

Habitat: Oyster Reefs

Aswani K. Volety
Florida Gulf Coast University

In a nutshell:

- Oyster reefs provide a habitat for over 300 species, including fish and invertebrates, and play a major role in improving water quality and clarity via their filtration capacity, thereby removing phytoplankton, detritus, contaminants, and bacteria.
- People value oyster reefs as a place to find a large number and variety of fish. Oyster reefs stabilize sediments, protect against boat wakes, and provide a critical habitat for larval stages of fish and crustaceans. They also play a role as sentinels in contaminant monitoring.
- The damage to reefs from overharvesting, dredging, sedimentation, and altered freshwater inflows into the estuarine system can lead to a complete loss of oyster reefs in heavily-affected areas.
- Watershed alteration resulting from increasing human development and changes in salinity and contaminants has been implicated in the loss of oyster reefs in many areas of the world, including southwest Florida.

Eastern oysters, *Crassostrea virginica*, are natural components of estuaries along the eastern seaboard of the U.S., as well as the estuaries in the Gulf of Mexico, and were once abundant in the estuaries of southwest and southeast Florida (RECOVER, 2007). In the Caloosahatchee, Loxahatchee, Lake Worth, and St. Lucie estuaries (northern estuaries of the Everglades), oysters have been identified as a valued ecosystem component (Chamberlain and Doering, 1998a,b). The eastern oyster once supported a Native American subsistence fishery prior to and during early European colonization of North America (Quitmyer and Massaro, 1999) and today continues to be an important economic and ecological resource to coastal inhabitants (Ingle and Smith, 1949; Coen *et al.*, 1999; Gutierrez *et al.*, 2003). Along the southwest Florida coast, oysters exist within the estuarine and coastal areas as extensive reefs or isolated clusters or are attached to prop roots of red mangroves, often extending out at the base of mangroves (Figure 1).

The historical coastal complex of South Florida was distinctly estuarine with freshwater discharging through natural channels, as sheet flow across coastal wetlands and ground water flow, as general pore seepage, and as individual artesian springs emerging from karst pipes. As a result, conditions were favorable for the oyster to flourish and build small to extensive oyster banks and bars. In a few areas on the southwest coast, new oyster growths have shifted further inland along channels and interior bays. Oysters have an even greater temporal and spatial impact to south and southwest Florida because of the sedimentation associated with their reef development. Oyster reef development occurred along the southwest Florida coast over the last 3500 years, with reef development having a significant impact on coastal geomorphology. As reefs become emergent at low tide, they become the centers for red mangrove propagule settlement, and reefs transform into mangrove-forested islands. These islands entrap freshwater and predispose the



Figure 1. Oyster reefs beds in the Southwest Florida Shelf ecosystem.

region to estuarine conditions (Parkinson, 1989; Wohlpart, 2007). In the present day, oyster reefs are extensive along the Charlotte Harbor to the Ten Thousand Islands, with reef development decreasing southeast of Chatam River towards Everglades National Park (Savarese *et al.*, 2004; Volety *et al.*, 2009). In estuaries north of Lostman’s and Broad rivers, oysters are also found on the prop-roots of red mangroves fringing the inner bays. In most of the estuaries, oyster reef coverage ranges between 5-20 acres (Volety and Savarese, 2001; Savarese *et al.*, 2004; Volety *et al.*, 2009).

Ecological Role of Oyster Reefs

Secondary Habitat and Trophic Transfer

Oysters provide habitat for other estuarine species that have significant recreational and commercial value. Grabowski and Peterson (2007) estimated that an acre of oyster reef sanctuary will result in ~\$40,000 in additional value of commercial finfish and crustacean fisheries. Oysters are also ecologically important: they improve water quality by filtering particles from the water and serve as prey and habitat for many other animals (Coen *et al.*, 1999). For

example, oyster reefs have been identified as essential fish habitat for resident and transient species (Breitburg, 1999; Coen *et al.*, 1999). Wells (1961) collected 303 different species that utilized oyster reefs and segregating species that used the reef primarily as shelter from those that depend on the reef for food. These organisms are then consumed by finfish and crustacean species that may be recreationally or commercially valuable (Grabowski *et al.*, 2005; Grabowski and Peterson, 2007).

Harding and Mann (2001) found that transient generalist fishes do not rely exclusively on oyster reef habitats; therefore, it may not be appropriate to identify oyster reefs as essential fish habitat for these opportunistic fishes. According to the Magnuson-Stevens Fishery Conservation and Management Act, essential fish habitat is defined as “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity” and fish is defined as “finfish, mollusks, crustaceans, and all other forms of marine animal and plant life other than marine mammals and birds” (USDOC, 1997). In general, oyster reefs provide habitat and shelter for many estuarine species (Zimmerman *et al.*, 1989; Myers and Ewel, 1990; Breitburg, 1999), especially during periods of hypoxia (Lenihan *et al.*, 2001). Harding and Mann (2001)

suggested that oyster reefs may provide a higher diversity and availability of food or a greater amount of higher quality food compared to other habitats. Oyster reefs restored on mudflats have higher juvenile fish abundances compared to reefs restored in vegetated areas that could potentially cause an increase in fish productivity in an estuary (Grabowski *et al.*, 2005). The reefs can also be called essential fish habitat for oysters themselves, especially when reef height and quality and quantity of interstitial spaces for recruiting oysters are considered (Coen *et al.*, 1999). Both of these characteristics increase the recruitment, growth, and survival of oysters on reefs (Coen *et al.*, 1999).

Several species of fishes have been identified as oyster reef residents and include the naked goby (*Gobiosoma bosc*), Florida blenny (*Chasmodes saburrae*), striped blenny (*Chasmodes bosquianus*), feather blenny (*Hypsoblennius hentz*), skilletfish (*Gobiesox strumosus*), gulf toadfish (*Opsanus beta*), and oyster toadfish (*Opsanus tau*) (Zimmerman *et al.*, 1989; Wenner *et al.*, 1996; Breitburg, 1999; Coen *et al.*, 1999; Lenihan *et al.*, 2001; Tolley and Volety, 2005; Tolley *et al.*, 2006). These fishes use the oyster reef as a spawning and feeding habitat and as shelter from predators. Resident oyster reef fishes typically feed on benthic invertebrates such as amphipods, mud crabs, and grass shrimp but can also prey on benthic fishes (Breitburg, 1999; Lenihan *et al.*, 2001). The naked goby, striped blenny, and skilletfish attach their eggs to the insides of recently dead, clean, articulated oyster shells, and the oyster toadfish attaches its eggs to the underside of consolidated oyster shells (Breitburg, 1999; Coen *et al.*, 1999). Resident reef fishes have been observed to swim quickly into the shell matrix of the oyster reef in the presence of a predatory fish or due to the sudden movement of a diver instead of swimming along the substrate surface or up into the water column (Coen *et al.*, 1999).

