Ecological Indicators 44 (2014) 108–119

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Ecological condition and value of oyster reefs of the Southwest Florida shelf ecosystem

Aswani K. Volety[a],[*], Lesli Haynes[a], Patricia Goodman[a], Patricia Gorman[b]

[a] Vester Marine Field Station and Coastal Watershed Institute, Florida Gulf Coast University, 10501 FGCU Boulevard, Fort Myers, FL 33965, United States
[b] South Florida Water Management District, 3301 Gun Club Road, West Palm Beach, FL 33406, United States

ARTICLE INFO

Article history:
Received 25 August 2013
Received in revised form 3 March 2014
Accepted 12 March 2014

Keywords:
Ecological indicator
Oysters
Everglades restoration
Water quality
Conceptual model

ABSTRACT

The eastern oyster *Crassostrea virginica* is prolific and their reefs are dominant features along the estuaries and coastal areas in the Gulf of Mexico including those along the Southwest Florida coast. This paper examines the ecological and indirect economic value of oysters and the ecosystem services they provide. Drivers of change in reefs as well as various factors (pressures) that affect oyster reefs are examined. Using the monitoring data from on-going studies, this study examined various metrics of oyster health, reproduction and survival to develop an index to create an overall state of oyster reefs in the Southwest Florida estuaries. Based on existing data, oyster reefs in Southwest Florida estuaries are at “caution”, but stable. Restoration of a more natural freshwater inflow, minimizing nutrient and contaminant input as well as decreased sedimentation will enable oyster reefs to expand and thrive.

1. Introduction

Oysters, *Crassostrea virginica*, are natural components of estuaries along the eastern seaboard of the US as well as estuaries in the Gulf of Mexico and were once abundant in the estuaries in both southwest and southeast Florida (RECOVER, 2007). In the Caloosahatchee, Loxahatchee, Lake Worth Lagoon, and St. Lucie Estuaries (Northern Estuaries of the Everglades), oysters have been identified as a Valued Ecosystem Component (VEC; Chamberlain and Doering, 1998a,b). The Eastern oyster (*C. virginica*) 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 attach to prop roots of red mangroves, often extending out at the base of mangroves.

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, *C. virginica*, to flourish and build small to extensive oyster banks and bars. In a few areas on the southwest coast, new oyster growth appears to have shifted farther inland along channels and interior bays (Volety, unpublished results). 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 (Volety et al., 2008, 2009a; Wohlpart, 2007). 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 region to estuarine conditions (Parkinson, 1989; Wohlpart, 2007). In the present day, oyster reefs are extensive along Charlotte Harbor to the Ten Thousand Islands, with reef development decreasing southeast of Chatham River toward Everglades National Park (Savarese et al., 2004; Volety et al., 2009b). In estuaries north of Lostman’s and Broad Rivers, oysters are also found on the prop roots of red mangroves fringing the inner bays (Fig. 1). In most of the estuaries, oyster reef coverage ranged between 5 and 20 acres (Volety and Savarese, 2001; Savarese et al., 2004; Volety et al., 2009a).

Information presented in this manuscript was collected as part of the MARine and EStuarine goal-setting (MARES) project that aims to develop characteristics of south Florida coastal Marine Ecosystems that are sustainable and provide diverse ecosystem services encompassing ecological and human dimensions (Loomis et al., 2014). There was a significant harvest as recently as the 1990s (Charlotte, Lee and Collier Counties) and continues as a very

---

[*] Corresponding author. Tel.: +1 239 590 7216.
E-mail addresses: avolety@fgcu.edu, avolety@yahoo.com (A.K. Volety).

http://dx.doi.org/10.1016/j.ecolind.2014.03.012
1470-160X/

minor industry today (Lee County); illegal and unmonitored recreational harvest occurs. However, oyster reefs and other shellfish are extremely important for their ecological services. Therefore, in addition to describing measures of oyster health, human dimension attributes such as "why do we care about oyster reefs" are included in this paper with most of the emphasis on their ecological services. Based on the measured attributes, we propose a "state-of-the-oyster reefs" indicator in the Southwest Florida shelf ecosystem and describe various factors that influence the state of oyster reefs.

1.1. *Ecological role of oyster reefs – attributes that people care about*

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

- Diverse fish, crustaceans and other invertebrate populations by providing critical nursery, food and habitat for recreationally and commercially important species
- Natural filter for phytoplankton, detritus, bacteria and contaminants resulting in enhanced water clarity and improved water quality
- Prevention of coastal erosion and boat wake mitigation
- Carbon sequestration
- Sentinels for environmental monitoring

1.1.1. *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 with a life span of about 50 years 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). The reef-resident and transient organisms (Wells, 1961; Zimmerman et al., 1989; Myers and Ewel, 1990; Breitburg, 1999; Lenihan et al., 2001) are 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) and thus oyster reefs are considered essential fish habitat (USDOC, 1997).

Harding and Mann (2001) suggested that oyster reefs may provide 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 and this could potentially cause an increase in fish productivity in an estuary (Grabowski et al., 2005). Additionally, oyster shells and the interstitial spaces provide space for settlement and refuge from predation, thereby increasing 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*

Fig. 1. Geographical distribution of oyster reefs along the estuarine and coastal region of the Southwest Florida shelf system.

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; Abeels et al., 2012). These fishes use the oyster reef as spawning and feeding habitat and as shelter from predators.

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 undulates*), bluefish (*Pomatomus saltatrix*), Atlantic menhaden, 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).

Fishes are not the only species that utilize oyster reefs as habitat. Several species of decapod crustaceans are found on oyster reefs: Porcelain crab *Petrolisthes armatus*, mud crab *Panopeus* spp. and the flatback mud crab *Eurypanopeus depressus*, stone crab *Menippe mercenaria*, snapping shrimp *Alpheus heterochaelis* and grass shrimp *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). In addition, many organisms use the oyster reef in varying ways. Benthic reef invertebrates, such as amphipods, are food for crabs and shrimps that then are eaten by resident and transient fish species. The oyster reef serves as shelter to species such as resident mud crabs and grass shrimp (Posey et al., 1999) that use the spaces in and around oysters to avoid predation.

