. 2011). Substrate loss due to mining historically was common across Florida (particularly in Tampa Bay and Charlotte Harbor). Continued loss to live harvesting remains a concern and has had a particularly detrimental impact on reef extent in Apalachicola Bay and Suwannee Sound (Camp et al. 2015, Pine et al. 2015, Kaufman 2017).

Hypoxia: While oysters can tolerate occasional exposure to low dissolved oxygen, hypoxia and anoxia decrease settlement, growth rate, and survival (Baker and Mann 1992, Johnson et al. 2009). Dissolved oxygen under 2 mg/L can cause mortality in subtidal oysters and associated reef fauna (Lenihan and Peterson 1998). Benthic hypoxia may arise when water bodies are stratified as a result of freshwater flow or limited vertical mixing (Woithe and Brandt-Williams 2006). Water bodies with limited flushing, such as the Indian River Lagoon, are also susceptible

to hypoxia, particularly in warm summer temperatures when oxygen solubility is low (FDEP 2014). Areas with high sedimentation of organic matter are also prone to decomposition-induced benthic hypoxia (Volety et al. 2008). Subtidal oyster reefs with sufficient vertical relief that elevates them off the bottom are less often exposed to hypoxic conditions (Coen and Humphries 2017). Intertidal oyster reefs encounter hypoxia less often as they are periodically submerged in surface water that has higher concentrations of dissolved oxygen (Coen and Humphries 2017).

Disease and parasitism: Two protozoan diseases can cause high mortality in oyster populations. Perkinsus marinus causes the disease dermo and Haplosporidium nelsoni causes the disease MSX (Ford and Tripp 1996, Fisher et al. 1999). Dermo is present in waters throughout Florida, although typically at a low intensity (Volety et al. 2009). The disease is usually recognized as a weakening factor for oysters rather than a primary cause of mortality in Florida. Dermo may have been a contributing factor to an oyster die-off in Pensacola Bay in 1971, although there was also poor water quality at the same time (USEPA 2004). MSX, first noted in the United States in the late 1950s, is present from Maine to northeast Florida and can cause local die-offs of as much as 90% mortality (Burreson et al. 2000). MSX has never been detected in the Gulf of Mexico (Ford et al. 2011), and its presence in Atlantic Florida waters is not pathogenic (Burreson and Ford 2004, Walters et al. 2007). Infestations of boring sponges (Fig. 1.9), polychaetes, and boring mollusks can also harm oysters and make shells more vulnerable to predators or breakage; this forces the oyster to dedicate more energy toward shell repair and away from growth and reproduction (Buschbaum et al. 2007, VanderKooy 2012). Oysters are more susceptible to these diseases and parasites at higher salinity (Camp et al. 2015, Coen and Bishop 2015).

Boating impacts: Boat wakes can cause significant local damage and erosion on intertidal oyster reefs, harming both established adults and new recruits (Grizzle et al. 2002, Wall et al. 2005). Erosion of intertidal reefs and salt marshes from boat wakes is a significant problem in many parts of northeast Florida, particularly along the Intracoastal Waterway. Mosquito Lagoon oyster reefs have extensive dead margins and in some cases have been reduced to intertidal sand flats as a result of erosion from boat wakes (Grizzle et al. 2002).

Sedimentation: Excessive sedimentation due to dredging or the lack of water currents can bury oysters and impede filter feeding and respiration (Thayer et al. 2005, Coen and Humphries 2017). Many of the reefs in Naples Bay were buried due to dredging, and seismic profiling has revealed remnant reefs buried below sediment

(Savarese et al. 2006). Shell removal can also increase sedimentation on reefs, which can smother remaining oysters on low-relief reefs (Berrigan et al. 1991, Breitburg 1999, Lenihan 1999). Bottom currents help protect subtidal oysters from burial in sediments or their own feces and pseudofeces.

Overharvesting: Until recently, the oyster fisheries in the Gulf of Mexico were described as one of the last remaining areas in the United States (and perhaps globally) for which oyster conservation and sustainable wild fisheries were feasible (Beck et al. 2011). Areas such as Apalachicola Bay that have historically been central to the oyster fishery along the Gulf now face significantly reduced harvests as a result of numerous stressors including salinity variability, tropical storms and hurricanes, and substrate loss (Camp et al. 2015, NASEM 2017). While overharvesting is seldom considered a primary threat to oyster populations in Florida (in the sense that harvest does not limit recruitment; NOAA 2007, FWC 2012, FWC 2013), the substrate depletion associated with harvest may constitute a form of overfishing that results in loss of essential habitat (Pine et al. 2015, NASEM 2017). The effects of fishing pressure and substrate removal are of growing concern, particularly when paired with altered hydrology and sea-level rise.

Chemical contamination: Pesticides, fungicides, and herbicides enter the estuarine environment through runoff. Herbicides or antifouling chemicals such as tributyltin (TBT) can inhibit oyster growth, cause shell thickening, increase disease abundance, or decrease disease resistance (Alzieu 1998, Fisher et al. 1999, Bushek et al. 2007). According to Mussel Watch, a U.S. program that monitors bivalve contaminants, oysters at many sites in Florida have elevated levels of arsenic, copper, mercury, or lead (Kimbrough et al. 2008). Contamination by crude oil can also have detrimental impacts on oyster health (Barszcz et al. 1978). Following the Deepwater Horizon oil spill, the densities of spat, juvenile to young adult oysters, and market-size oysters decreased in several Gulf states (Grabowski et al. 2017, NASEM 2017). However, there is no evidence that the oil spill contaminated seafood from Apalachicola Bay (Havens et al. 2013).

Competition: Invasive species such as the striped barnacle (*Balanus amphitrite*), Asian green mussel (*Perna viridis*), charru mussel (*Mytella charruana*), and pink titan acorn barnacle (*Megabalanus coccopoma*) compete against native oysters for space and resources (Boudreaux 2003, Baker et al. 2007, Yuan et al. 2016). The presence of nonnative species can decrease larval settlement and survival of juveniles (Yuan et al. 2016). When present in high densities, native oysters and nonnative mussels may also



Figure 1.10. Asian green mussels (*Perna viridis*) on an oyster reef in Tampa Bay, Florida. Photo credit: Scott Adams.

compete with each other as they grow and mature (Galimany et al. 2017). A native of the Indo-Pacific, the Asian green mussel (Fig. 1.10) has established populations on both the Gulf and Atlantic coasts of Florida (Baker et al. 2007). While cold weather can cause die-offs and restrict expansion of the mussel, the range of this invasive species is expected to grow in the southeastern United States as a result of climate change (Firth et al. 2011, Urian et al. 2011).