Many transient fish species have been found on oyster reefs, and several are recreationally or commercially valuable, including Atlantic menhaden (*Brevoortia tyrannus*), tautog (*Tautoga onitis*), striped bass (*Morone saxatilis*), and Spanish mackerel (*Scomberomorus maculatus*) (Breitburg, 1999; Harding and Mann, 2001; Lenihan *et al.*, 2001). Atlantic croaker (*Micropogonias undulatus*), Atlantic menhaden, bluefish (*Pomatomus saltatrix*), and striped bass are all found in greater abundances near oyster reefs compared to habitats such as sand bars (Harding and Mann, 2001). Many transient species, including speckled seatrout (*Cynoscion*

nebulosus), weakfish (*Cynoscion regalis*), southern flounder (*Paralichthys lethostigma*), and Spanish mackerel have been found to eat reef resident fish species (Lenihan *et al.*, 2001). Striped bass frequent reefs to feed on the benthic fishes (e.g., naked gobies) and crabs found in and around dead and live oysters (Breitburg, 1999; Harding and Mann, 2001). Juvenile striped bass also feed on naked goby larvae, one of the most abundant fish larvae in Chesapeake Bay tributaries during the summer (Breitburg, 1999). Other species of fish that feed on benthic invertebrates found on oyster reefs include spot (*Leiostomus xanthurus*) and black drum (*Pogonias cromis*) (Breitburg, 1999).

Fish are not the only species that utilize oyster reefs as habitat. Several species of decapod crustaceans are found on oyster reefs: *Petrolisthes armatus*, *Panopeus* spp., *Eurypanopeus depressus*, *Menippe mercenaria*, *Alpheus heterochaelis*, and *Palaemonetes pugio* (Zimmerman *et al.*, 1989; Wenner *et al.*, 1996; Coen *et al.*, 1999; Luckenbach *et al.*, 2005; Tolley and Volety, 2005; Tolley *et al.*, 2005, 2006). The xanthid crab (*Panopeus herbstii*) is a predator of the eastern oyster and is generally found along the boundaries of oyster reefs (McDermott, 1960; McDonald, 1982). In contrast, the flatback mud crab (*E. depressus*) is an omnivore that uses the narrow spaces between dead shells and living oysters as shelter from predation and to avoid desiccation (Grant and McDonald, 1979; McDonald, 1982). The porcelain crab (*P. armatus*) is also abundant in oyster clusters and among dead articulated shells, reaching up into the water column perched atop oyster clusters to filter feed (Caine, 1975; Tolley and Volety, 2005). Penaeid and caridean shrimp such as grass shrimp (*Palaemonetes* sp.) are also frequently found on oyster reefs and serve as an important trophic link in both detrital and higher food webs (Coen *et al.*, 1999). Grass shrimp also probably use the reef to avoid predators (Posey *et al.*, 1999). In addition, many organisms use the oyster reef in varying ways. Benthic reef invertebrates, such as amphipods, are food for crabs and shrimp that then are eaten by resident and transient fish species. The oyster reef is also used as shelter by species such as resident mud crabs and grass shrimp that use the spaces in and around oysters to avoid predation.

In a comprehensive study, using carbon and nitrogen isotopes, Abeels (2010) examined the trophic transfer from the water column to various organisms in an oyster reef ecosystem. The organic matter sources, amphipods, and

worms are at the lowest level and are consumed by oysters, resident crabs, shrimp, and fishes. The oysters, crabs, and shrimp are then consumed by other resident crabs and fish species. Transient fish species such as *Lutjanus* spp. come to the reef to feed on the resident crab, shrimp, and fish species. In a separate study, Wasno *et al.* (2009) investigated the trophic transfer from within the oyster reef community to 12 species of predatory fish. While the species of fish varied with season, the diet of fish caught during the wet and dry seasons did not differ significantly. Prey species belonging to the decapod crustaceans (*Eurypanopeus depressus*, *Panopeus* spp., and *Xanthidae* spp.) that are almost exclusive to oyster reefs occurred in the majority of stomachs and contributed to >43 percent of the relative importance index. Combined, results from both of these studies illustrate the importance of oyster reefs not only in oyster reefs serving as a habitat, but also in trophic transfer and secondary production.

Filtration

Oysters filter tremendous amounts of water while feeding (Newell, 1988). By filtering water column particulates, nutrients, sediment, and phytoplankton, oyster reefs increase light penetration to deeper layers, thus promoting the growth of SAV and, via denitrification, reduce anthropogenic nitrogen and minimize impacts of eutrophication (Grabowski and Peterson, 2007; Newell, 2004; Newell *et al.*, 2002). For example, the decline in oyster populations in the estuaries along the eastern seaboard has coincided with increases in nutrient loading and a decrease in water quality (Paerl *et al.*, 1998). This has resulted in ecosystem perturbations such as hypoxia and food webs dominated by microbes, phytoplankton, and nuisance pelagic species such as jellyfish (Breitberg, 1992; Jackson *et al.*, 2001; Lenihan and Peterson, 1998; Paerl *et al.*, 1998; Ulanowicz and Tuttle, 1992). Experiments have also indicated that oysters, through their filtration, increased light penetration by consuming algal production and increasing microphytobenthos (Dame *et al.*, 1989; Porter *et al.*, 2004). Field studies have demonstrated that oysters in North Carolina decreased chlorophyll-a levels in the water column by 10-25 percent and fecal coliform bacteria by 45 percent (Cressman *et al.*, 2003). Increased nutrient loading and/or turbidity is extremely detrimental to SAV habitats. For example, nitrogen loading of 30 Kg N ha⁻¹ yr⁻¹ resulted in a decrease of 80-96 percent loss in

SAV coverage in Waquoit Bay, Massachusetts. A 20 percent reduction in seagrass coverage in Chesapeake Bay resulted in an annual loss of \$1-4 million of fishery value annually (Kahn and Kemp, 1985). In addition, a study by National Research Council (2004) estimated that a 20 percent improvement in water quality along the western shore of Maryland was worth \$188 million for shore beach users, \$26 million for recreational boaters, and \$8 million for striped bass fishermen.

Mitigation of Wave Activity and Carbon Sequestration

In addition to providing habitat and secondary production, oyster reefs, with their calcareous shells and three-dimensional structure, also attenuate wave action and reduce erosion, thereby protecting other valuable habitats such as mangroves, sea grasses, and marshes in the estuarine environment (Henderson and O'Neil, 2003; Meyer *et al.*, 1997). Oyster reefs also promote sedimentation and, therefore, benefits the growth of SAVs. Additionally, oysters also sequester CO₂ from the water column via formation of calcium carbonate shells and, thus, potentially reduce the concentration of greenhouse gases (Peterson and Lipcius, 2003).