Oyster reefs are important locations for recreational anglers in Southwest Florida. For example, two studies in Southwest Florida have examined the trophic transfer from the water column to the oyster reef ecosystem and from the oyster reef ecosystem to higher trophic levels, such as predatory fish that are recreationally and commercially important. In a comprehensive study, using carbon and nitrogen isotopes, Abeels et al. (2012) 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 trophic levels and are consumed by oysters, resident crabs, shrimp, and fishes, which are then consumed by other resident crabs and fish species Transient fish species such as *Lutjanus* sp. come to the reef to feed on the reef 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 decapods crustaceans (*E. depressus, Panopeus* sp., and *Xanthidae* sp.) that are almost exclusive to oyster reefs occurred in the majority of stomachs and contributed to >43% of their diet (relative importance index). Live oyster reefs have higher diversity and species richness compared to reefs with dead oysters or no oysters (Tolley and Volety, 2005) and harbor tremendous diversity of organisms (Grabowski and Peterson, 2007; Wells, 1961). Oyster reefs and adjoining sea grass beds and/or mangrove areas are commonly targeted by recreational fishermen and fishing guides in SW Florida. Combined, results from all of these studies illustrate the importance of oyster reefs not only as habitat for maintaining diverse fish, crustacean and other invertebrate populations, but also in trophic transfer and secondary production resulting in recreationally and commercially important fisheries.

1.1.2. Filtration

One of the important benefits of oyster reefs to an ecosystem is their tremendous filtration capacity. According to Newell (1988), individual oysters filter 4–40 L/h. By filtering water column particulates, nutrients, sediment, and phytoplankton, oyster reefs increase light penetration to deeper layers thus promoting the growth of submerged aquatic vegetation and via denitrification, they 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 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 Chl *a* levels in the water column by 10–25% and fecal coliform bacteria by 45% (Cressman et al., 2003). In addition to oysters themselves, sedentary and reef-resident organisms that occupy an established reef (e.g., barnacles, *P. armatus*) also filter water. Therefore, the total amount of water filtered is greater when the oyster reef is healthy and occupied by such organisms.

Increased nutrient loading and/or turbidity is extremely detrimental to submerged aquatic vegetation (SAV) habitats. For example, Nitrogen loading of 30 kg N $\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$ resulted in an 80–96% loss in SAV coverage in Waquoit Bay, MA. A reduction in 20% seagrass coverage in Chesapeake Bay results 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% improvement in water quality along the western shore of Maryland is worth $188 million for shore beach users, $26 million for recreational boaters and $8 million for striped bass fishermen. While oyster reefs in Southwest Florida, given their coverage and area of the watershed, may not contribute to as much to improvement in water quality, they still filter enormous amount of water.

1.1.3. Coastal erosion and protection against boat wakes

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 benefit the growth of SAVs. By reducing wave height, current velocities, and sediment re-suspension, oyster reefs protect sea grasses and mangroves from erosion, saving these valued ecosystem communities (Meyer et al., 1997; Piazza et al., 2005; Coen et al., 2007). 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, at least when the environment is stable and no harvest is taking place, as is the case in many southwest Florida estuaries.

1.1.4. Carbon sequestration

Oyster reef habitats have also been observed to sequester significant quantities of carbon (Wingard and Lorenz, 2014). Oysters secrete calcium carbonate shells from seawater, thereby removing CO_2 from the water column (and thus atmosphere) and contribute to reduction in greenhouse gases (Peterson and Lipcius, 2003). The shells have very low rates of dissolution and thus form a carbon sink in the coastal and estuarine realms, especially when the shells are buried.

1.1.5. Environmental sentinels

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

2. Materials and methods

2.1. Study area

The study area is the coastal shelf ecosystem in Southwest Florida encompassing the coastal and estuarine areas in the Charlotte Harbor and the Ten Thousand Islands. Since data on the responses of oyster reefs is available via monitoring program(s), information from the Caloosahatchee River and Estuary (Charlotte Harbor), Faka Union Estuary, Pumpkin Bay and Fakahatchee Estuary in the Ten Thousand Islands area (Fig. 2) are used as case studies to evaluate the indicator and describe the general state of oyster reefs. Typical topography of estuaries and coastal systems in Southwest Florida is dominated by numerous mangrove islands or barrier islands providing an estuarine–marine setting where oyster reefs abound. Oysters exist either as continuous reefs, or loose clusters that forms bars. In this manuscript, the terminology "oyster reefs" is used to encompass oyster reefs, bars, and small clusters of oysters.

2.2. Indicator selection

Various indicators (e.g., water column index, economic index) including indicator species (e.g. oysters) were selected through a series of workshops involving scientists, resource managers and Non-Governmental Organizations (NGOs). Given the ecological and economic importance of oyster reefs in the estuaries and coastal areas of the east coast of the United States and the Gulf Coast as well as their abundance in the Gulf Coast estuaries, oysters were chosen as one of the indicator species for the Southwest Florida shelf ecosystem. While numerous responses of oysters or oyster reefs are measured in various estuaries and coastal systems by scientists and resource managers, physiological and ecological responses mentioned in this manuscript are used to assess the state of oyster reefs in the Southwest Florida shelf ecosystem due to the availability of on-going monitoring data. In addition, these estuaries are representative of most estuaries along Southwest Florida coastal system. Previous conceptual models have focused on factors influencing oyster abundance and health in Southwest Florida estuaries (Barnes, 2005; Volety et al., 2008). These conceptual models are a product of the known cause and effect relationships between stressors and *C. virginica* ecologic and physiologic responses from published studies for this region (cited previously) and elsewhere throughout the species' range. The oyster reef sub-model diagram for Southwest Florida shelf builds upon these conceptual models by linking them with pressures that alter the status of oyster reefs and describes how oyster reefs contribute to the benefits valued by humans (Fig. 3). The oyster conceptual model in this paper describes the linkages from pressures identified through the MARES process to the oyster indicator responses identified in Table 1 (what do we measure to look at the health of oysters) to the ecosystem attributes that people care about (Kelble et al., 2013).

Based on feedback from the scientists, resource managers, and NGOs that contributed to the MARES process and using the best available scientific knowledge, MARES developed an Ecosystem-based management (EBM) EBM-DPSER conceptual model for the Southwest Florida shelf ecosystem (Nuttle and Fletcher, 2013). The EBM-DPSER framework involves: (1) Drivers – the ultimate cause of large-scale ecosystem changes (e.g., climate change, land- and water-based anthropogenic activities); (2) Pressures – regional scale effects that are the cause of change in the immediate environment, often as response to drivers (e.g., sea-level rise, rainfall, input of contaminants, storms, dredging, stormwater runoff, nutrient loading, timing and quantity of freshwater input); (3) State – encompasses the focal components of the ecosystem; (4) Ecosystem services – benefits that humans derive from the ecosystem; (5) Responses – changes in the human activities that come about from changes in the State caused by Drivers and Pressures (Kelble