Climate change: Rising sea level, altered precipitation patterns, increasing temperatures, and ocean acidification all pose significant threats for oysters (Hoegh-Guldberg and Bruno 2010, Rodriguez et al. 2014).

• Sea-level rise: Intertidal exposure offers oysters refuge from predation, pests, and disease (Bahr and Lanier 1981). Increased submergence times and salinity lead to increased susceptibility to predation and pathogens (Shumway 1996). As the rate of sea-level rise continues to accelerate, intertidal oysters will need to migrate landward or accrete sufficient substrate if they are to keep pace with water depth (Rodriguez et al. 2014). Similarly, subtidal reefs will need to colonize substrates with higher elevations or grow vertically to maintain viable depths. Oyster reefs with balanced shell budgets and manageable stressors are the most likely to keep pace with sea-level rise, as new shell material will enable the

reef to grow vertically into the space provided by the rising water (Rodriguez et al. 2014). Reduced recruitment due to sea-level rise may move oyster reefs toward a shell budget deficit, as shell loss reduces carbonate supply and hampers reef building (Waldbusser et al. 2013, Solomon et al. 2014). Sea-level rise also causes estuaries to be increasingly saline and pushes seawater further up the estuary. Depending on the shape of the estuary, this shift can decrease the geographic area for which the salinity is suitable for oyster growth. As estuaries become more saline, oysters will become more vulnerable to predation, disease, and harmful algal blooms (Petes et al. 2012, Gobler et al. 2013, Garland and Kimbro 2015).

• Altered precipitation patterns: Global warming alters precipitation patterns by increasing evaporation and increasing the water-holding capacity of the atmosphere (Trenberth 2011). This effect can exaggerate weather patterns, including droughts and floods. Regions in Florida, such as parts of the southeast and southwest coast, Apalachicola Bay, and Suwannee Sound, that have historically been susceptible to high salinity as a result of both low precipitation and freshwater withdrawal, will continue to be vulnerable to more extreme variations in precipitation (Kelly and Gore 2008, Petes et al. 2012, SWFWMD 2015).

- Increasing temperatures: Oysters in Florida are already coping with temperatures near the upper limit of their physiological tolerance. Not only are oysters more susceptible to disease in high temperatures, but they can suffocate because the solubility of oxygen decreases as temperatures rise. Increased temperatures also can change the timing and frequency of oyster spawning (Hofmann et al. 1992, Wilson et al. 2005) and reduce larval survival and settlement (Shumway 1996). Not only will increasing temperatures expose ovsters to temperature extremes more often, but also a lack of critical cool temperatures during winter months may force oysters to allocate energy toward survival and reduce energy input toward growth and reproduction (Kraeuter et al. 1982, Thompson et al. 1996). High temperatures have also been shown to disproportionately affect large oysters as oxygen diffusivity decreases and disease intensity increases with body size (Forster et al. 2012, Waples and Audzijonyte 2016). This phenomenon can result in the loss of large oysters (Lehman 1974), which are disproportionately important to reproduction and shell budgets (Waldbusser et al. 2013).
- Ocean acidification: Ocean acidification results from an increase in atmospheric carbon dioxide which dissolves in water, reducing carbonate ion concentrations in the water column and lowering pH. These changes make it difficult for calcifying organisms such as oysters to produce shell and can enhance dissolution of existing shell material (Hofmann 2010, Waldbusser et al. 2011, Waldbusser et al. 2013). Eastern oyster larvae reared under acidic conditions have shown stunted shell growth and reduced calcium content (Miller et al. 2009).

Mapping oyster reefs

The choice of techniques used to map oyster reefs depends on the size of the area to be mapped, which can vary from an individual restored reef (typically < 1 ha) to the regional or even statewide scale (thousands of ha). Relatively small intertidal reefs can be mapped directly by walking around the perimeter of oyster beds while they are exposed at low tide with a real-time kinematic global positioning system (RTK GPS) or differential GPS (dGPS) (Gambordella et al. 2007, Baggett et al. 2014). A surveyor's measuring wheel or transect tape may also be used to measure the perimeter, length, or width of the reef. Geographic information system (GIS) software may then be used to document the location and calculate reef areal coverage or reef footprint. For larger scales, oyster reefs are mapped from georeferenced multispectral or hyper-

spectral imagery (Grizzle et al. 2002, Le Bris et al. 2016). These remote images may be collected at low tide using satellites, airplanes, balloons, or drones. Oyster reefs are identifiable in aerial photographs by patterns of light and dark, texture, and shape (Grizzle et al. 2002). In traditional photo-interpretation, a person visually identifies oyster reefs in aerial images. This process can be automated or semiautomated using various object-recognition software packages (O'Keife et al. 2006, SCDNR 2008). All methods of remote sensing require some ground truthing for assessing the accuracy of the mapping products, which, for intertidal reefs, may be conducted by visual validation at low tide (SCDNR 2008, Meaux 2011).

Reef identification from aerial photography can be confounded if oysters are covered in mud or intermixed with algae, seagrass, rubble, or darkly colored sediment (O'Keife et al. 2006, Vincent 2006, SCDNR 2008, Le Bris et al. 2016). The spectral signature of reflectance will also vary depending on vertical or horizontal orientation of individual oysters, the sun's angle, and seasonally variable algal growth (Vincent 2006, SCDNR 2008, Le Bris et al. 2016). In Florida, the mangrove canopy can hide fringing oyster reefs and oysters growing on mangrove roots (Fig. 1.11). Mapping based on remote imagery is only possible on reefs with a horizontal footprint. Oysters growing on mangrove roots or seawalls are seldom mapped because these peripheral habitats are difficult to see in aerial photography, but those oysters still contribute significantly to an estuary's population (Drexler et al. 2014).

Subtidal reefs can be mapped indirectly with sidescan or multibeam sonar and simultaneous acquisition of



Figure 1.11. Oysters that grow on prop roots and as fringes under mangrove canopy are difficult to map using aerial imagery. Photo credit: Kara Radabaugh.

Table 1.1. Selected habitat classification schemes including oyster reefs. See text for affiliation acronyms. (Continues next page.)