Environmental Sentinels

Sedentary, benthic filter-feeding organisms, such as oysters, clams, and mussels, given their enormous filtration capacity, are particularly effective in taking up hydrocarbons via filtration and ingestion and are, therefore, susceptible to the negative effects of these contaminants. For this reason, bivalve mollusks, such as oysters and mussels, are used worldwide as sentinel organisms in coastal environments to examine trends of contaminant levels, as well as ecological impairment (NOAA Status and Trends Program; O'Connor and Laurenstein, 2006).

Attributes People Care About

Oyster reefs in the SWFS support attributes of the marine environment that people care about. These attributes are directly related to ecosystem services provided by the southwest Florida coastal and marine ecosystem:

- Diverse fish, crustaceans, and other invertebrate populations
- Coastal erosion and boat wake mitigation
- Critical nursery and food habitat for recreationally- and commercially-important species
- Natural filter for phytoplankton, detritus, bacteria, and contaminants, resulting in enhanced water clarity and increased water quality
- Carbon sequestration

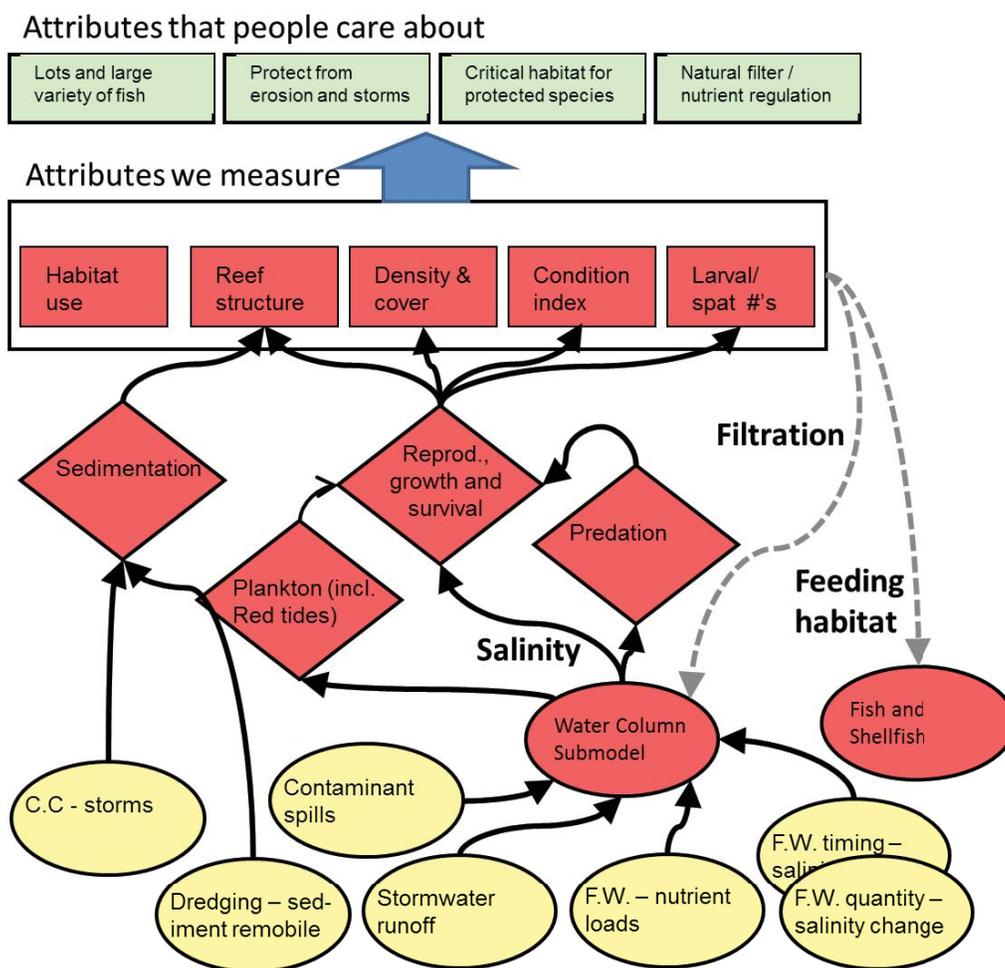
by Wasno *et al.* (2009) showed that fish such as sheephead, snook, redfish, catfish, snapper, etc., obtain 43 percent of their diet (relative importance index) from four crustacean species that only live within an oyster reef. Live oyster reefs have higher diversity and species richness compared to reefs with dead oysters or no oysters (Tolley and Volety, 2005) and harbor a tremendous diversity of organisms (Grabowski and Peterson, 2007; Wells, 1961). Oyster reefs and adjoining seagrass beds and/or mangrove areas are commonly targeted by recreational fishermen and fishing guides in southwest Florida.

Diverse Fish, Crustaceans, and Other Invertebrate Populations

Oyster reefs are important locations for recreational fisherman in southwest Florida. For example, a recent study

Coastal Erosion and Protection Against Boat Wakes

By reducing wave height, current velocities, and sediment resuspension, oyster reefs protect sea grasses and mangroves from erosion, saving these valued ecosystem communities.



Oyster reef submodel diagram for the Southwest Florida Shelf.

The reduction in turbidity, sedimentation, and erosion not only aids the ecology, but also has economic benefit derived from these habitats. Similar to sea grasses, oyster reefs are self-perpetuating and require little or no time or expense in maintaining them.

Natural Filtration

The biggest and most important benefit of oyster reefs to an ecosystem is their tremendous filtration capacity. According to Newell (1988), individual oysters filter 4-40 L/h. This filtration removes detritus, phytoplankton, contaminants, and bacteria, resulting in greater light penetration, thus promoting the growth of seagrasses and benthic microalgae. Sequestration of nitrogen via removal of organic matter from the water column also decreases impacts of eutrophication and promotes denitrification.

Carbon Sequestration

Oysters secrete calcium carbonate shells from seawater, thereby removing CO₂ from the water column (and thus atmosphere) and contributing to a reduction in greenhouse gases. The shells are insoluble and, thus, form a carbon sink in the coastal and estuarine realms.

Attributes We Can Measure

Given the ecological and economic benefits of oyster reefs, monitoring of oyster reefs by various local, state, and federal agencies has been in place for many years. In southwest Florida, a monitoring program to support the Comprehensive Everglades Restoration Plan (CERP) includes monitoring of oyster responses (RECOVER, 2007). Typical oyster responses that are measured include:

- Spatial extent
- Living density
- Larval recruitment
- Growth and survival of juvenile oysters
- Intensity and prevalence of diseases
- Reproductive condition

Spatial Extent

Along the southwest Florida estuaries and coast, the distribution and coverage of oyster reefs is influenced by salinity, substrate and food availability, larval recruitment, as well as the timing and duration of freshwater inflows into the estuaries (Volety, 2008; Volety *et al.*, 2009). Recent decades have witnessed declining oyster populations throughout the world. For example, Beck *et al.* (2011) estimated that oyster reefs are at less than 10 percent of their prior abundance and that ~85 percent of oyster reefs have been lost globally. Such decreases have coincided with decreases in water quality and clarity (Newell *et al.*, 1988). Some of the main reasons for declines in oyster reef abundance and distribution include diseases (Burreson and Ragone-Calvo, 1996; Soniat, 1996; Volety *et al.*, 2000), overharvesting, dredging, altered watershed, and salinity (Volety *et al.*, 2009).