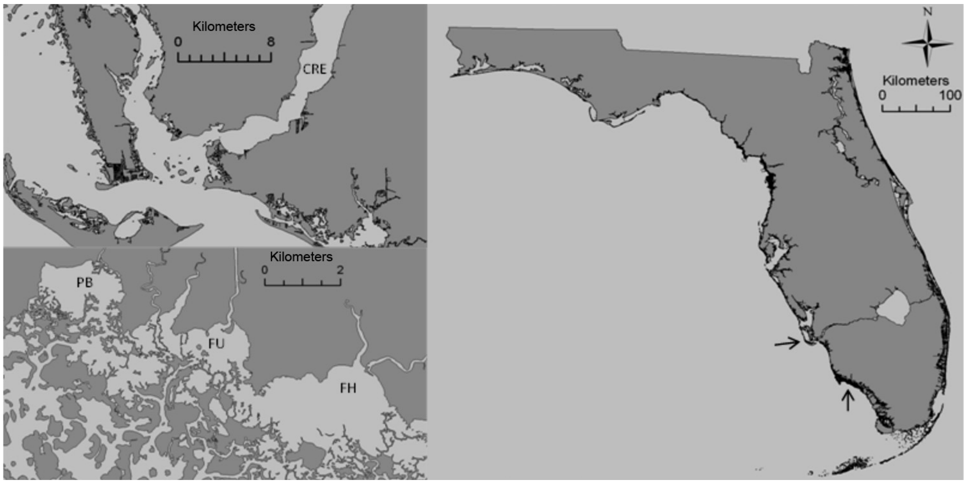

Fig. 2. Map of sampling locations. Map A is the Caloosahatchee River Estuary (CRE). Map B is the Ten Thousand Islands area. PB, Pumpkin Bay Estuary; FU, Faka Union Estuary; and FH, Fakahatchee Estuary.

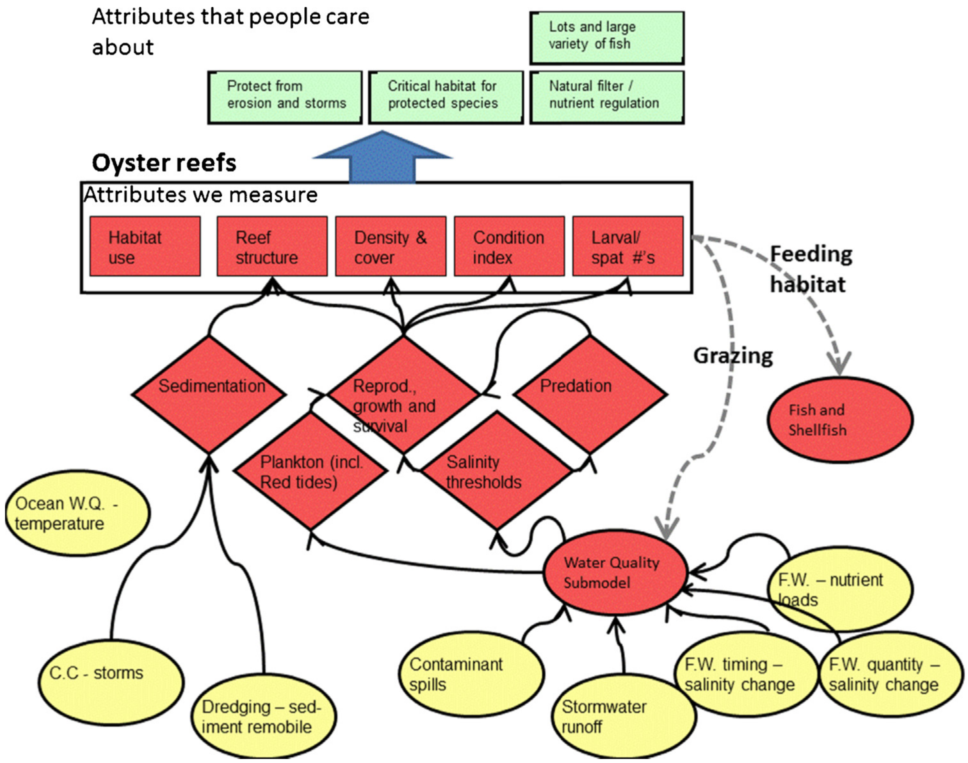

Fig. 3. Oyster reef sub-model of Drivers, Pressures, State, Ecosystem Services in the Southwest Florida shelf system.

et al., 2013). A nested conceptual model for each focal ecosystem component in the state box was developed that links pressures to quantifiable state indicators to ecosystem attributes people care about (Fig. 3). Similar to the broader EBM-DPSER model, the model for oyster reefs was developed based upon the best available scientific and local knowledge and input from scientists, resource managers, and stakeholders. This model leads to the selection of indicators by highlighting how pressures affect quantifiable attributes of oyster reefs and how these quantifiable attributes produce ecosystem attributes people care about (e.g., diversity of organisms, critical habitat, filtration benefits, habitat and food for various organisms) that directly produce ecosystem services. Given the importance of oyster reefs to the ecosystem, there is greater awareness and interest in creating favorable conditions

Table 1
Decision rule questions for performance measure/suitability relationships for the oyster indicator.

1. What is the current living density, in individuals per m^2, of oysters in the estuary? Use yearly average of twice a year (wet and dry season) sampling.	
(a). 0–200	Score: 0
(b) >200–800	Score: 0.5
(c) >800–4000	Score: 1.0
2. What is the current condition index of oysters in the estuary? Use yearly average of year round monthly sampling.	
(a) 0–1.5	Score: 0
(b) >1.5–3.0	Score: 0.5
(c) >3.0–6.0	Score: 1.0
3. What is the current gonadal condition of oysters in the estuary? Use yearly average of year round monthly sampling.	
(a) 0–1	Score: 0
(b) >1–2	Score: 0.5
(c) >2–4	Score: 1
4. What is the current spat recruitment of oysters (spat/shell) in the estuary? Use mean spat/shell/month for the estuary of year round monthly sampling.	
(a) 0–5	Score: 0
(b) >5–20	Score: 0.5
(c) >20–200	Score: 1.0
5. What is the current growth of juvenile oyster in mm/month? Use yearly average of year round monthly sampling.	
(a) 0–1	Score: 0
(b) >1.0–2.5	Score: 0.5
(c) >2.5–5	Score: 1.0
6. What is the prevalence of *Perkinsus marinus* (% of infected oysters) in oysters from the estuary? Use yearly average of year round monthly sampling.	
(a) 0–20	Score: 1.0
(b) >20–50	Score: 0.5
(c) >50–100	Score: 0
7. What is the intensity of *Perkinsus marinus* (scale 0–5) in oysters from the estuary? Use yearly average of year round monthly sampling.	
(a) 0–1	Score: 1
(b) >1–3	Score: 0.5
(c) >3–5	Score: 0

for the sustenance and enhancement of oyster reefs in Southwest Florida both through adaptive management and through habitat restoration.