Name	Affiliation	Region	Classification scheme	Reference
Florida Land Use and Cover Classification System (FLUCCS)	FDOT	Florida	Wetlands o Non-vegetated o Oyster bars	FDOT 1999
System for Classification of Habitats in Estuarine and Marine Environments (SCHEME)	FWC	Florida	Reef/hardbottom • Mollusk reef • Bivalve reef	Madley et al. 2002
Guide to the Natural Communities of Florida	FNAI	Florida	Marine and estuarine • Mollusk reef	FNAI 2010
Florida Land Cover Classification System	FWC	Florida	Estuarine • Intertidal • Oyster bar	Kawula 2009, 2014, Kawula and Redner 2018
Sarasota County Water Quality Planning Methods Manual for Field Mapping of Oysters	Sarasota County	Sarasota and Tampa bays	Oyster habitat characterization codes Shell Scattered shell Oyster clumps Scattered oyster clumps Oyster reef Oyster clumps/reef Mangrove apron Mangrove root oysters Seawall Riprap Pilings	Meaux 2011
South Carolina Intertidal Oyster Survey and Related Reef Restoration/ Enhancement Program	SCDNR and NOAA Coastal Services Center	South Carolina	Background (no oysters) Vertical and horizontal oysters • Dense oyster clusters • Oysters tightly clustered on rocks • Vertical clusters on shell • Vertical clusters on horizontal oysters • Vertical oysters on mud • Separate vertical clusters on mud • Vertical clusters on mud Horizontal oysters • Very few clusters on shell • Few live oysters on shell Washed shell	SCDNR 2008

RTK GPS or dGPS data (Allen et al. 2005, Baggett et al. 2014). Acoustic backscatter of side-scan sonar data allow for differentiation between strong and weak acoustic returns, which provide, respectively, some indication of hard and soft substrate (Preston and Collins 2003, Twichell et al. 2007). A high-quality depth finder that uses side-scan technology may also be used to detect changes in bottom type. Multibeam sonar can extract additional directional information from the acoustic return of hundreds to thousands of points simultaneously, providing a high-resolution image with wide swath coverage. Single-beam so-

nar methods are less expensive than multibeam, but they provide data from a narrower footprint (Twitchell et al. 2007, Grizzle et al. 2008). Tidal depth is a critical concern in mapping using acoustic methods because shallow water limits boat access and the width of the sonar swath (Preston and Collins 2003). Divers, poles, or tongs can be used to validate the presence of live subtidal oysters (Baggett et al. 2014).

In areas with high water clarity, mapping can be completed using underwater video imagery with simultaneous collection of RTK GPS or dGPS data. Underwater

Table 1.1. (Continued.)

Name	Affiliation	Region	Classification scheme	Reference
Classification of Wetlands and Deepwater Habitats of the United States	USFWS	National	Estuarine Subtidal Reef Mollusk Intertidal Reef Mollusk Reef Mollusk Regularly flooded Irregularly flooded	Cowardin et al. 1979, FGDC 2013
Coastal Change Analysis Program (C-CAP) Classification System	NOAA	National	Marine/estuarine reef • Mollusk reef	Klemas et al. 1993, Dobson et al. 1995
Coastal and Marine Ecological Classification Standard (CMECS)	FGDC	National	Geoform origin: biogenic Geoform: mollusk reef Fringing mollusk reef Linear mollusk reef Patch mollusk reef Patch mollusk reef Washed shell mound Substrate: biogenic Shell substrate Shell reef substrate Oyster reef substrate Shell rubble Oyster rubble Shell hash Oyster hash Biotic setting: Benthic/attached biota Reef biota Mollusk reef biota Oyster reef Faunal bed Attached fauna Attached oysters Soft sediment fauna Oyster bed	FGDC 2012

videography can map oyster reefs with high accuracy, but it covers a small swath and is greatly restricted by low-visibility conditions (Grizzle et al. 2005, 2008). Videography may also be used in combination with ground truthing to obtain information such as ratio of live to dead oysters, mean oyster size, or density (Grizzle et al. 2005, 2008). Subtidal oyster mapping is complicated by murky water, variable water depth, limited vertical relief, and oyster reefs interspersed with multiple benthic habitats such as seagrass beds and hardbottom.

Classification of oyster reef habitats

Benthic habitat maps use a variety of classification schemes, which are often hierarchical in structure. Most maps simply group all oyster structures into one category, but oyster habitats may be further subdivided based upon characteristics such as shell density, mean size, live/dead,

reef complexity, dominant species, tidal exposure, or reef height (Table 1.1, Baggett et al. 2014). This report does not distinguish between reefs of differing vertical heights and refers to all oyster structures as reefs. However, some publications may refer to an oyster structure with a relief of less than 0.5 m (1.6 ft) as an oyster bed (Beck et al. 2009, Baggett et al. 2014, Gillies et al. 2015). Oysters growing on structures, such as mangrove roots, seawalls, or pilings, have sometimes been termed aggregations (ASMFC 2007, Beck et al. 2009). Relevant statewide and national classification schemes that include classification of oyster reefs are summarized in Table 1.1 and explained in further detail below.

The Florida Land Use and Cover Classification System (FLUCCS) was created by the Surveying and Mapping Office of the Florida Department of Transportation (FDOT). The original classifications were published in 1985 (FDOT 1985) and revised in 1999 (FDOT 1999).

Florida water management districts use FLUCCS for land classifications within their districts but may modify them for their region. Relevant FLUCCS classifications include:

- 6000 Wetlands: areas where the water table is at or near the surface of the land for a significant portion of most years
 - 6500 Non-vegetated: Hydric surfaces lacking vegetation

■ 6540 Oyster bars

The System for Classification of Habitats in Estuarine and Marine Environments (SCHEME) was developed for the U.S. Environmental Protection Agency (USEPA) by FWC in an effort to make a standardized, hierarchical classification system for Florida (Madley et al. 2002). Relevant SCHEME classifications include:

- 3. Reef/hardbottom: region dominated by calcium carbonate substrate formed by reef building organisms
 - **32. Mollusk reefs:** concentration of sessile mollusks attached to a hard substrate
 - **321. Bivalve reef:** oyster reef, partially exposed at low tide

The Guide to the Natural Communities of Florida was first published in 1990 by the Florida Natural Areas Inventory (FNAI 1990) and updated in 2010. Relevant FNAI (2010) classifications include:

- Marine and estuarine: includes subtidal, intertidal, and supratidal zones
 - Mollusk reef: subtidal or intertidal area with concentration of sessile mollusks

The Florida Land Cover Classification System (Kawula 2009, updated in Kawula 2014 and Kawula and Redner 2018) was developed to create a single land cover classification scheme for Florida by integrating established classification systems. The Florida Land Cover Classification System's hierarchy is based upon other mapping schemes including the FNAI's Guide to the Natural Communities of Florida (FNAI 1990) and FLUCCS classifications (FDOT 1999). Relevant classifications include:

- 5000 Estuarine
 - 5200 Intertidal
 - 5230 Oyster bar

Sarasota County developed a Methods Manual for Field Mapping of Oysters for detailed mapping in Sarasota Bay and adjacent tidal creeks (Meaux 2011). Methods are based upon FWC protocols that were used to map oyster habitat in Tampa Bay. The training manual fully describes each category with accompanying photo-

graphs and provides protocols and data sheets for mapping (Meaux 2011). Specific classifications include the following:

