

## A HABITAT SUITABILITY INDEX MODEL FOR THE EASTERN OYSTER (*CRASSOSTREA VIRGINICA*), A TOOL FOR RESTORATION OF THE CALOOSAHATCHEE ESTUARY, FLORIDA

T. K. BARNES,<sup>1</sup> A. K. VOLETY,<sup>2\*</sup> K. CHARTIER,<sup>3</sup> F. J. MAZZOTTI<sup>3</sup> AND L. PEARLSTINE<sup>3</sup>

<sup>1</sup>PBS&J, 3501 North Causeway Blvd., Suite 725, Metairie, Louisiana 70002; <sup>2</sup>Florida Gulf Coast University, 10501 FGCU Blvd. South, Fort Myers, Florida 33965; <sup>3</sup>University of Florida, Fort Lauderdale Research and Education Center, 3205 College Ave., Davie, Florida 33314

**ABSTRACT** A tool in the form of a habitat suitability index model (HSI) for the eastern oyster, *Crassostrea virginica*, was adapted to evaluate and compare the effects of alternative restoration plans in southwest Florida. A component of a large forecasting model, this tool simulates system response by examining the impact of freshwater inputs into the system. The eastern oyster is a good indicator species for modeling because of its sedentary nature and its susceptibility to natural and artificial changes. In addition, oysters form a complex three-dimensional reef structure, which provides habitat and food for numerous species of fish and invertebrates. The model focuses on salinity, temperature, depth, substrate, and high flow frequency as the particular requirements to determine habitat suitability for the eastern oyster. A geographic information system (GIS) incorporates the oyster HSI model, which includes larval and adult components, to determine responses spatially and temporally to facilitate the decision making process. This paper evaluates four hydrologic and land use scenarios for the C-43 West Basin Reservoir Project. Model results indicate that the Preferred Flow scenario and the future conditions with the Comprehensive Everglades Restoration Plan have higher HSI values than either the existing conditions or the future without the Comprehensive Everglades Plan.

**KEY WORDS:** eastern oyster, Habitat Suitability Index, *Crassostrea virginica*, Caloosahatchee, restoration, alternative evaluation, Freshwater impacts

### INTRODUCTION

Florida's Everglades was once an expansive, ecologically productive system (Davis & Ogden 1994). Water flowed through the Kissimmee River into Lake Okeechobee, spilling over the southern rim of the lake during high precipitation events and into an extensive Everglades system flowing as a sheet of water until it reached the southern estuaries. Fragmentation and hydrologic alterations (Light & Dineen 1994, Ogden et al. 2005a, Ogden et al. 2005b) have led to the loss of this sheet-flow across the system (Science Coordination Team 2003) and into estuaries (McIvor et al. 1994).

The Caloosahatchee Estuary is located on the southwest coast of Florida between the cities of Cape Coral and Fort Myers (Fig. 1). Most of the freshwater flowing into the estuary comes from the Caloosahatchee River. Historically, the Caloosahatchee River was a meandering system with numerous oxbows, flowing from its headwaters at the marshlands of Lake Flirt, west of Lake Okeechobee, to the Gulf of Mexico. Activities that led to its degradation began in the late 1800s, with Hamilton Disston's dredging and channelization project, which included a connection to Lake Okeechobee and construction of an extensive canal network associated with agricultural development in the watershed. The channelization and canal building process (C-43) has changed the timing, quantity, quality, and direction of runoff within the watershed; and it led to abnormal salinity fluctuations. The operation of three water control structures allowing large periodic regulatory releases from Lake Okeechobee has reduced the tidally influenced portion of the estuary.

Two seasonal trends influence Southwest Florida estuaries, including the Caloosahatchee estuary: seasonal variation in air

and water temperature and seasonal variation in rainfall and water releases (Tolley & Volety 2005). During dry, cooler months (November to May) little or no rainfall is present and very little freshwater flows from Lake Okeechobee into the Caloosahatchee estuary, resulting in estuarine salinities ranging from 28–38 ppt. In warmer, wet months (June to October), the Caloosahatchee estuary experiences heavy rainfall as well as significant freshwater releases from Lake Okeechobee for flood control (~1,000–20,000 cubic feet per second), resulting in physical flushing of the estuary as well as depressed estuarine salinities (~0–10 ppt, Volety et al. 2003). Thus, the key stressor in the Caloosahatchee estuary is an altered hydrology, which includes unnatural high and low water deliveries to the estuary.