2.3. Indicators (attributes that we can measure) methodology

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). Typically, the quantifiable attributes of oyster reefs measured by these programs include:

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

Given the paucity of concurrent data related to growth and survival of oysters along the Southwest Florida coast, results related to this measure are not presented here.

2.3.1. Spatial extent

Along the southwest Florida estuaries and coasts, the distribution and coverage of oyster reefs is influenced by salinity, substrate and food availability, larval recruitment, and the timing and duration of freshwater inflows into the estuaries (Volety, 2008; Volety et al., 2009a). 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% their prior abundance and that ~85% of oyster reefs have been lost globally. Such decreases have coincided with decreases in water quality and clarity (Newell, 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., 2009a). It appears that spatial extent of oyster coverage in southwest Florida estuaries has been relatively stable (Volety et al., unpublished results).

2.3.2. Living density

Density of living oysters in Southwest Florida estuaries varies between estuaries (100–3000+ oysters/m^2; Volety et al., 2008). 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, Florida (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 a profound influence on spat recruitment, predation, survival, and fecundity (Volety et al., 2009a,b, 2010), differences in the living density of oysters between estuaries is not surprising. In addition to salinity, the amount of freshwater that flows into the estuaries due to regulatory freshwater releases and/or watershed runoff may result in physical flushing of larvae to downstream locations, where substrate may be limited. For this reason, in relatively un-altered 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).

2.3.3. 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 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 expressed as the number of spat settled per oyster shell per month. Oysters reproduce from late spring to early fall in SW Florida and monitoring of spat recruitment is typically conducted year round in SW Florida estuaries (Volety, 2008; Volety et al., 2009a,b, 2010). Since oyster reproduction and spat recruitment is influenced by salinity, temperature, food availability and substrate quality, any environmental perturbations will impact spat recruitment and survival and hence the next year's class of oysters, thus influencing living density of oysters during subsequent years.

2.3.4. Survival and growth of juvenile oysters

Juvenile oysters, as measured by shell height, grow at a faster rate than adult oysters and thus make better indicators to measure the role of water quality on the survival and growth of oysters (Volety et al., 2010). In addition, juvenile and younger stages of oysters are more susceptible to stressors such as salinity, temperature, food quality and quantity, predators, and dissolved oxygen (Shumway, 1996; Volety et al., 2010). Higher salinities typically attract more predators and disease; thus, oysters at high salinities 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 plastic-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. (2010) in the Caloosahatchee River.

Adult oysters normally occur at salinities between 10 and 30, but they tolerate salinities of ~2–40 (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 and Tolley, 2005; Bergquist et al., 2006). Therefore, controlled freshwater releases could be used in adaptive management to mitigate disease and predation pressure on oysters.

2.3.5. Intensity and prevalence of *P. marinus*

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 *P. marinus* (a.k.a. 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, 2009a). Presence and intensity of the disease organism is typically assayed using Ray's fluid thioglycollate medium technique (Ray, 1954; Volety et al., 2003, 2009a,b, 2010). Samples of gill and digestive diverticulum are incubated in the medium for 5–7 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 % 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, 5 = heavy.

Temperature and salinity profoundly influence the disease susceptibility of oysters, with higher temperatures and salinities resulting in higher prevalence and intensity of *P. marinus* infections (Chu and Volety, 1997; Soniat, 1996; La Peyre et al., 2003; Volety, 2008; Volety et al., 2009a,b). 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% 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 late fall through early spring months (∼November–March), 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 prevalence and intensity 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 wk), 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.

2.3.6. *Reproductive condition*

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 (see below). This method has previously been successfully used 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 through 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 SW 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 are more favorable to predators and diseases (Shumway, 1996, White and Wilson, 1996; Volety, 2007; Volety et al., 2009a,b) 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.

Table 2
Parameter value and score for oysters in Pumpkin Bay (2009–2012).

Parameter	Mean	Parameter score
Living density (per m^2)	1014 ± 6	1.0
Condition index	2.6 ± 0.1	0.5
Gonadal condition	1.9 ± 0.6	0.5
Spat recruitment (spat/shell)	5.4 ± 10	0.5
P. marinus prevalence (%infected)	72.9 ± 5.7	0
P. marinus intensity (scale 0–5)	1.3 ± 0.1	0.5
Grand mean		0.5

Values are mean ± standard deviation.

Table 3
Parameter value and score for oysters in Faka Union Bay (2009–2012).

Parameter	Mean	Parameter score
Living density (per m^2)	1839 ± 6	1.0
Condition index	2.5 ± 0.2	0.5
Gonadal condition	2.5 ± 0.4	1.0
Spat recruitment (spat/shell)	3.8 ± 6.8	0
P. marinus prevalence (% infected)	67.6 ± 6.7	0
P. marinus intensity (scale 0–5)	1.1 ± 0.1	0.5
Grand Mean		0.5

Values are mean ± standard deviation.

Table 4
Parameter value and score for oysters in Fakahatchee Bay (2012).

Parameter	Mean	Parameter score
Living density (per m^2)	1791 ± 4	1.0
Condition index	2.4 ± 0.7	0.5
Gonadal condition	N/A	Incomplete
Spat recruitment (spat/shell)	16 ± 3.4	0.5
P. marinus prevalence (%infected)	81.8 ± 6.1	0
P. marinus intensity (scale 0–5)	1.5 ± 1.3	0.5
Grand mean		0.5

Values are mean ± standard deviation.

Development of the oyster index (state of oysters) is based on the methodology developed by Volety et al. (2008) for communicating the status of oysters as an indicator, with minor modifications. This index uses the range of oyster metrics to come up with three thresholds (Success, Caution, Failure) corresponding to 1, 0.5 and 0, respectively, for each of the metrics based on what is typical for each metric in local estuaries. While oyster data for the Caloosahatchee Estuary was available for a longer period, data for other estuaries was not available for more than 1–4 years. Therefore, data from the last four years were used for Caloosahatchee Estuary, Pumpkin Bay and Faka Union (2009–2012) while only one year (2012) of data was available for Fakahatchee Estuary. Therefore, available data are used to illustrate this example.

3. Results

3.1. *Living density*

Density of living oysters in Southwest Florida estuaries was high and mean density for years under consideration were between 1014 and 1839 per m^2 oysters (Tables 2–5). As spat recruitment, predation, survival, and fecundity of oysters are profoundly influenced by salinity (Volety et al., 2009a,b, 2010), differences in the living density of oysters between and within estuaries is not

Table 5
Parameter value and score for oysters in the Caloosahatchee Estuary (2009–2012).