- Shell (S): single shells, usually dead, scattered densely enough along a shoreline that a person would step on shells when walking through the area
- Scattered shell (SS): same as above, but shells are less dense, such that a person could walk through the area without stepping on shells
- Oyster clumps (C): clusters of two or more oysters that are cemented together; oysters may be live or dead. Clumps are dense enough that a person would step on shells when walking through the area
- Scattered oyster clumps (SC): same as above, but clumps are less dense, such that a person could walk through the area without stepping on clumps
- Oyster reef (R): includes patch reefs and string reefs, which may or may not be attached to the mainland and may or may not include mangroves growing out of the shell substrate in the center of the reef
- Oyster clumps/reef (CR): central solid oyster reef surrounded by clumps or scattered clumps
- Mangrove apron (MA): solid oyster reef growing in a narrow band around mangroves that are growing in sediment (not on a reef substrate). May be attached to the mainland or surrounding a mangrove island. Also known as a fringe oyster reef
- Mangrove root oysters (MRO): oysters grow on the prop roots and drop roots of *Rhizophora mangle* (red mangrove). May be single shells or clumps
- Seawall (SW), riprap (RR), pilings (P), or floating docks (D): oysters grow on solid structures such as seawalls, bulkheads, and riprap rather than on bottom substrate. Thickness and vertical height of oyster aggregations are subdivided, and oysters are classified as solid or scattered along the substrate:
 - Light: 1 or 2 layers of oysters in a band less than 15 cm (6 in) wide
 - **Medium:** more than 1 layer of oysters in a band 15–30 cm (6–12 in) wide
 - **Heavy:** more than 1 layer of oysters in a band 30–46 cm (12–18 in) wide
 - Very heavy: more than 1 layer of oysters in a band >46 cm (18 in) wide
 - Solid: solid stretch of oysters along the seawall or riprap
 - **Scattered:** sporadic stretch of oysters along the seawall or riprap

The South Carolina Department of Natural Resources (SCDNR) and the NOAA Coastal Services Center mapped the coastline of South Carolina using multispectral imagery (SCDNR 2008). The effort included the development of classification system for oyster reefs, largely using different spectral signatures as a result of vertical or horizontal orientation of the oysters. The project report (SCDNR 2008) describes each category with accompanying photographs and provides protocols for classifying aerial imagery. Classes and oyster strata include the following:

- Class 1: background (no oysters)
- Class 2: vertical and horizontal oysters mixed, little or no mud or washed shell
 - **Stratum A:** dense oyster clusters with little exposed dead shell or mud
 - **Stratum E:** oysters tightly clustered on rocks, may have mud or *Spartina alterniflora* (smooth cordgrass) between clusters
 - Stratum F: vertical clusters with spatial separation. Substrate between clusters consists of shells with few horizontal live oysters and little mud
 - Stratum F1: small, vertical clusters on a substrate of single, horizontal oysters. Very little exposed mud
- Class 3: vertical oysters on a substrate of mud with few to no horizontal oysters
 - **Stratum C:** vertical clusters with up to 1 m spatial separation. Substrate between clusters is usually mud with little surrounding shell
 - **Stratum G:** close vertical clustered oysters separated by mud with little to no shells or oysters
- Class 4: horizontal oysters mixed with washed shells
 - **Stratum B:** little to no vertical oysters and few clusters, oysters frequently single. Found on heavily shelled substrate in the lower intertidal zone
 - Stratum D: mostly horizontal dead oyster shell with little live crop, generally found in lower intertidal zone
- Class 5: washed shell

The Classification of Wetlands and Deepwater Habitats of the United States, developed by Cowardin et al. (1979) for the U.S. Fish and Wildlife Service, was updated by the Federal Geographic Data Committee in 2013 (FGDC 2013). Classification codes directly relevant to oyster reefs include E1RF2L, E2RF2M, and E2RF2N. Oysters that are mixed with unconsolidated substrate may be classified as E2RF2/US2N, E2RF2/USM. The hierarchical structure of these relevant classifications is as follows:

- **System: estuarine** (E): impacted by seawater and by freshwater runoff
 - Subsystem: subtidal (1): exposed substrate flooded by tides
 - Class: reef (RF): ridge or moundlike structure formed by sessile invertebrates
 - Subclass: mollusk (2): dominance types include *Ostrea* and *Crassostrea*
 - Water regime: subtidal (L): substrate continuously inundated
 - **Subsystem: intertidal (2):** exposed substrate that is flooded by tides
 - Class: reef (RF): ridge or moundlike structure formed by sessile invertebrates
 - Subclass: mollusk (2): dominance types include Ostrea and Crassostrea
 - Water regime: regularly flooded (N)
 - Water regime: irregularly exposed (M)
 - Class: unconsolidated shore (US): >70% cover of stones, boulders, or bedrock and <30% vegetation cover
 - Subclass: sand (2): unconsolidated particles predominantly sand, although particles of other sizes may be mixed in
 - Water regime: regularly flooded (N)
 - Water regime: irregularly exposed (M)

The National Oceanic and Atmospheric Administration's (NOAA) Coastal Change Analysis Program (C-CAP) uses its own classification system. The original classification system was described in Klemas et al. (1993), and an updated summary is available in Dobson et al. (1995), which also explains how the land cover categories compare to Cowardin et al.'s (1979) classes. Relevant classifications include:

- Class: marine/estuarine reef: ridge or moundlike structure made from sedentary invertebrates
 - Subclass: mollusk reef

The Coastal and Marine Ecological Classification Standard (CMECS) was created by the Federal Geographic Data Committee and the Marine and Coastal Spatial Data Subcommittee (FGDC 2012). CMECS is a hierarchical classification scheme designed to use common terminology to classify marine and estuarine habitats. CMECS includes classifications based on two settings (biogeographic and aquatic) and four components (wa-

ter column, geoform, substrate, and biotic). The relevant hierarchical classifications for oyster reefs in the geoform, substrate, and biotic components are listed below.