Prior to these impacts, the Caloosahatchee estuary was a highly productive system with an abundance of aquatic plants and animals. Today, abundance, health, and functionality of these species have been greatly reduced (Harris et al. 1983, Chamberlain & Doering 1998a, Doering & Chamberlain 1999).

The Comprehensive Everglades Restoration Plan (CERP), developed by the United States Army Corps of Engineers (USACE) and the South Florida Water Management District (SFWMD), provides a framework and guide to improve quality, quantity, timing, and distribution of water in the Everglades ecosystem (United States Army Corps of Engineers and South Florida Water Management District 1999). A series of eight expedited projects, together called Acceler8, implement the initial phase of Everglades restoration for the State of Florida. The C-43 West Basin Reservoir (an Acceler8 project and a component of a larger restoration effort for the Caloosahatchee River and estuary) focuses on storing regulatory releases from Lake Okeechobee and storm water runoff. Removing this surplus water will reduce excess water flow to the Caloosahatchee estuary during the wet season and provide essential flow during the dry season. The C-43 project will

\*Corresponding author. E-mail: avolety@fgcu.edu

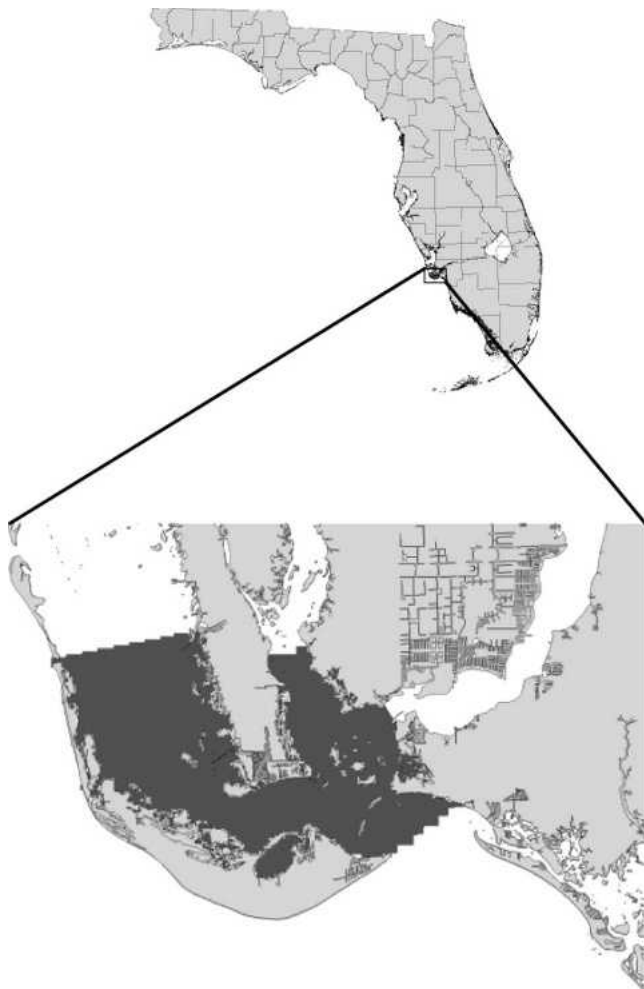


Figure 1. The Caloosahatchee estuary, Lee County Florida.

consist of an above-ground reservoir located along the Caloosahatchee River, Florida with a storage capacity of ~200 million cubic meters.

To arrive at a final plan design, a series of steps must be taken (Yoe & Orth 1996). Two critical steps of this process are the design and evaluation of alternative restoration plans and comparison of effects of each alternative. Through an evaluation process, each individual restoration alternative is assessed and its effects are quantified and evaluated. For the C-43 West Reservoir Project, the evaluation tool is a forecasting model. This forecasting model is a set of habitat suitability index (HSI) models for individual or multiple species, or both, which relate selected environmental metrics to habitat of each organism. The forecasting model applies each HSI to restoration alternatives with the assumption that as changes for each alternative occur, so will extent and quality of suitable habitat. Another assumption is that habitat suitability is related to distribution and abundance of the species (or life stage) modeled (Klopatek & Kitchens 1985).