Parameter	Mean	Parameter Score
Living density (per m^2)	1227 ± 3	1.0
Condition index	2.9 ± 0.1	0.5
Gonadal condition	2.3 ± 0.2	1.0
Spat recruitment (spat/shell)	7.9 ± 2.8	0.5
P. marinus prevalence (%infected)	73.2 ± 19.0	0
P. marinus intensity (scale 0–5)	1.3 ± 0.5	0.5
Grand mean		0.58

Values are mean ± standard deviation.

surprising. Wet season densities are in general higher downstream due to the amount of freshwater flowing into the estuary as regulatory freshwater releases and/or watershed runoff. For relatively un-altered estuaries, such as the Fakahatchee, 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).

As indicated in Tables 2 and 5, and referencing the performance measure/suitability relationships provided in Table 1, live densities in the southwest coast estuaries merit a parameter score of 1. Over the period of 2009 through 2011, the mean live densities along the southwest coast of Florida ranged from 565.3 ± 111.0 to 1892.7 ± 146.11 per m^2. In 2012, the living densities significantly increased in all 4 estuaries and ranged from 1529.8 ± to 2613.3 ± 443.7. These are significantly higher densities than observed in populations on the east coast of Florida in the St. Lucie Estuary, Lake Worth Lagoon and Loxahatchee River Estuary.

3.2. Recruitment

Larval recruitment in the estuaries ranged between 3.8 and 12 spat/shell/month between estuaries. While there were differences between estuaries and sampling years, spat recruitment occurred between March and November at all estuaries (Tables 2–5). As recruitment in Southwest Florida estuaries ranged from 5.4 ± 10 to 7.9 ± 2.8, the parameter score, as referenced in Table 1, is 0.5.

3.3. *P. marinus*

P. marinus (a major oyster disease) is prevalent in oysters on the Southwest coast of Florida with infection rates for 2009–2012 ranging from 54.0 ± 11.4 to elevated levels of 92.0 ± 22.9. Mean infection prevalence ranged between 67% and 82% in oysters for all the estuaries (Tables 2–5) and according to indicator parameters provided in Table 1, are scored as 0. The highest rates of infection occurred in 2012, with the Caloosahatchee experiencing the most significant increase (results not shown). All three estuaries in the Ten Thousand Islands met or exceeded previous levels of infection in 2012. Discharges from the canal system which still exists upstream of the Faka Union estuary result of freshwater inputs, which may explain why this estuary experienced the lowest mean rate of infections.

The intensity of the *P. marinus* infection was at a moderate to low level, as previously mentioned, unlikely to result in the mortalities experienced in Chesapeake Bay. Across the southwest coast of Florida intensity ranged from 0.79 ± 1.0 to 1.76 ± 1.4, with 2012 again being a significant year with respect to elevated levels of intensity. Across the period of study, the mean of all years in each of the estuaries never exceeded 1.5 ± 1.3, resulting in a parameter score of 0.5. The level of variability in each of the means does indicate that there are some oysters that do have elevated levels of infection, but the number of individuals experiencing this condition is not significant enough to influence the overall mean intensity for the populations.

3.4. Reproductive condition

As previously mentioned, oysters in Southwest Florida continuously spawn from April through October and the mean reproductive condition is an excellent indication of this as the annual mean reproductive condition ranges from 1.2 ± 0.3 to 2.8 ± 1.4, indicating that oysters are often in a “partially spent” condition, and a period of storing reserves in preparation of spawning. All four of the estuaries experienced a significant drop in gonadal condition in 2011. The parameter scores for the estuaries vary from 0.5 to 1, which may indirectly indicate the extended spawning season that has been documented in the estuaries of Southwest Florida.

4. Discussion

The choice of oysters as an indicator for coastal ecosystems is relevant for several reasons: (1) the indicator is relevant to the coastal ecosystems, including those in the Everglades, and responds to variability at a scale that makes it applicable to the entire estuarine portions of the ecosystem; (2) the indicator is feasible to implement and responses to natural and anthropogenic stressors are well established; (3) the indicator is sensitive to system drivers; (4) the indicator is integrative over time; and (5) the metrics of the indicator are already being measured through various monitoring programs such as the Comprehensive Everglades Restoration Program RECOVER – Monitoring and Assessment Plan (RECOVER, 2007, 2009; Volety et al., 2008). The RECOVER conceptual ecological models and ongoing monitoring programs in the Caloosahatchee Estuary and Ten Thousand Islands have identified three major stressors that affect the success of eastern oysters and associated invertebrate and vertebrate species: altered hydrology, altered habitat and sedimentation (Volety et al., 2009a,b, 2010). Water management practices in the watersheds in Southwest Florida have resulted in significant alterations of the timing, distribution, volume and quality of waters delivered to the estuaries (Volety et al., 2009a). These disruptions facilitated through water control structures such as weirs and dredged channels have reduced the watersheds ability to absorb nutrients, have contributed to poor water quality and increased sedimentation on substrate suitable for oyster larval settlement and growth of oyster reefs. Three main factors support oyster population growth in estuaries worldwide: brood or seed stock, appropriate substrate and favorable salinity regime. A number of the oyster responses monitored in the estuaries of Southwest Florida reflect these and simultaneously beg the question of how should these be weighed and are some more crucial or influential in impacting the survival of oysters? In a laboratory study, salinity was determined to be the most important factor in disease progression and infection intensity compared to temperature and dose of infective cells of *P. marinus* in oysters (Chu and Volety, 1997). However, this study did not examine the role of substrate or the size of broodstock. Given the abundance of larvae or recruitment of spat in southwest Florida estuaries and paucity of substrate, it is speculated that input of freshwater into the estuaries due to watershed alteration and regulatory releases as well as limited substrate availability limit the development and growth of oyster reefs in Southwest Florida estuaries (Volety et al., 2010).

As previously mentioned, spatial extent serves as an indicator of oyster response to environmental conditions within an estuary. The overall extent of oyster reefs on the southwest coast of Florida would seem to indicate that the estuaries while not in the more dire condition of some estuaries along the east coast of the United States, are not as healthy as one would expect with populations present over the last 3500 years (Volety et al., 2009b). While debate exists about the extent of aerial coverage of oyster reefs in the estuaries due to differences in the methodologies associated with measurement of oyster reefs, it is generally accepted that the aerial coverage of oyster reefs in the estuaries is far less than 1% of the accommodation space, defined as area with salinities suitable for oyster reef development. This would indicate that there are significant stresses on oyster populations in southwest Florida as is occurring to oyster populations around the world.