- Geoform origin: biogenic: physical features created by organisms, most commonly reefs made by corals, mollusks, or worm tubes
 - Geoform: mollusk reef: shell reefs intermixed with channels and unvegetated flats
 - Geoform type: fringing mollusk reef: narrow, linear reefs; generally intertidal and lower than the marsh along tidal creeks
 - Geoform type: linear mollusk reef: narrow, ridgelike reefs; generally intertidal and in areas with small tidal range
 - Geoform type: patch mollusk reef: mounded reefs with vertical relief above surrounding substrate; usual intertidal, occasionally subtidal
 - Geoform type: washed shell mound: accumulations of loose, dead shell in the high intertidal zone
- Substrate origin: biogenic substrate: majority of substrate is of nonliving biogenic origin rather than geologic or anthropogenic origin
 - Substrate class: shell substrate: substrate made of shells or shell fragments; may or may not include live reef-building fauna
 - Substrate subclass: shell reef substrate: cemented, conglomerated, or self-adhered shell reefs with median particle size >4 m
 - Substrate group: oyster reef substrate
 - Substrate subclass: shell rubble: shells with a median particle size of 0.064–4 m; may be loose, cemented, or conglomerated
 - Substrate group: oyster rubble
 - Substrate subclass: shell hash: loose shell, broken or whole, with median particle size of 2–64 mm
 - Substrate group: oyster hash
- Biotic setting: benthic/attached biota: biota live on or in the substrate
 - Biotic class: reef biota: reef-building fauna construct biogenic substrates
 - Biotic subclass: mollusk reef biota: living and dead mollusks or gastropods aggregate and attach in sufficient numbers to make a substrate
 - Biotic group: oyster reef: mounds or ridges formed by live oysters cementing to the substrate of live and dead conspecifics

Biotic communities: Crassostrea reef, Ostrea reef

- **Biotic class: faunal bed:** seabed dominated by benthic fauna that have not created a reef
 - Biotic subclass: attached fauna: dominated by fauna that maintain contact with a hard substrate
 - Biotic group: attached oysters: oysters attach to a hard substrate other than conspecifics
 - Biotic communities: attached Crassostrea, attached Ostrea
 - Biotic subclass: soft-sediment fauna: sand or mud with dominant presence of infauna, epifauna, or mobile fauna that create burrows
 - Biotic group: oyster bed: sand or mud with low densities of oysters that are not attached to a hard substrate.
 - Biotic communities: *Crassostrea* bed, *Ostrea* bed

Recent oyster mapping data in Florida

Oyster mapping data sets in Florida are often limited to a specific estuary or region. The FWC and OIMMP have combined many of these maps to create a statewide oyster map. This GIS shapefile is updated periodically and was used to create the maps in this report. The shapefile is available for download at http://geodata.myfwc.com/ datasets/oyster-beds-in-florida. A listing of selected largescale data providers, including the FWC compilation, is compiled in Table 1.2 and summarized in further detail below. These and other smaller-scale mapping efforts are described in the regional chapters of this report. While land classification schemes vary across agencies (Table 1.1) and may subdivide different types of oyster habitat, many maps simply plot oyster extent using one category. Land cover maps vary widely among agencies due to variable classification schemes, image resolution, and minimum mapping units. Oyster reef maps are subject to similar variability but also suffer from gaps as mapping efforts are generally regional and often focus on either subtidal or intertidal reefs.

For more than 30 years, the National Wetlands Inventory (NWI) has generated and updated highly detailed wetland maps following Cowardin et al.'s (1979) classification scheme using a variety of methods and data sources, including aerial images (Dahl et al. 2015). Most recently, NWI maps are available online at http://www.fws.gov/wetlands/index.html. The effort fo-

cused primarily on wetlands, but mollusk reefs are included in available maps. Not all bays in the state with oyster reefs included labeled mollusk reefs under the NWI scheme.

The Florida Water Management Districts (WMDs) periodically complete their own assessments of land use and land cover (LULC) in their jurisdictions. Land-cover analysis is based on remote imagery using FLUCCS categories (FDOT 1999) and does not always include oyster reefs. The Northwest Florida Water Management District (NWFWMD) sometimes includes oyster reefs (FLUCCS code 6540) in their LULC maps. The most recent Suwannee River Water Management District (SRWMD) LULC map that includes oyster reefs is from 2010. While LULC data are available from 2013–2014, this map does not include an oyster category. SRWMD also conducted an extensive oyster mapping effort in 2001 (Patterson 2002). LULC data are available on the water management district websites (Table 1.2).

The Southwest Florida Water Management District (SWFWMD) conducts periodic seagrass and oyster mapping within its district boundaries using a modified version of FLUCCS (FDOT 1999). Subtidal habitats are mapped using natural color aerial photography collected in winter at a scale of 1:24,000. Mapped habitats include tidal flats, oyster bars, beaches, patchy seagrass, and continuous seagrass. Dead and live oysters were mapped together to form the oyster bar classification. Map files may be downloaded from the district website https://data-swfwmd.opendata.arcgis.com/.

The St. Johns River Water Management District (SJRWMD) mapped live and dead oyster reefs within the Northern Coastal Basin of Florida with the use of aerial photographs and a custom photo-interpretation key of oyster reef types. There was no minimum mapping unit. Field verification determined that the maps were 96% accurate. The data set is available for download at http://data-floridaswater.opendata.arcgis.com/.

FWC created the Oyster Beds in Florida GIS data set by compiling mapping data from a variety of sources. This map is a compilation of multiple studies and methodologies and was greatly expanded upon by OIMMP. Sources of data include the WMDs, FWC, U.S. Geological Survey (USGS), and university and city mapping efforts for seagrass, oysters, or general benthic habitat mapping. The data set is regularly updated and is available for download at http://geodata.myfwc.com/datasets/oyster-beds-in-florida. Although this is the most comprehensive oyster map available for Florida, gaps remain. There is need for updated detailed mapping in the panhandle (Perdido, Pensacola, Choctawhatchee, and St.

Andrew bays), Big Bend and Springs Coast (for Apalachee Bay and subtidal oysters), much of the Everglades, and the Indian River Lagoon (outside of its tributaries).

The Cooperative Land Cover Map (CLC) is a collaboration between FNAI and FWC to support the goals of the Florida Comprehensive Wildlife Conservation Strategy (FNAI and FWC 2010). The CLC project compiles data from various sources and integrates them using aerial photography and local data collections. Data were obtained from Florida WMD LULC data, local mapping efforts, aerial photographs, and interviews with local experts (FNAI and FWC 2010). Each data set is assigned a confidence category to determine which data set takes precedence over other data sets with conflicting maps. Due to the diverse array of data sources, multiple land classification systems are used (FNAI 1990, FDOT 1999, Kawula 2014, and others). All classifications are related to the Florida Land Cover Classification System (Kawula 2009). Mapping layers are updated approximately every six months and can be downloaded at http://mvfwc.com/ research/gis/applications/articles/Cooperative-Land-Cover.

The Gulf of Mexico Data Atlas (http://gulfatlas.noaa.gov/), created by NOAA, compiles data from other sources. The oyster mapping layer for Florida is compiled from sources such as the water management districts, USGS, FWC, The Nature Conservancy, and the National Estuarine Research Reserves in the state. The data atlas includes an online mapping program that enables the viewing of maps for distribution of oysters and other invertebrates.