This paper selected the species used in this evaluation process because of a combination of ecological, recreational, and economic importance. Additionally, they must have an established link to stressors of management interest (Barnes 2005). The eastern oyster, *Crassostrea virginica*, one species

chosen for this process, is important commercially and recreationally in fisheries along the Atlantic Ocean and Gulf of Mexico coasts of North America. Whereas this role of oysters as a fishery is well known, their ecological significance remains under appreciated and under studied (Coen et al. 1999a). Individual oysters filter 4–34 L of water per hour, removing phytoplankton, particulate organic carbon, sediments, pollutants, and microorganisms from the water column (Newell 1988, Newell & Langdon 1996). This filtration results in greater light penetration immediately downstream promoting growth of submerged aquatic vegetation. Although oysters assimilate most of the organic matter that they filter, they deposit the remainder on the bottom where it provides food for benthic organisms. Furthermore, the oyster's ability to form large biogenic reefs (Coen et al. 1999b) qualifies it as a keystone species.

Oysters and the complex, three-dimensional, reef structure they form attract numerous species of invertebrates and fishes (Ingle & Smith 1956, Woodburn 1965, McDonald 1982, Peters 1981, Meyer 1994). To date, over 300 species have been identified as depending, either directly or indirectly, on oyster reefs (Wells 1961, Tolley et al. 2006). Many of these organisms in turn serve as forage for important fishery species (Marshall 1958, Tabb & Manning 1961, Fore & Schmidt 1973, Gilmore et al. 1983, Peters & McMichael 1987, McMichael & Peters 1989).

Because of its sedentary nature, the eastern oyster is susceptible to natural and artificial ecosystem changes, making it a good indicator species for this restoration effort. Environmental disruptions are responsible for reducing oyster populations and their traditional habitats (Cake 1983). Although not currently harvested in the Caloosahatchee estuary, oysters have been identified in this area as a valued ecosystem component (VEC) (Chamberlain & Doering 1998a, Chamberlain & Doering 1998b). Historical records indicate that oyster reefs were once significant features of the Caloosahatchee estuary and adjacent San Carlos Bay. However, populations have declined significantly to less than 7.5 ha<sup>2</sup> (18 acres) (Volety et al. unpublished results).

Adult oysters can temporarily tolerate a wide range of salinities ranging from 0–42.5 ppt. Normal species distribution occurs between 5 and 40 ppt (Ingle & Dawson 1953, Loosanoff 1953a, Wells 1961, Galtsoff 1964, Menzel et al. 1966) with optimal salinities in Southwest Florida ranging between 14 and 28 ppt (Volety et al. 2003), but varying by latitude and geography. They can survive at salinities 4–5 ppt indefinitely (Loosanoff 1932, Volety et al. 2003) and can occur at salinities as low as 0.2–3.5 ppt for up to five consecutive months (Butler 1952), including those in the upstream Caloosahatchee estuary where they can encounter zero salinities for several months when regulatory freshwater releases are made (Volety & Savarese 2001, Savarese et al. 2003, Volety et al. 2003). Reefs located near the head of an estuary, where salinities range from 0–15 ppt, are characterized by oyster populations that are small, rounded, and sparse because of frequent flooding and high mortality rates (Butler 1954, Volety & Savarese 2001, Savarese et al. 2003). Spat recruitment and growth rates are also low in this region. Where salinities are between 15 and 20 ppt, populations are dense, reproductive activity high, predator numbers low, and spat recruitment and growth rates high. Near the mouth of a typical Gulf Coast estuary with a salinity of 25 ppt, growth and reproductive rates are typically high;

however, predation and competition are also high. Where the estuary opens into the high-salinity Gulf waters, oyster reefs are sparse, spat recruitment and growth are low, diseases and predators are high, and suitable substrate is lacking. Volety et al. (2003), Volety and Savarese (2001), and Savarese et al. (2003) observed similar conditions in Florida estuaries.