Living Density

The density of living oysters varies between estuaries (100-4000+ oysters/square meter). Live oyster density, an indirect measure of reef productivity, also varies considerably along an estuarine salinity gradient and in response to various stressors that affect oyster growth and survival. Patterns attributable to human alterations in freshwater flow were detected previously in the Blackwater and Faka Union estuaries in the Ten Thousand Islands (Volety and Savarese, 2001; Volety, 2007). Similarly, oyster-living density varies with yearly freshwater inflows in the Caloosahatchee Estuary (Volety *et al.*, 2010). Since salinity has profound influence on spat recruitment, predation, survival, and fecundity (Volety *et al.*, 2009, 2010), differences in the living density of oysters between estuaries is not surprising. In addition to salinity, depending on the amount of freshwater that flows into the estuaries due to regulatory freshwater releases and/or watershed runoff, this may result in physical flushing of larvae to downstream locations, where substrate may be limited. For this reason, for relatively unaltered estuaries, the focus of oyster reef development occurs at mid-estuary, where salinity and food conditions tend to be favorable for oysters (Volety and Savarese, 2001; Savarese and Volety, 2008; Volety *et al.*, 2010).

Larval Recruitment

Oyster spat recruitment is typically monitored using old adult oyster shells strung together by a weighted galvanized wire or settling plates made of calcium carbonate cement and deployed at a sampling location. Oyster spat settlement is monitored monthly by counting the number of spat settled on the underside of strung shells (or plate), and spat settlement is expressed as the number of spat settled per oyster shell per month. Oysters reproduce during late spring-early fall in southwest Florida, and monitoring of spat recruitment is typically conducted between the months of May and October in southwest Florida estuaries (Volety, 2008; Volety *et al.*, 2009; Volety *et al.*, 2010). Since oyster reproduction and spat recruitment are influenced by salinity, temperature, food availability, and substrate quality, any environmental perturbations will negatively impact spat recruitment and survival and, hence, next year's class of oysters, resulting in poor living density of oyster during subsequent years.

Growth and Survival of Juvenile Oysters

Juvenile oysters grow at a faster rate than adult oysters and, thus, make excellent indicators to measure the role of water quality on the survival and growth of oysters (Volety *et al.*, 2010). Juvenile survival and growth is influenced by salinity, temperature, food quality and quantity, predators, and dissolved oxygen (Shumway, 1996). Higher salinities typically attract more predators and disease and, thus, oysters are more susceptible to predation and mortality (White and Wilson, 1996). To discriminate between growth and survival of juvenile oysters due to water quality and/or predation, juvenile oysters are deployed in open and closed bags and their survival and growth monitored (Volety *et al.*, 2010). The responses of juvenile oysters placed in closed wire-mesh bags indicate growth and/or mortality due to water quality; responses of oysters in open cages denote growth and/or mortality due to predation and water quality, thus giving us an estimation of the role of predation in these estuaries. These results are extremely useful in modeling or estimating oyster populations at various salinity and inflow regimes. This method was successfully employed by Volety *et al.* (2003) in the Caloosahatchee River and estuary and by Volety and Savarese (2001) in the Ten Thousand Islands.

Adult oysters normally occur at salinities between 10 and 30‰, but they tolerate salinities of ~2 to 40‰ (Gunter and Geyer, 1955). Occasional, short pulses of freshwater inflow can greatly benefit oyster populations by reducing predator (e.g., oyster drill, whelk) and parasite (e.g., *Perkinsus marinus*) impacts (Owen, 1953), but excessive freshwater inflow may kill entire populations of oysters (Gunter, 1953; Schlesselman, 1955; MacKenzie, 1977; Volety *et al.*, 2003; Volety *et al.*, 2010; Bergquist *et al.*, 2006). Therefore, controlled freshwater releases could be used in adaptive management to mitigate disease and predation pressure on oysters.

Intensity and Prevalence of Disease

For nearly 50 years, eastern oyster populations along the east and Gulf coasts of the United States have been ravaged by the highly pathogenic protozoan parasite, *Perkinsus marinus* (aka Dermo; Mackin, 1962; Andrews and Hewatt, 1957; Andrews, 1988; Burreson and Ragone-Calvo, 1996; Soniat, 1996). Higher salinities and temperatures significantly enhance *P. marinus* infections in oysters (Andrews, 1988; Burreson and Ragone-Calvo, 1996; Chu and Volety, 1997; Soniat, 1996; Volety *et al.*, 2003, 2009). The presence and intensity of the disease organism is typically assayed using Ray's fluid thioglycollate medium technique (Ray, 1954; Volety *et al.*, 2000; Volety *et al.*, 2003, 2009). Samples of gill and digestive diverticulum are incubated in the medium for four to five days. *P. marinus* meronts enlarge in the medium and stain blue-black with Lugol's iodine, allowing for visual identification under a microscope. Prevalence of infection is calculated as the percentage of infected oysters (Mackin, 1962). The intensity of infection is recorded using a modified Mackin scale (Mackin, 1962) in which 0 = no infection, 1 = light, 2 = light-moderate, 3 = moderate, 4 = moderate-heavy, and 5 = heavy.

Temperature and salinity profoundly influence the disease susceptibility of oysters, with higher temperatures and salinities resulting in a higher prevalence and intensity of *P. marinus* infections (Chu and Volety, 1997; Soniat, 1996; La Peyre *et al.*, 2003; Volety, 2008; Volety *et al.*, 2009). This trend has been confirmed in other southwest Florida estuaries, including those in the Ten Thousand Islands (Volety and Savarese, 2001; Savarese and Volety, 2008).

Oysters with infections above moderate levels quickly die out if temperatures and salinities remain high. Given that >80 percent of infected oysters can encounter mortality (Andrews, 1988), the impact of salinity on the survival of adult oysters cannot be underestimated. During warmer months (summer–fall), southwest Florida estuaries experience heavy rainfall and watershed runoff, as well as regulatory freshwater releases that depress salinities. During winter, when temperatures are cooler, there is little or no rainfall or watershed runoff, resulting in high salinities and, at times, hypersaline conditions within the estuary. The antagonistic effects of high temperature/low salinity (summer), and low temperature/high salinity (winter) keeps disease in check at low to moderate levels; however, in the absence of freshwater releases during winter, salinities become high and oysters are prone to disease, as well as predation. Similarly, if high volumes of freshwater are released, especially for extended periods (>1-2 weeks), salinities tend to be depressed, resulting not only in mitigation of the parasite and predators, but also in increased mortality of larval, juvenile, and adult oysters.