Oyster reef monitoring

Oyster monitoring in Florida is performed by a variety of state and local governments, water management districts, preserves, reserves, universities, and nongovernmental organizations. The goals of these efforts include monitoring the efficacy of the Comprehensive Everglades Restoration Program (CERP) (Volety et al. 2009), the health of oyster fisheries (FDACS 2012), the success of restoration efforts (Brumbaugh et al. 2006), identifying long-term changes (Seavey et al. 2011), and providing general ecological assessments (Garland and Kimbro 2015). Examples of protocols for oyster monitoring are cited in Table 1.3. Many focus specifically on monitoring restored reefs.

Monitoring parameters

Recommended universal monitoring metrics for oyster reef restoration efforts include reef areal dimension, reef height, oyster density, tidal emersion, and oyster size-frequency distribution (Baggett et al. 2014, Walles et

Table 1.2. Selected large-scale providers of oyster reef data in Florida. See text for affiliation acronyms.

Program	Affiliation	Region of map extent, live reef area mapped in Florida	Data origin, most recent data	Classification scheme	Website
National Wetlands Inventory (NWI)	USFWS	national, 197 ha/488 ac	Composite of multiple data and aerial image sources, image years vary from 1970s to 2010s	Cowardin et al. 1979	http://www.fws.gov/ wetlands
Florida water management districts land use land cover (LULC) maps	NWFWMD	NWFWMD, 124 ha/306 ac	Color infrared or true color aerial photography, 2009–2010	FDOT 1999	https://www. fgdl.org/ metadataexplorer/ explorer.jsp
	SRWMD	SRWMD, 75 ha/185 ac	Color infrared or true color aerial photography, 2010–2011	FDOT 1999	http://www.srwmd. state.fl.us/319/ Data-Directory
SRWMD oyster mapping	SRWMD	SRWMD, 590 ha/1,457 ac	Composite of multiple data and aerial image sources, 2001	customized FDOT 1999	http://www.srwmd. state.fl.us/319/ Data-Directory
SWFWMD seagrass mapping	SWFWMD	SWFWMD, 1,330 ha/3,286 ac	Color aerial photography, oysters included in seagrass mapping efforts, 2016	customized FDOT 1999	http://data-swfwmd. opendata.arcgis. com/
Northern Coastal Basin Intercoastal Oysters	SJRWMD, UCF	Northeast Florida, 589 ha/1,456 ac	Color aerial photography, 2009–2016	custom classification	http://data- floridaswater. opendata.arcgis. com/
Oyster beds in Florida	FWC	Florida, 7,923 ha/19,579 ac	Compilation of many sources, see metadata. Source years vary; updated regularly	FDOT 1999 and others	http://geodata. myfwc.com/datasets/ oyster-beds-in-florida
Cooperative land cover (CLC) map	FNAI, FWC	Florida, 235 ha/585 ac	Compilation of many sources, see metadata. Version 3.3 published 2018	FNAI 1990, FDOT 1999, Kawula 2014, and others	FNAI and FWC 2010 http://myfwc. com/research/gis/ applications/articles/ Cooperative-Land- Cover
Gulf of Mexico Data Atlas	NOAA	Gulf coast and east coast of Florida 6,906 ac	Compilation of many sources, see metadata. Source years vary; published 2011	FNAI 1990, FDOT 1999, and others	http://gulfatlas. noaa.gov/catalog/ living-marine/

al. 2016). A variety of other parameters is also used, depending on objectives and goals of the monitoring. These parameters are briefly described below; see cited references for further detail.

Reef areal dimensions and footprint include the area of the reef (the summed area of patches of living and nonliving oyster shell or other substrate material) and reef footprint (entire area of the reef complex, including gaps between small patch reefs) (Baggett et al. 2014). Al-

ternatively, data may be collected on the percent cover of oysters within the footprint (Coen et al. 2004). Data on reef area is collected with the same methodologies used to map oyster reefs (see previous section), which includes walking the perimeter of the reef with an RTK GPS or dGPS, use of aerial or underwater imagery, or use of side-scan or multibeam sonar.

Reef height and reef depth provide information on reef accretion and stability and offer an indicator of the reef's utility as habitat for associated species (Baggett et al. 2014). Subtidal reefs that are sufficiently elevated above the bottom substrate tend to be less vulnerable to hypoxia and sedimentation (Lenihan and Peterson 1998, Coen et al. 2004). A high-precision GPS unit or traditional surveying equipment may be used to determine intertidal reef elevation and topography (Baggett et al. 2014). Subtidal reefs can be assessed using side-scan sonar across a reef to determine the reef's relief and water depth. A sounding pole may also be used at intervals across a subtidal reef to determine variation in elevation of a given reef footprint.

Tidal emersion: The length of time portions of a reef are exposed to air at low tide can result in clear zonation in oyster development, performance, and ecosystem services (Walles et al. 2016, Hanke et al. 2017). Tidal emersion can be determined from temperature loggers or water-level gauges. It can also be assessed with the use of bathymetric or topographic maps, or the elevation of the top of the reef can be measured using an RTK GPS or dGPS. The elevation can then be converted to emersion time based on local sea level and tidal cycles (Rodriguez et al. 2014, Walles et al. 2016).

Oyster density is determined by counting live individuals of a particular size within quadrats on an oyster reef (0.25-m² quadrats recommended in high oyster densities, 1-m² in low densities) (Baggett et al. 2014). If necessary, the oysters in a given quadrat should be excavated to a depth of 10-15 cm to allow the counting of live oysters and articulated shells. Articulated shells, also called boxes, often indicate recent mortality (Christmas et al. 1997). Percent cover by live oysters can also be determined using a point-intercept method in a grid within a quadrat (Fig. 1.12). Grizzle et al. (2005) paired underwater videography with divers excavating oysters in grids in order to evaluate the accuracy of estimating live oyster counts from video stills. This method was found to work best in regions of low oyster density that did not have large numbers of spat or juveniles or a lot of dead shell.

Oyster size-frequency distribution is determined by using a ruler or caliper to measure the shell height of a subset of the oysters in a quadrat (Galtsoff 1964). A digital caliper system that wirelessly inputs data directly into a computer can also be used to efficiently measure a large number of oysters (Coen et al. 2004). The same set of oysters can generally be used for both density and size-frequency measurements (Coen et al. 2004, NASEM 2017). Baggett et al. (2014) recommend measuring at least 50 oysters per sample (or 250 oysters per reef). Size-frequency metrics can be used to gauge recruitment, to track a cohort over time, or to compare the age (size) structures of restored and natural reefs. Note that this can be diffi-



Figure 1.12. Researchers use quadrats to assess cover of live and dead oysters. Photo credit: Kara Radabaugh.

cult to implement on reefs with high recruitment or a high density of oysters.