High living density of adult oysters and spat recruitment of oysters in Southwest Florida estuaries under favorable conditions suggests that significant breeding populations exist. However, these adult densities are depressed and spat recruitment poor, owing to unfavorable low or high salinities that occur during periods of high levels of freshwater input into the estuaries during wet years or during dry years when little or no freshwater input occurs. This repeated cycle cannot bode well for oyster populations or for their overall health. High salinities in a dry season followed by a wet season characterized by below average rainfall or drought can reduce brood stock populations, and expose them to conditions more favorable for increased prevalence and intensity of *P. marinus* infection. This can directly affect overall health and fecundity of the oysters, impacting recruitment. In addition, high salinities are favorable to predators resulting in increased mortality, decreased spat recruitment and low living density of oysters.

In the short term, these measurements enable a resource manager to get a quick understanding of the estuary's current condition and implement adaptive management protocols, potentially minimizing the frequency and severity of adverse conditions. This information, in the long term, allows resource managers the opportunity to determine the most beneficial timing and scale of regulatory releases. This information will also provide valuable input into the design and implementation of restoration components, including flexibility in design, and lends itself to support the design of test or pilot projects capable of answering larger design questions and potentially offer significant economic benefits.

4.1. Drivers of change in oyster reefs

Pressures are the direct cause of change in the ecosystem. The source of pressures affecting oyster reefs in the SW Florida shelf 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, which has tremendous impact on the development of oyster larvae and formation/dissolution of calcium carbonate shell under acidic conditions.

4.1.1. Coastal development

Local-scale alterations in the watershed from coastal and watershed development result in run-off of nutrient- and contaminant-laden sediment as well as anomalistic timing and severity of freshwater input into the rivers and estuaries. This contributes to the development of macroalgae and harmful algal blooms. Blooms smother 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 exacerbates the depletion of suitable substrate and negatively affects oyster reef development.

4.1.2. 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 CO_2 concentrations of 385 ppm represent a nearly 30% increase over preindustrial values, with concentrations forecast to surpass 700 ppm by the end of the century (IPCC, 2007). These increases in CO_2 concentrations are believed to cause increases in atmospheric and oceanic temperatures, changes in carbonate chemistry of seawater and widespread melting of snow and ice and rising of sea-level (IPCC, 2007). Recent studies have shown that the CO_2 trends anticipated by the IPCC (2007) study can have significant impacts on the calcification rates and physiology of planktonic and benthic organisms including shellfish (see 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 CO_3^{2-} 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 increased mortality (Talmage and Gobler, 2009) in different species and life-stages of marine bivalves.

4.2. Mechanisms of change in oyster reefs

The principal threats to oyster reefs in Southwest Florida shelf occur through three primary pathways: watershed development and input of nutrients and contaminants as well as freshwater runoff from the watershed and regulatory freshwater releases; increased sedimentation; and, dredging and removal of substrate required for larval settlement and reef growth. In Southwest Florida as well in other places, dredging was undertaken to enhance navigable waterways and dredged material was used for road construction.

5. Oyster reef status and trends

Anecdotal evidence as well as archived photographic evidence suggests that the coverage of oyster reefs in SW Florida has drastically decreased. Current coverage of oyster reefs in the Caloosahatchee Estuary – Ten Thousand Islands is about 0.1–1% 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 reefs coverage of about 1–5% 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% of their prior abundance in most bays and eco-regions. It has been estimated that there is an 85% 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 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. With increasing awareness of the ecological role of oysters, there is a renewed interest across the United States to restore and enhance oyster reefs in all the estuaries. In Florida, oysters are considered a valued ecosystem component and their responses are being used as a measure of the success of Everglades Restoration.

6. Topics of scientific debate, 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 Ragone-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 SW 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 not clear. 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 not clear. Recent studies investigating the effect of elevated CO_2 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 CO_2 levels in seawater and how it may impact growth and survival of larval oysters is unclear.

Acknowledgements

This paper is a result of research under the Marine and Estuarine Goal Setting (MARES) for South Florida Project funded by the National Oceanic and Atmospheric Administration Center for Sponsored Coastal Ocean Research (Coastal Ocean Program), under award NA08OAR4320889 to the University of Miami, NA09NOS4780224 to Nova Southeastern University, NA09NOS4780225 to the University of Massachusetts Amherst, NA09NOS4780226 to the National Audubon Society, NA09NOS4780227 to Florida Gulf Coast University, NA09NOS4780228 to Florida International University, and to the NOAA Atlantic Oceanographic and Meteorological Laboratory. We would like to acknowledge the technical help of Ms. Pamela Fletcher and Mr. Bill Nuttle during the MARES process and for graphic illustrations. Critical feedback from Drs. Chris Kelble, Peter Doering, Susan Gray and three anonymous reviewers has significantly contributed to this manuscript. Numerous undergraduate and graduate students have contributed to the lab and field work through grants from the South Florida Water Management District and Army Corps of Engineers – RECOVER program.

References

Abeels, H.A., Loh, A.N., Volety, A., 2012. Trophic transfer and habitat use of oyster *Crassostrea virginica* reefs in southwest Florida using stable isotope analysis. Marine Ecology Progress Series 462, 125–142, http://dx.doi.org/10.3354/meps09824.

Anderson, R.S., 1993. Modulation of nonspecific immunity by environmental stressors. In: Couch, J.A., Fournie, J.W. (Eds.), Pathobiology of Marine and Estuarine Organisms. CRC Press, London, pp. 482–510.

Anderson, R.S., Unger, M.A., Burreson, E.M., 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., Hewatt, W.G., 1957. Oyster mortality studies in Virginia: II. The fungus disease caused by *Dermocystidium marinum* in oysters in Chesapeake Bay. Ecological Monographs 27, 1–26.

Barnes, T.K., 2005. Caloosahatchee estuary conceptual ecological model. Wetlands 25 (4), 884–897.

Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Cien, L.D., Crawfors, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.A., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61, 107–116.

Berge, J.A., Bjerkeng, B., Petersen, O.R., Schaanning, M.T., Oxnevad, S., 2006. Effects of increased seawater concentrations of CO_2 on growth of the bivalve *Mytilus edulis* L. Chemosphere 62 (4), 681–687.

Bergquist, D.C., Hale, J.A., Baker, P., Baker, S.M., 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: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA.

Burreson, E.M., Ragone-Calvo, L.M., 1996. Epizootiology of Perkinsus marinus disease of oysters in Chesapeake Bay with emphasis on data since 1985. Journal of Shellfish Research 15, 17–34.

Capuzzo, J.M., 1996. The bioaccumulation and biological effects of lipophilic organic contaminants. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), The Eastern Oyster: *Crassostrea virginica*. Maryland Sea Grant College Publication, College Park, MD, pp. 539–557.