Reproductive Condition

The reproductive condition is used to estimate fecundity or the potential of oysters to engage in normal reproductive activity (or lack thereof). Histological analysis is typically used to examine gonadal state and reproductive potential of oysters and gametogenic stage identified under a microscope according to Fisher *et al.* (1996) and the International Mussel Watch Program (1980). Gonadal portions of the sections were examined by light microscopy to determine gender and gonadal condition. This method has been previously used successfully to identify reproductive patterns of oysters in southwest Florida estuaries (Volety and Savarese, 2001; Volety *et al.*, 2003) and to recommend alteration of inflow patterns to ensure survival of oyster spat during the reproductive season.

It appears that oysters in the Caloosahatchee Estuary continuously spawn from April to October, a result corroborated by changes in the condition index and spat recruitment at various sampling locations (Volety *et al.*, 2010). This trend contrasts with that of oysters from the northeastern United States (Shumway, 1996) and Chesapeake Bay (Southworth *et al.*, 2005), where reproduction of oysters is limited to a few months in the

summer (August–September). This reproductive trend of oysters in southwest Florida estuaries has significant management implications. For example, minimizing large freshwater releases during summer–fall, when oysters are spawning in the estuary, would result in favorable salinity conditions and larval retention within the estuary, resulting in higher recruitment and possibly higher adult densities in subsequent months. Due to high freshwater flows during summer months, larvae are flushed to downstream locations where substrate may not be available. High spat recruitment at downstream locations due to flushing activity may not be beneficial to the system as a whole, as higher salinity conditions at these locations attract predators and diseases (Shumway, 1996; White and Wilson, 1996; Volety, 2007; Volety *et al.*, 2009), resulting in mortality. Decreasing the duration and magnitude of high flows during summer (wet) and releasing base flows during winter (dry) will minimize extreme salinity fluctuations that are detrimental to oysters.

Drivers of Change in Oyster Reefs

Pressures are the direct cause of change in the ecosystem. The source of pressures affecting oyster reefs beds in the SWFS area, on a local scale, include coastal development and freshwater inflows into the estuaries due to regulatory releases and/or watershed runoff, increased sedimentation, input of excessive nutrients, and contaminants. On a more regional or global scale, pressures result from regional inputs of nutrients, which contribute to a general increase in nutrient concentrations in the coastal ocean, climate change, and the effects of rising carbon dioxide concentrations on ocean water chemistry. These pressures have a tremendous impact on the development of oyster larvae and the formation/dissolution of calcium carbonate shell under low acidic conditions.

Coastal Development

Local-scale alterations in the watershed from coastal/watershed development results in run-off of nutrient- and contaminant-laden sediment into rivers and estuaries. This contributes to the development of macroalgae and harmful algal blooms. Blooms smother the oyster beds and deplete oxygen when they decompose and negatively impact oysters and their early life stages with biotoxin production (Leverone *et al.*, 2006, 2007). Contaminants also negatively impact

oysters by increasing disease susceptibility and survival (Chu and Hale, 1994). Dredging and filling of coastal areas for navigation and utilization of shell in construction also depletes suitable substrate and negatively affects oyster reef development.

Climate Change and Sea-Level Rise

Carbon dioxide levels in the atmosphere have been rising since the beginning of the Industrial Revolution. Present day atmospheric CO₂ concentrations of 385 ppm represent a nearly 30 percent increase over pre-industrial values, with concentrations forecast to surpass 700 ppm by the end of the century (IPCC, 2007). These increases in CO₂ concentrations are believed to cause increases in atmospheric and oceanic temperatures, changes in the carbonate chemistry of seawater and widespread melting of snow and ice, and rising sea levels (IPCC, 2007). Recent studies have shown that the CO₂ trends anticipated by the IPCC (2007) study can have significant impacts on the calcification rates and physiology of planktonic and benthic organisms, including shellfish (Fabry *et al.*, 2008). In fact, the impact of acidic waters on bivalves has been investigated since the 1940s (Loosanoff and Tommers, 1947). More recently, reduced CO₂ levels have been shown to decrease calcification (Gazeau *et al.*, 2007; Kurihara *et al.*, 2009; Miller *et al.*, 2009), reduce shell growth (Berge *et al.*, 2006; Michaelidis *et al.*, 2005), and increase mortality (Talmage and Gobler, 2009) in different species and life stages of marine bivalves.

Mechanisms of Change in Oyster Reefs

The principal threats to oyster reefs in the SWFS mostly occur through four pathways: watershed development and input of nutrients and contaminants; freshwater runoff from the watershed and regulatory freshwater releases; increased sedimentation; and dredging and removal of substrate required for larval settlement and reef growth.

Oyster Reef Status and Trends

Anecdotal evidence, as well as archived photographic evidence, suggests that the coverage of oyster reefs in southwest Florida has drastically decreased. Current coverage of oyster reefs in the Caloosahatchee Estuary-Ten Thousand

Islands is about 0.1-1 percent of the accommodation space (as defined by the area where salinity is favorable for oyster growth). Healthy estuaries along the Gulf of Mexico have oyster reef coverage of about 1-5 percent accommodation space (RECOVER, 2009; Volety *et al.*, unpublished results). The situation along the southwest Florida coast follows a general decline in oysters worldwide. Oyster reefs are at less than 10 percent of their prior abundance in most bays and ecoregions. It has been estimated that there is an 85 percent loss of oyster reef ecosystems globally (Beck *et al.*, 2011). Most of the loss is due to timing, duration, and quantity of freshwater inflows into the estuaries, as well as increased sedimentation and contaminants resulting from watershed runoff. With a reduction and redirection of freshwater Everglades discharge (along with many other changes to the coastal wetlands), many of these historical oyster bars and banks have been lost.

Topics of Scientific Debate and Uncertainty

While the relationship between salinity and *P. marinus* prevalence and intensity has been well established through laboratory (Chu and Volety, 1997; La Peyre *et al.*, 2003) and field studies (Burreson and Ragono-Calvo, 1996; Soniat, 1996), the importance of duration, frequency, and magnitude of freshwater inflows into estuaries and how they influence *P. marinus* infections is not clear. In addition, the role of freshwater inflows on the early life stages of oysters is unclear and is necessary for managing freshwater inflows into southwest Florida estuaries. While it has been shown that contaminants affect immune responses (Anderson, 1993; Pipe and Coles, 1995), energy reserves (Capuzzo, 1996), and exacerbates *P. marinus* infections in oysters (Chu and Hale, 1994; Anderson *et al.*, 1996), their effects on the early life stages and, especially, on the F-2 generation is unclear. Similarly, the effects of harmful algal blooms on the survival and metamorphosis of early life stages of oysters and long-term reproductive impacts on oysters are unclear. Recent studies investigating the effect of elevated CO₂ levels under scenarios of predicted global climate change have yielded contrasting results depending on the species examined. Little or no information exists on the effects of elevated CO₂ levels in seawater, and how it may impact growth and survival of larval oysters is unclear.