Settlement can be monitored using arrays of replicate ceramic tiles, shells, or other materials appropriate for colonization to determine recruitment of spat (Figs. 1.13 and 1.14). Regular collection of these materials and counting the spat that have settled on the surfaces enables determination of the seasonal timing and rate of oyster settlement (Brumbaugh et al. 2006). On subtidal reefs with significant relief, separate measurements of oyster spat densities on different areas (e.g., the reef crest, slope, and base) can provide information on recruitment variability with depth (Lenihan 1999, Brumbaugh et al. 2006, Hanke et al. 2017).

Salinity, dissolved oxygen, and temperature are the three environmental metrics universally recommended for inclusion in an oyster monitoring plan (Baggett et al. 2014, NASEM 2017). These water quality metrics should be monitored continuously with automated sondes, and data should be collected as close to the reef as possible. Automated sampling is recommended because water quality measurements during infrequent site visits (weekly or monthly) provide only a snapshot of local conditions. These data are not very helpful for assessing impact of these parameters on growth, survival, or diseases. Estuarine water-quality parameters vary widely with tides, seasons, winds, and rainfall (see http://recon.sccf.org/ for real-time water-quality data associated with a number of oyster restoration efforts). Additional parameters such as total suspended solids, chlorophyll a, and water clarity also aid in ecosystem-wide water quality assessments (Brumbaugh et al. 2006). For intertidal reefs, air temperature at low tide should also be measured.

Condition index: The oyster condition index provides a method of comparing oyster condition across multiple locations (Lawrence and Scott 1982, Crosby and Gale 1990,

Table 1.3. Selected monitoring protocols for natural oyster reefs or shellfish restoration projects. See text for affiliation acronyms.

Name	Affiliation	Focus	Reference
Design and monitoring of shellfish restoration projects	The Nature Conservancy	Instructional guide for bivalve restoration projects and monitoring	Brumbaugh et al. 2006
Oyster habitat restoration monitoring and assessment handbook	NOAA, TNC, University of South Alabama, Florida Atlantic University	Instructional guide for monitoring and characterization of oyster restoration sites	Baggett et al. 2014
Science-based restoration monitoring of coastal habitats	NOAA	Volume 1: A framework for monitoring plans under the estuaries and clean waters act of 2000; Volume 2: Tools for monitoring coastal habitats	Thayer et al. 2003, Thayer et al. 2005
Best management practices for shellfish restoration	Interstate Shellfish Sanitation Conference, TNC, NOAA	Methods for shellfish restoration including community outreach and harvesting concerns	Leonard and Macfarlane 2011
Restoration goals, quantitative metrics and assessment protocols for evaluating success on restored oyster reef sanctuaries	Chesapeake Bay Program	Monitoring protocols and success metrics for restored oyster reefs	Oyster Metrics Workgroup 2011
Effective monitoring to evaluate ecological restoration in the Gulf of Mexico	National Academies of Sciences, Engineering, and Medicine	General and specific guidelines for monitoring numerous restored habitats, including oyster reefs	NASEM 2017
Oyster condition assessment protocol	UCF, SJRWMD, GTMNERR, NE Florida Aquatic Preserves	Instructional guide for standardized oyster reef monitoring	Walters et al. 2016
A South Carolina Sea Grant report of a 2004 workshop to examine and evaluate oyster restoration metrics to assess ecological function, sustainability, and success	South Carolina Sea Grant	Site selection parameters and metrics to assess reef restoration efforts	Coen et al. 2004
Sampling and analytical methods of the national status and trends program national benthic surveillance and Mussel Watch projects	NOAA Mussel Watch, national status and trends program	Chemical contamination monitoring for organic and inorganic contaminants in bivalves and sediment	Lauenstein and Cantillo 1993

Baggett et al. 2014). Condition index (CI) is calculated as follows (Crosby and Gale 1990, Baggett et al. 2014):

 $CI = (tissue dry weight \times 100) / (whole wet weight - shell wet weight)$

This dry-to-wet-weight ratio can provide a metric of the proportion of water in the tissue of a given oyster. A high amount of water within the tissue is a sign of depleted energy reserves (as occurs after spawning) or food limita-

tion (Lucas and Beninger 1985, Rheault and Rice 1996). At least 25 oysters should be used to determine oyster condition at a location; the same oysters used for the size and density measurements as described above can be used for this purpose as well.

Oyster growth and survival can be determined by placing premeasured oysters in trays, mesh bags, or cages, and placing them back out on the reef. These oysters are then tracked for growth and survival over time (e.g., Kingsley-Smith et al. 2009). Comparison of survival in closed



Figure 1.13. Example spat on the interior side of an oyster shell. Photo credit: Christine Russo.

vs. open cages allows for determination of predation on oysters of various sizes.

Oyster disease: Monitoring for the presence, frequency, and severity of diseases such as dermo and MSX can be achieved by collecting and examining 20-25 oysters per location (Coen et al. 2004). Dermo infections can be diagnosed by using Ray's fluid thioglycolate method (Ray 1952, Bushek et al. 1994, Dungan and Bushek 2015). In this method, oyster tissue is incubated in Ray's fluid thioglycolate medium, stained with iodine, and then examined for parasites under a microscope. The intensity of a dermo infection is scored on a scale of 0 to 5, where 0 indicates no infection and 5 indicates that protist density almost entirely obscures the oyster tissue (Fig. 1.15; Mackin 1962). Frequency of disease monitoring should be tailored to seasonal and annual variability of a given location. In some cases, seasonal variability of disease prevalence necessitates a sampling frequency of 4–5 times per year (Coen et al. 2004).

MSX is not found on the Gulf coast of Florida (Ford et al. 2011) and has not shown pathogenicity on the east coast of Florida (Burreson and Ford 2004, Walters et al. 2007). Disease monitoring may therefore be necessary only if disease prevalence is a problem in an area or there is unexplained high mortality (Baggett et al. 2014). MSX is more difficult to detect than is dermo and can be determined using the paraffin histology method (Burreson et al. 1988, Burreson and Ford 2004) or by polymerase chain reaction (PCR) amplification (Stokes et al. 1995), but suspected infections should be verified with histology (Burreson 2008).

Chemical contamination: Oysters are useful indicators of water quality and pollution because, as sessile filter feeders, their tissues provide a record of water quality



Figure 1.14. Suspended clean oyster shells are used to collect spat and assess oyster settlement. Photo credit: Kara Radabaugh.

and they can be used to quantify spatial variation in contaminant levels. Compounds of interest include polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), pesticides, and heavy metals. The methods used by NOAA's Mussel Watch program to monitor organic contaminants and trace elements in bivalve tissue and sediments are summarized in Lauenstein and Cantillo (1993), and two decades of results are summarized in Kimbrough et al. (2008) and Kim et al. (2008).