Chamberlain, R.H., Doering, P.H., 1998a. Freshwater inflow to the Caloosahatchee Estuary and the resource-based method for evaluation. In: Proceedings of the Charlotte Harbor Public Conference and Technical Symposium, Technical Report No. 98-02, pp. 81–90.

Chamberlain, R.H., Doering, P.H., 1998b. Preliminary estimate of optimum freshwater inflow to the Caloosahatchee Estuary: a resource-based approach. In: Proceedings of the Charlotte Harbor Public Conference and Technical Symposium, Technical Report No. 98-02, pp. 121–130.

Chu, F.L.E., Hale, R.C., 1994. Relationship between pollution and susceptibility to infectious disease in eastern oyster, *Crassostrea virginica*. Marine Environmental Research 38, 243–256.

Chu, F.L.E., Volety, A.K., 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., Luckenbach, M.W., Breitburg, D.L., 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.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers, S.E., Tolley, S.G., 2007. As we see it: Ecosystem services related to oyster restoration. Marine Ecology Progress Series 341, 303–307.

Cressman, K.A., Posey, M.H., Mallin, M.A., Leonard, L.A., Alphin, T.D., 2003. Effects of oyster reefs on water quality in a tidal creek estuary. Journal of Shellfish Research 22, 753–762.

Dame, R.F., Spurrier, J.D., Wolaver, T.G., 1989. Carbon, nitrogen and phosphorous processing by an oyster reef. Journal of Experimental Marine Biology and Ecology 83, 249–256.

Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science 65 (3), 414–432.

Fisher, W.S., Winstead, J.T., Oliver, L.M., Edminston, H.L., Bailey, G.O., 1996. Physiological variability of eastern oysters from Apalachicola Bay, Florida. Journal of Shellfish Research 15, 543–555.

Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J.P., Middelburg, J.J., Heip, C.H.R., 2007. Impact of elevated CO_2 on shellfish calcification. Geophysical Research Letters 34, L07603.

Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86 (7), 1926–1935.

Grabowski, J.H., Peterson, C.H., 2007. Restoring oyster reefs to recover ecosystem services. In: Cuddington, K., Byers, J.E., Wilson, W.G., Hastings, A. (Eds.), Ecosystem Engineers. Elsevier Inc., Burlington, MA.

Gunter, G., 1953. The relationship of the Bonnet Carre spillway to oyster beds in Mississippi sound and the Louisiana marsh, with a report on the 1950 opening. Publication of the Institute of Marine Science, University of Texas 3 (1), 17–71.

Gunter, G., Geyer, R.A., 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., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Harding, J.M., Mann, R., 2001. Oyster reefs as fish habitat: opportunistic use of restored reefs by transient fishes. Journal of Shellfish Research 20 (3), 951–959.

Henderson, J., O'Neil, L.J., 2003. Economic Values Associated with Construction of Oyster Reefs by the Corps of Engineers, EMRRP Technical Notes and Collection (ERDC TN-EMRRP-ER-01). US Army Corps of Engineer Research and Development Center, Vicksburg, MS.

Ingle, R.M., Smith, F.G.W., 1949. Oyster Culture in Florida. State of Florida Board of Conservation, Educational Series 5, 25 pp.

1980. International Mussel Watch. National Academy of Sciences, Washington, DC, 248 pp.

IPCC, 2007. Summary for policymakers. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom/New York, NY, USA.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.

Kahn, J.R., Kemp, W.M., 1985. Economic losses associated with the degradation of en ecosystem: the case of submerged aquatic vegetation in Chesapeake Bay. Journal of Environmental Economics and Management 12, 246–263.

Kelble, C.R., Loomis, D.K., Lovelace, S., Nuttle, W.K., Ortner, P.B., Fletcher, P., Cook, G.S., Lorenz, J.J., Boyer, J.N., 2013. The EBM-DPSER conceptual model: integrating ecosystem services into the DPSIR framework. PLoS ONE 8 (8), e70766, http://dx.doi.org/10.1371/journal.pone.0070766.

Kurihara, H., Asai, T., Kato, S., Ishimatsu, A., 2009. Effects of elevated CO_2 on early development in the mussel *Mytilus galloprovincialis*. Aquatic Biology 4 (3), 225–233.

La Peyre, M.K., Nickens, A.D., Volety, A.K., Tolley, S.G., La Peyre, J.F., 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., Peterson, C.H., 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecological Applications 8, 128–140.

Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecological Applications 11 (3), 764–782.

Leverone, J.R., Blake, N.J., Pierce, R.H., Shumway, S.E., 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., Blake, N.J., Shumway, S.E., 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.

Loomis, D.K., Ortner, P., Kelble, C., 2014. Developing integrated ecosystem indices. Ecological Indicators 44, 57–62.

Loosanoff, V.L., Tommers, F.D., 1947. Effect of low pH upon rate of water pumping of oysters, *Ostrea virginica*. Anatomical Record 99 (4), 668–669.

Luckenbach, M.W., Coen, L.D., Ross Jr., P.G., Stephen, J.A., 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 Jr., C.L., 1977. Development of an aquaculture program for rehabilitation of damaged oyster reefs in Mississippi. Marine Fisheries 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.

Meyer, D.L., Townsend, E.C., Thayer, G.W., 1997. Stabilization and erosion control of oyster cultch for intertidal marsh. Restoration Ecology 5, 93–99.

Michaelidis, B., Ouzounis, C., Paleras, A., Portner, H.O., 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., Reynolds, A.C., Sobrino, C., Riedel, G.F., 2009. Shellfish face uncertain future in high CO_2 world: influence of acidification on oyster larvae calcification and growth in estuaries. PLoS ONE 4 (5), e5661.

Myers, R.L., Ewel, J.J., 1990. Ecosystems of Florida. University of Central Florida Press, ISBN: 0-8130-1012-5.

National Research Council, 2004. Nonnative oysters in the Chesapeake Bay: Committee on the Nonnative Oysters in the Chesapeake Bay, Ocean Studies Board, Division on Earth and Life Studies. The National Academic Press, Washington, DC.

Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the eastern oyster (*Crassostrea virginica*). In: Lynch, M. (Ed.), Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Publication 129, pp. 536–546.

Newell, R.I.E., Cornwell, J.C., Owens, M.S., 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. Limnology and Oceanography 47, 1367–1379.

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.

Nuttle, W.K., Fletcher, P., 2013. Integrated Conceptual Ecosystem Model for the Southwest Florida Shelf Coastal Marine Ecosystem. NOAA Technical Memorandum. OAR AOML-102, 1–108 p.

O'Connor, T., Lauenstein, G.G., 2006. Trends in chemical concentrations in mussels and oysters collected along the US 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 3 (1), 34–43.