References

- Abeels, H.A. 2010. Trophic transfer and habitat use of oyster *Crassostrea virginica* reefs in southwest Florida using stable isotope analysis. Masters' Thesis, Florida Gulf Coast University, Fort Myers, FL, 77 pp.
- Anderson, R.S. 1993. Modulation of nonspecific immunity by environmental stressors. In *Pathobiology of Marine and Estuarine Organisms*, J.A. Couch and J.W. Fournie (eds.). CRC Press, London, 482-510.
- Anderson, R.S., M.A. Unger, and E.M. Bureson. 1996. Enhancement of *Perkinsus marinus* disease progression in TBT exposed oysters (*Crassostrea virginica*). *Marine Environmental Research*, 42:177-180.
- Andrews, J.D. 1988. Epizootiology of the disease caused by oyster pathogen, *Perkinsus marinus*, and its effects on the oyster industry. American Fisheries Society Special Publication, 18:47-63.
- Andrews J.D., and W.G. Hewatt. 1957. Oyster mortality studies in Virginia, II. The fungus disease caused by *Dermocystidium marinum* in oysters in Chesapeake Bay. *Ecological Monographs*, 27:1-26.
- Beck, M.W., R.D. Brumbaugh, L. Airoidi, A. Carranza, L.D. Cien, C. Crawford, O. Defeo, G.J. Edgar, B. Hancock, M.C. Kay, H.S. Lenihan, M.W. Luckenbach, C.A. Toropova, G. Zhang, and X. Guo. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience*, 61(2):107-116.
- Berge, J.A., B. Bjerkeng, O. Pettersen, M.T. Schaanning, and S. Oxnevad. 2006. Effects of increased seawater concentrations of CO₂ on growth of the bivalve *Mytilus edulis* L. *Chemosphere*, 62(4):681-687.
- Bergquist, D.C., J.A. Hale, P. Baker, and S.M. Baker. 2006. Development of ecosystem indicators for the Suwannee River estuary: Oyster reef habitat quality along a salinity gradient. *Estuaries and Coasts*, 29:353-360.
- Breitberg, D.L. 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behavior, and physical disturbance. *Ecological Monographs*, 59:329-364.
- Breitburg, D.L. 1999. Are three-dimensional structure and healthy oyster populations the key to an ecologically interesting and important fish community? In *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*, M.W. Luckenbach, R. Mann, and J.A. Wesson (eds.). Virginia Institute of Marine Science Press, Gloucester Point, VA, 239-250.
- Bureson, E.M., and L.M. Ragone-Calvo. 1996. Epizootiology of *Perkinsus marinus* disease of oysters in Chesapeake Bay with emphasis on data since 1985. *Journal of Shellfish Research*, 15:17-34.
- Caine, E.A. 1975. Feeding and masticatory structures of selected Anomura (Crustacea). *Journal of Experimental Marine Biology and Ecology*, 18:277-301.
- Capuzzo, J.M. 1996. The bioaccumulation and biological effects of lipophilic organic contaminants. In *The Eastern Oyster: Crassostrea Virginica*, V.S. Kennedy, R.I.E. Newell, and A.F. Eble (eds). Maryland Sea Grant College Publ., College Park, MD, 539-557.
- Chamberlain, R.H., and P.H. Doering. 1998a. Freshwater inflow to the Caloosahatchee Estuary and the resource-based method for evaluation. Proceedings, Charlotte Harbor Public Conference and Technical Symposium, Technical Report No. 98-02, 81-90.
- Chamberlain, R.H., and P.H. Doering. 1998b. Preliminary estimate of optimum freshwater inflow to the Caloosahatchee Estuary: A resource-based approach. Proceedings, Charlotte Harbor Public Conference and Technical Symposium, Technical Report No. 98-02, 121-130.
- Chu, F.L.E., and R.C. Hale. 1994. Relationship between pollution and susceptibility to infectious disease in eastern oyster, *Crassostrea virginica*. *Marine Environmental Research*, 38:243-256.
- Chu, F.L.E., and A.K. Volety. 1997. Disease processes of the parasite *Perkinsus marinus* in eastern oyster *Crassostrea virginica*: Minimum dose for infection initiation, and interaction of temperature, salinity, and infective cell dose. *Diseases of Aquatic Organisms*, 28:61-68.
- Coen, L.D., M.W. Luckenbach, and D.L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. American Fisheries Society Symposium, 22:438-454.
- Cressman, K.A., M.H. Posey, M.A. Mallin, L.A. Leonard, and T.D. Alphin. 2003. Effects of oyster reefs on water quality in a tidal creek estuary. *Journal of Shellfish Research*, 22:753-762.
- Dame, R.F., J.D. Spurrier, and T.G. Wolaver. 1989. Carbon, nitrogen, and phosphorus processing by an oyster reef. *Journal of Experimental Marine Biology and Ecology*, 83:249-256.
- Fabry, V.J., B.A. Seibel, R.A. Feely, and J.C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65(3):414-432.
- Fisher, W.S., J.T. Winstead, L.M. Oliver, H.L. Edminston, and G.O. Bailey. 1996. Physiological variability of eastern oysters from Apalachicola Bay, Florida. *Journal of Shellfish Research*, 15:543-555.
- Gazeau, F., C. Quiblier, J.M. Jansen, J.P. Gattuso, J.J. Middelburg, and C.H.R. Heip. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letters*, 34:L07603 (doi:10.1029/2006GL028554), 5 pp.
- Grabowski, J.H., and C.H. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. In *Ecosystem Engineers*, K. Cuddington, J.E. Byers, W.G. Wilson, and A. Hastings (eds). Elsevier Inc., Burlington, MA, 281-298.
- Grabowski, J.H., A.R. Hughes, D.L. Kimbro, and M.A. Dolan. 2005. How habitat setting influences restored oyster reef communities. *Ecology*, 86(7):1926-1935.
- Grant, J., and J. McDonald. 1979. Desiccation tolerance of *Eurypanopeus depressus* (Smith) (Decapoda: Xanthidae) and the exploitation of microhabitat. *Estuaries*, 2(3):172-177.
- Gunter, G. 1953. The relationship of the Bonnet Carre spillway to oyster beds in Mississippi Sound and the "Louisiana March": With a report on the 1950 opening and a study of beds in the vicinity of the Bohemia spillway and Baptiste Collete Gap. Publication of the Institute of Marine Science, University of Texas, 3(1):17-71.