Monitoring of associated species: The presence and diversity of transient and resident species on oyster reefs provide an indicator of ecosystem status and function (Tolley et al. 2006, Coen et al. 2007). The biomass, abundance, and diversity of the fish and invertebrates that live near the oyster reef can be assessed with various types of nets (lift nets, drop nets, seines, gill nets, etc.), traps, embedded sampling trays, and visual surveys (Brumbaugh et al. 2006, ASMFC 2007, zu Ermgassen et al. 2016, Hanke et al. 2017, NASEM 2017). Animals may also be collected when shells are excavated during an oyster density survey; resident organisms such as crabs, mollusks, and other invertebrate species can be sampled in this way. While monitoring associated fauna may be time consuming and require significant knowledge of taxonomy, the resulting data are valuable for understanding the ecology of the reef (Coen et al. 2004, Tolley et al. 2005, Coen and Humphries 2017). In the case of restored reefs, faunal monitoring may focus on similarity of species composition with adjacent natural reefs (Walters and Coen 2006). Seagrass surveys may also be of interest after oyster restoration efforts, because enhanced water clarity as a result of oyster reefs has been noted to increase seagrass productivity (Peterson and Heck 2001a, 2001b, Newell and Koch 2004).

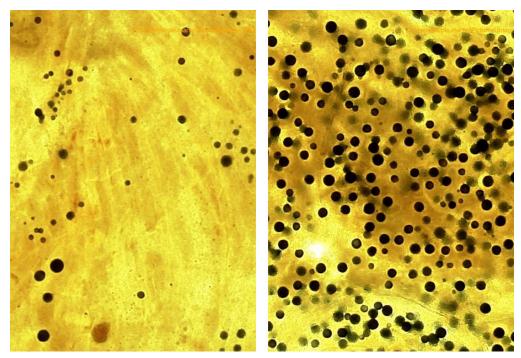


Figure 1.15. Example of dermo infections in oyster tissue. The intensities of these infections were classified as a three (left) and five (right) on the Mackin (1962) scale. Photo credit: Nicole Martin.

Restoration monitoring: Monitoring restoration sites calls for special consideration of sampling design (NASEM 2017). Monitoring data (physical and biological) collected before restoration activities begin allows for evaluation of the suitability of the habitat and its hydrology (Thayer et al. 2005, Coen and Humphries 2017). Frequent postrestoration monitoring of survival and erosion rates allows for early assessment of restoration success or any needed improvements (Baggett et al. 2014, NASEM 2017). Use of a before-after-control-impact (BACI) sampling design, which includes monitoring both the oyster restoration site and a control site before and after the restoration effort, enables identification of change as a result of restoration efforts rather than environmental factors (Thayer et al. 2005, Baggett et al. 2014, NASEM 2017). An interesting direction in restoration monitoring includes the estimation of ecosystem services derived from natural and restored oyster reefs. These can include production of fish and invertebrates, shoreline protection, or reduction of nutrients (Peterson et al. 2003, Grabowski et al. 2012, zu Ermgassen et al. 2016). Using an easily accessible tool (see http:// oceanwealth.org/tools/oyster-calculator/), one can even calculate filtering capabilities of potential oyster habitat by area, estuary volume, residence time, and other variables.

Region-specific chapters

The remainder of this report documents region-specific ecosystems, monitoring, and mapping programs for oyster reefs across Florida. The eight OIMMP regions are separated as shown in Fig. 1.16. Each chapter includes a general introduction to the region, mapped oyster reefs, oyster harvesting records, location-specific threats to oyster reefs, a summary of selected mapping and monitoring programs, and recommendations for management, monitoring, and mapping efforts.

General references and additional information

OIMMP resources and workshop presentations: http://ocean.floridamarine.org/OIMMP/

FWC compilation of oyster maps in Florida: http://geodata.myfwc.com/datasets/oyster-beds-in-florida

FWC eastern oyster information: http://myfwc.com/ research/saltwater/mollusc/eastern-oysters/

Commercial fisheries landings in Florida: https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/

Florida saltwater fishing regulations: https://myfwc.com/fishing/saltwater/

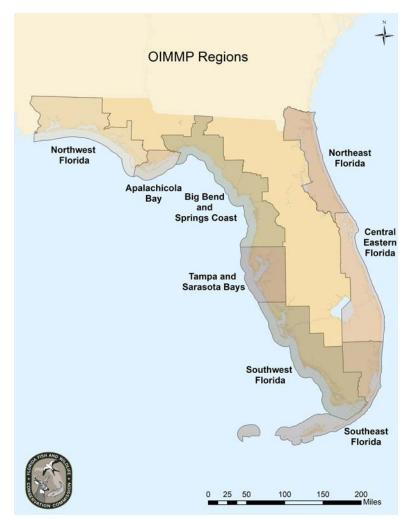


Figure 1.16. Regions of focus for the OIMMP report chapters.

Oyster restoration workgroup:

http://www.oyster-restoration.org/

NOAA's National Status and Trends program (includes Mussel Watch): https://products.coastalscience.noaa.gov/collections/ltmonitoring/nsandt/default.aspx

NOAA Chesapeake Bay Office: technical aspects of oyster restoration: https://chesapeakebay.noaa.gov/oysters/technical-aspects-of-oyster-restoration

NOAA Chesapeake Bay Office: oyster substrate literature review: https://chesapeakebay.noaa.gov/habitats-hot-topics/ oyster-reef-alternative-substrate-literature-review

The Nature Conservancy's oyster calculator for water filtration and fish production provided by oyster reefs: http://oceanwealth.org/tools/oyster-calculator/

Shellfish Reef Restoration Network: https://www.shellfishrestoration.org.au/

Chesapeake Bay Foundation eastern oyster information: http://www.cbf.org/about-the-bay/

more-than-just-the-bay/chesapeake-wildlife/eastern-oysters/

University of Maryland oyster hatchery information: http://hatchery.hpl.umces.edu/

Oyster Recovery Partnership: https://oysterrecovery.org/

North Carolina Coastal Federation oyster information: https://www.nccoast.org/protect-the-coast/restore/ oyster-habitat/

North Carolina Oyster Blueprint: oyster restoration, education, and research information: https://ncoysters.org/

The Nature Conservancy: restoring North Carolina's oysters: https://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/northcarolina/explore/oyster-reef-restoration-in-north-carolina-1.xml

Sink Your Shucks oyster recycling program: http://oysterrecycling.org/

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