Paerl, H.W., Pinckney, J.L., Fear, J.M., Peierls, B.L., 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, 960.

Peterson, C.H., Lipcius, R.N., 2003. Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. Marine Ecology Progress Series 264, 297–307.

Piazza, B.P., Banks, P.D., La Peyre, M.K., 2005. The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. Restoration Ecology 13, 499–506, http://dx.doi.org/10.1111/j.1526-100X.2005.00062.x.

Pipe, R.K., Coles, J.A., 1995. Environmental contaminants influencing immune function in marine bivalve mollusks. Fish and Shellfish Immunology 5, 581–595.

Porter, E.T., Cornwell, J.C., Sanford, L.P., 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., Alphin, T.D., Powell, C.M., Townsend, E., 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, VIMS Press.

Quitmyer, I.R., Massaro, M.A., 1999. Seasonality and subsistence in a Southwest Florida estuary: a faunal analysis of pre-Columbian Useppa. In: Marquardt, W.H. (Ed.), The Archaeology of Useppa Island, Monograph Number 3. Institute of Archaeology and Paleoenvironmental Studies, University of Florida, Gainesville, FL, pp. 99–128.

Ray, S.M., 1954. Biological studies of *Dermocystidium marinum*. The Rice Institute Pamphlet 41 (special issue), 65–76.

RECOVER, 2007. Systems Status Report: Development and Application of Comprehensive Everglades Restoration Plan System-Wide Performance Measures. Restoration Coordination and Verification, South Florida Water Management District/US Army Corps of Engineers, Jacksonville District, West Palm Beach, FL/Jacksonville, FL.

RECOVER, 2009. Systems Status Report: Development and Application of Comprehensive Everglades Restoration Plan System-Wide Performance Measures. Restoration Coordination and Verification, South Florida Water Management District/US Army Corps of Engineers, Jacksonville District, West Palm Beach, FL/Jacksonville, FL (accessed: http://www.evergladesplan.org/pm/recover/recover.aspx).

Savarese, M., Volety, A., Tolley, S.G., 2004. Oyster Health and Habitat Quality in Fakahatchee Estuary: Establishing a Baseline Performance for Ten Thousand Island estuarine restoration. South Florida Water Management District, Technical Report, 27 pp.

Savarese, M., Volety, A.K., 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.

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: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant College, University of Maryland System, College Park, MD.

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., Harding, J.M., Mann, R., 2005. The Status of Virginia's Public Oyster Resource. Virginia Institute of Marine Science, VA 23062, 49 pp.

Talmage, S.C., Gobler, C.J., 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., Volety, A.K., 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., Volety, A.K., Savarese, M., 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., Volety, A.K., Savarese, M., Walls, L.D., Linardich, C., Everham III, E.M., 2006. Impacts of salinity and freshwater inflow on oyster-reef communities in Southwest Florida. Aquatic Living Resource 19, 371–387.

Ulanowicz, R.E., Tuttle, J.H., 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. Estuaries 15, 298–306.

USDOC (US Department of Commerce), 1997. Magnuson-Stevens Fishery Conservation and Management Act, as Amended through October 11, 1996. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-23, US Government Printing Office, Washington, DC.

Volety, A.K., Perkins, F.O., Mann, R., Hershberg, P.R., 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., Savarese, M., 2001. Oysters as indicators of ecosystem health: determining the impacts of watershed alterations and implications for restoration. In: 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., Tolley, S.G., Winstead, J., 2003. Investigations into effects of seasonal and water quality parameters on oysters (*Crassostrea virginica*) and associated fish populations in the Caloosahatchee Estuary. In: Interpretive Report (Award #C 12412-A 1) Submitted to the South Florida Water Management District.

Volety, A.K., Tolley, S.G., 2005. Analyses of the effects of freshwater inflow alteration on oysters (*Crassostrea virginica*) in Lower Alafia River. In: Final Report Submitted To Southwest Florida Water Management District 2379 Broad Street, Brooksville, FL 34604, 31 pp.

Volety, A.K., 2007. Caloosahatchee estuary oyster monitoring and research. In: Final Report, Submitted to the South Florida Water Management District. Contract # 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, http://dx.doi.org/10.1007/s10646-008-0242-9.

Volety, A.K., Wohlpart, S.L., Savarese, M., Loh, A.N., 2008. Characterization of Community Assemblages in Oyster-Reef Habitats of the Estero Estuary through the Late Holocene: Monitoring the Ecological Impact of Watershed Management and Sea-Level Rise, SW Florida Regional Planning Council, Final Technical Report, 86 pp.

Volety, A.K., Savarese, M., Hoye, B., Loh, A.N., 2009a. Landscape Pattern: Present and Past Distribution of Oysters in South Florida Coastal Complex (Whitewater Bay/Oyster Bay/Shark to Robert's Rivers), South Florida Water Management District, Final Technical Report, 195 pp.

Volety, A.K., Savarese, M., Tolley, S.G., Arnold, W., Sime, P., Goodman, P., Chamberlain, R., Doering, P.H., 2009b. Eastern oysters (*Crassostrea virginica*) as an indicator for restoration of Everglades' ecosystems. Ecological Indicators 9 (Suppl. 6), S120–S136.

Volety, A.K., Tolley, G., Loh, A.N., Abeels, A., 2010. Oyster Monitoring Network for the Caloosahatchee Estuary. Final Report, South Florida Water Management District. Award # 4600000815, 145 pp.

Wasno, R.M., Volety, A.K., Doering, P.H., Crean, D., 2009. The Importance of Oyster Reef Community in the Diet of Predatory Fish. American Society of Limnology and Oceanography, Nice, France.

White, M.E., Wilson, E.A., 1996. Predators, pests and competitors. In: Kennedy, V.S., Newell, R.I.E., Able, A.F. (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant College Publication UM-Sg-Ts-96-01, pp. 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., Beatty, H.R., Coen, L., 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. Journal of Shellfish Research 15 (3), 769–775.

Wingard, L., Lorenz, J., 2014. Integrated conceptual ecological model and habitat indices for the southwest Florida coastal wetlands. Ecological Indicators 44, 92–107.

Wohlpart, S.L., (master's thesis) 2007. The development of estuarine systems in Southwest Florida: a perspective from the Late Holocene history of oyster reef development. Florida Gulf Coast University, Fort Myers, FL, pp. 160 p.

Zimmerman, R.J., Minello, T.J., Baumer, T.J., Castiglione, M.C., 1989. Oyster Reef as Habitat for Estuarine Macrofauna. NOAA Technical Memorandum, NMFS-SEFC-249, 16 pp.