- Gunter, G., and R.A. Geyer. 1955. Studies of fouling organisms in the northwestern Gulf of Mexico. Publication of the Institute of Marine Science, University of Texas, 4(1):114-116.
- Gutierrez, J.L., C.G. Jones, D.L. Strayer, and O.O. Iribarne. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos*, 101:79-90.
- Harding, J.M., and R. Mann. 2001. Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes. *Journal of Shellfish Research*, 20(3):951-959.
- Henderson, J., and L.J. O'Neil. 2003. Economic values associated with construction of oyster reefs by the Corps of Engineers. EMRRP Technical Notes and Collection (ERDC TN-EMRRP-ER-01), Vicksburg, MS, U.S. Army Corps of Engineer Research and Development Center.
- Ingle, R.M., and F.G.W. Smith. 1949. Oyster culture in Florida. State of Florida Board of Conservation, Educational Series 5, 25 pp.
- International Mussel Watch. 1980. National Academy of Sciences, Washington, DC, 248 pp.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for Policymakers. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR4)*, S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (eds.). Cambridge University Press, Cambridge, UK and New York, NY, 996 pp.
- Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293:629-638.
- Kahn, J.R., and W.M. Kemp. 1985. Economic losses associated with the degradation of an ecosystem: The case of submerged aquatic vegetation in Chesapeake Bay. *Journal of Environmental Economics and Management*, 12:246-263.
- Kurihara, H., T. Asai, S. Kato, and A. Ishimatsu. 2009. Effects of elevated pCO₂ on early development in the mussel *Mytilus galloprovincialis*. *Aquatic Biology*, 4(3):225-233.
- La Peyre, M.K., A.D. Nickens, A.K. Volety, S.G. Tolley, and J.F. La Peyre. 2003. Environmental significance of freshets in reducing *Perkinsus marinus* infection in eastern oysters, *Crassostrea virginica*: Potential management applications. *Marine Ecology Progress Series*, 248: 165-176.
- Lenihan, H.S., and C.H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications*, 8:128-140.
- Lenihan, H.S., C.H. Peterson, J.E. Byers, J.H. Grabowski, G.W. Thayer, and D.R. Colby. 2001. Cascading of habitat degradation: Oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications*, 11(3):764-782.
- Leverone, J.R., N.J. Blake, R.H. Pierce, and S.E. Shumway. 2006. Effects of the dinoflagellate *Karenia brevis* on the larval development in three species of bivalve molluscs from Florida. *Toxicon*, 48:75-84.
- Leverone, J.R., N.J. Blake, and S.E. Shumway. 2007. Comparative effect of the toxic dinoflagellate *Karenia brevis* on clearance rates in juveniles of four bivalve molluscs from Florida, USA. *Toxicon*, 49:634-645.
- Loosanoff, V.L., and F.D. Tommers. 1947. Effect of low pH upon rate of water pumping of oysters, *Ostrea virginica*. *Anatomical Record*, 99(4):668-669.
- Luckenbach, M.W., L.D. Coen, P.G. Ross, Jr., and J.A. Stephen. 2005. Oyster reef habitat restoration: Relationships between oyster abundance and community development based on two studies in Virginia and South Carolina. *Journal of Coastal Research, Special Issue*, 40:64-78.
- MacKenzie, C.L., Jr. 1977. Development of an aquaculture program for rehabilitation of damaged oyster reefs in Mississippi. *Marine Fishery Review*, 39(8):1-13.
- Mackin, J.G. 1962. Oyster disease caused by *Dermocystidium marinum* and other microorganisms in Louisiana. Publication of the Institute of Marine Science, University of Texas, 7:132-229.
- McDermott, J. 1960. The predation of oysters and barnacles by crabs of the family *Xanthidae*. *Proceedings of the Pennsylvania Academy of Science*, 34:199-211.
- McDonald, J. 1982. Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Brachyura: Xanthidae). *Marine Ecology Progress Series*, 8:173-180.
- Meyer, D.L., E.C. Townsend, and G.W. Thayer. 1997. Stabilization and erosion control of oyster cultch for intertidal marsh. *Restoration Ecology*, 5:93-99.
- Michaelidis, B., C. Ouzounis, A. Paleras, and H.O. Portner. 2005. Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series*, 293:109.
- Miller, A.W., A.C. Reynolds, C. Sobrino, and G.F. Riedel. 2009. Shellfish face uncertain future in high CO₂ world: Influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS ONE*, 4(5):e5661.
- Myers, R.L., and J.J. Ewel (eds.). 1990. *Ecosystems of Florida*. University of Central Florida Press, 765 pp. (ISBN 0-8130-1012-5).
- National Research Council. 2004. Non-native oysters in the Chesapeake Bay: Committee on the non-native oysters in the Chesapeake Bay. Ocean Studies Board, Division on Earth and Life Studies, Washington, DC, The National Academies Press.
- Newell, R.I.E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the eastern oyster (*Crassostrea virginica*). In *Understanding the Estuary: Advances in Chesapeake Bay Research*, M. Lynch (ed.). Chesapeake Research Consortium, Publication 129, 536-546.
- Newell, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. *Journal of Shellfish Research*, 23:51-61.

- Newell, R.I.E., J.C. Cornwell, and M.S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology and Oceanography*, 47(5):1367-1379.
- O'Connor, T., and G.G. Laurenstein. 2006. Trends in chemical concentrations in mussels and oysters collected along the U.S. coast: Update to 2003. *Marine Environmental Research*, 26:261-285.
- Owen, H.M. 1953. The relationship of high temperature and low rainfall to oyster production in Louisiana. *Bulletin of Marine Science*, (1): 34-43.
- Paerl, H.W., J.L. Pinckney, J.M. Fear, and B.L. Peierls. 1998. Ecosystem responses to internal and watershed organic matter loading: Consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. *Marine Ecology Progress Series*, 166:17-25.
- Parkinson, R.W. 1989. Decelerating Holocene sea-level rise and its influence on southwest Florida coastal evolution: A transgressive/regressive stratigraphy. *Journal of Sedimentary Petrology*, 59(6): 960-972.
- Peterson, C.H., and R.N. Lipcius. 2003. Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. *Marine Ecology Progress Series*, 264:297-307.
- Pipe, R.K., and J.A. Coles. 1995. Environmental contaminants influencing immune function in marine bivalve mollusks. *Fish and Shellfish Immunology*, 5:581-595.
- Porter, E.T., J.C. Cornwell, and L.P. Sanford. 2004. Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic-pelagic coupling and estuarine water quality. *Marine Ecology Progress Series*, 271:61-75.
- Posey, M.H., T.D. Alphin, C.M. Powell, and E. Townsend. 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. In *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*, M.W. Luckenbach, R. Mann, and J.A. Wesson (eds). Virginia Institute of Marine Science Press, 229-237.
- Quitmyer, I.R., and M. Massaro. 1999. Seasonality and subsistence in a southwest Florida estuary: A faunal analysis of pre-Columbian Useppa. In *The Archaeology of Useppa Island*, W.H. Marquardt (ed.). Institute of Archaeology and Paleoenvironmental Studies, University of Florida, Gainesville, FL, Monograph No. 3, 99-128.
- Ray, S.M. 1954. Biological studies of *Dermocystidium marinum*. The Rice Institute Pamphlet, Special Issue, 65-76.
- RECOVER (Restoration Coordination and Verification). 2007. Development and application of Comprehensive Everglades Restoration Plan system-wide performance measures. South Florida Water Management District, West Palm Beach, FL and U.S. Army Corps of Engineers, Jacksonville District, Jacksonville, FL, October 12, 2007 (available at http://www.evergladesplan.org/pm/recover/perf_systemwide.aspx).
- RECOVER (Restoration Coordination and Verification). 2009. Development and application of Comprehensive Everglades Restoration Plan system-wide performance measures. South Florida Water Management District, West Palm Beach, FL and U.S. Army Corps of Engineers, Jacksonville District, Jacksonville, FL, October 12, 2007 (Accessed at http://www.evergladesplan.org/pm/recover/perf_systemwide.aspx).
- Savarese, M., and A.K. Volety. 2008. Oyster reef health in Pumpkin and Fakahatchee estuaries: Baseline monitoring for Ten Thousand Islands restoration. South Florida Water Management District, Technical Report, 58 pp.
- Savarese, M., A. Volety, and S.G. Tolley. 2004. Oyster health and habitat quality in Fakahatchee Estuary: Establishing a baseline performance for Ten Thousand Islands estuarine restoration. South Florida Water Management District, Technical Report, 27 pp.
- Schlesselman, G.W. 1955. The gulf coast oyster industry of the United States. *Geographical Reviews*, 45(4):531-541.
- Shumway, S.E. 1996. Natural environmental factors. In *The Eastern Oyster: Crassostrea virginica*, V.S. Kennedy, R.I.E. Newell, and A.F. Eble (eds.). Maryland Sea Grant College Publ., College Park, MD, 467-513.
- Soniat, T.M. 1996. Epizootiology of *Perkinsus marinus* disease of eastern oysters in the Gulf of Mexico. *Journal of Shellfish Research*, 15:35-43.
- Southworth, M., J.M. Harding, and R. Mann. 2005. The status of Virginia's public oyster resource. Virginia Institute of Marine Science, 49 pp.
- Talmage, S.C., and C.J. Gobler. 2009. The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and eastern oysters (*Crassostrea virginica*). *Limnology and Oceanography*, 54(6):2072-2080.
- Tolley, S.G., and A.K. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *Journal of Shellfish Research*, 24(4):1007-1012.
- Tolley, S.G., A.K. Volety, and M. Savarese. 2005. Influence of salinity on the habitat use of oyster reefs in three southwest Florida estuaries. *Journal of Shellfish Research*, 24(1):127-137.
- Tolley, S.G., A.K. Volety, M. Savarese, L.D. Walls, C. Linardich, and E.M. Everham, III. 2006. Impacts of salinity and freshwater inflow on oyster-reef communities in southwest Florida. *Aquatic Living Resource*, 19:371-387.
- Ulanowicz, R.E., and J.H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries*, 15:298-306.
- USDOC (U.S. Department of Commerce). 1997. Magnuson-Stevens Fishery Conservation and Management Act, as amended through October 11, 1996. NOAA Technical Memorandum, NMFS-F/SPO-23. U.S. Government Printing Office, Washington, DC, 121 pp.
- Volety, A.K. 2007. Caloosahatchee Estuary oyster monitoring and research. Final Report, submitted to the South Florida Water Management District, Contract No. CP040626, 28 pp.
- Volety, A.K. 2008. Effects of salinity, heavy metals, and pesticides on health and physiology of oysters in the Caloosahatchee Estuary. *Ecotoxicology*. 17:579-590 (doi:10.1007/s10646-008-0242-9).

- Volety, A.K., and M. Savarese. 2001. Oysters as indicators of ecosystem health: Determining the impacts of watershed alterations and implications for restoration. Final Report submitted to National Fish and Wildlife Foundation, South Florida Water Management District (Big Cypress Basin), and Florida Gulf Coast University Foundation, 104 pp.
- Volety, A.K., F.O. Perkins, R. Mann, and P.R. Hershberg. 2000. Progression of diseases caused by the oyster parasites, *Perkinsus marinus* and *Haplosporidium nelsoni*, in *Crassostrea virginica* on constructed artificial reefs. *Journal of Shellfish Research*, 19:341-347.
- Volety, A.K., S.G. Tolley, and J. Winstead. 2003. Investigations into effects of seasonal and water quality parameters on oysters (*Crassostrea virginica*) and associated fish populations in the Caloosahatchee Estuary. Interpretive Report (Award #C 12412-A 1) submitted to the South Florida Water Management District.
- Volety, A.K., M. Savarese, S.G. Tolley, W. Arnold, P. Sime, P. Goodman, R. Chamberlain, and P.H. Doering. 2009. Eastern oysters (*Crassostrea virginica*) as an indicator for restoration of Everglades' ecosystems. *Ecological Indicators*, 9(Suppl. 6):S120-S136.
- Volety, A.K., S.G. Tolley, A.N. Loh, and A. Abeels. 2010. Oyster monitoring network for the Caloosahatchee Estuary. Final Report, South Florida Water Management District, Award No. 4600000815, 145 pp.
- Wasno, R.M., A.K. Volety, P.H. Doering, and D. Crean. 2009. The importance of oyster reef community in the diet of predatory fish. *American Society of Limnology and Oceanography*, Nice, France.
- White, M.E., and E.A. Wilson. 1996. Predators, pests, and competitors. In *The Eastern Oyster: Crassostrea virginica*, V.S. Kennedy, R.I.E. Newell, and A.F. Eble (eds.). Maryland Sea Grant College Publ., College Park, MD, 559-579.
- Wells, H.W. 1961. The fauna of oyster beds with special reference to the salinity factor. *Ecological Monographs*, 31:239-266.
- Wenner, E., H.R. Beatty, and L. Coen. 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. *Journal of Shellfish Research*, 15(3):769-775.
- Wohlpert, S.L. 2007. The development of estuarine systems in southwest Florida: A perspective from the late Holocene history of oyster reef development. Master's Thesis, Florida Gulf Coast University, Fort Myers, FL, 160 pp.
- Zimmerman, R.J., T.J. Minello, T.J. Baumer, and M.C. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Technical Memorandum, NMFS-SEFC-249, 16 pp.