Juvenile oysters less than one year old can survive at salinities of 5 ppt (Chanley 1958, Volety et al. 2003); however, very little growth is observed below 5 ppt, slow growth observed at 12 ppt, and normal growth occurs between 12 and 27 ppt (Chanley 1958). Under laboratory conditions, Volety et al. (2003) observed high mortality (40% to 75%) of juvenile oysters exposed to <5 ppt and >35 ppt salinities for 2 wk, whereas very little mortality (5%) was seen at salinities of 15–25 ppt.

Salinity also affects gametogenesis, condition index, and spawning in oysters (Shumway 1996). Low salinities impair gametogenesis at <5 ppt, whereas normal gametogenesis occurred above 7.5 ppt (Loosanoff 1953a, Loosanoff 1953b). Oysters from Texas showed suppressed gonadal activity at salinities <6 ppt (Butler 1949). Similar trends were observed in the Caloosahatchee river oysters in 2003 when the estuary water was significantly fresh because of regulatory freshwater releases (Volety, unpublished results).

The protozoan parasite, *Perkinsus marinus*, has devastated oyster populations in the Atlantic (Burreson & Ragone-Calvo 1996), as well as in the Gulf of Mexico (Soniati 1996), where it is currently the primary pathogen of oysters. Andrews (1988) estimates that *P. marinus* can kill ~80% of the oysters on a reef. Temperature and salinity influence the distribution and prevalence of *P. marinus* with higher values favoring the parasite (Burreson & Ragone-Calvo 1996, Soniat 1996, Chu & Volety 1997, La Peyre et al. 2003). Laboratory studies by Volety (1995) and Chu and Volety (1997) suggest salinity to be the most important factor influencing the disease susceptibility and disease progression of *P. marinus* in oysters. High salinities also invite various predators such as crabs, starfish, boring sponges, oyster drills, and diseases (Butler 1954, Hopkins 1962, Galtsoff 1964, Livingston et al. 2000, Menzel et al. 1966, MacKenzie 1970, Manzi 1970, Shumway 1996). Other species that are tolerant of low salinities but pose serious threat to oysters include starfish *Asteria forbesi*, whelks *Fasciolaria hunteria* (Loosanoff 1945, Wells 1961), flatworms *Stylocos ellipticus* (Loosanoff 1956), and blue crabs *Callinectes sapidus* (Menzel et al. 1966). Field studies by Wilbur (1992) in Apalachicola Bay, Florida, and by Wilbur and Bass (1998) in Matagorda Bay, Texas showed reduced oyster landings two years after low freshwater flow periods, possibly because of higher estuarine salinities and resulting predation of oyster spat by marine predators. Similarly, higher predation rates caused by oyster drills were observed in the Apalachicola Bay by Livingston et al. (2000).

In the Caloosahatchee estuary there is a seasonal cycle of water temperature with temperatures around 24°C to 34°C during the late spring through fall (April to October) and between 14°C and 23°C from late fall through early spring (November to March). Oysters in the Caloosahatchee estuary reproduce continuously between April and October. The combination of shallow environments, warm water temperature, and food availability may account for the long spawning period, which also coincides with low salinities and high flows in the estuary. This paper presents the process that was used to adapt a

habitat suitability model for the eastern oyster and demonstrate its use for the assessment of restoration alternatives in the Caloosahatchee Estuary, Florida.

## MATERIALS AND METHODS

### *Model Development and Application*

The HSI for the eastern oyster was developed using adult and larval components to capture highest sensitivities of oysters to environmental changes resulting from restoration activities. The HSI model assesses habitat quality and suitability with a monthly or yearly numerical output ranging from 0 (least suitability) to 1 (most suitability) (Cake 1983, Soniat & Brody 1988). The models calculate habitat suitability, where component indices are the weighted geometric mean of the metrics. The geometric mean is derived from the product of the metrics rather than the sum (as in the arithmetic mean) and has the appropriate property that, if any of the individual metrics are unsuitable for species success (i.e., the value of the metric is zero), then the entire index goes to zero. The final HSI is the minimum score of the larval and adult component indices. Each metric can be weighted (w) with regard to importance; however, the sum of the weights is constrained to be one.

Livingston et al. (2000) previously modeled the relationship between freshwater inputs using a hydrodynamic model and various life history stages in the Apalachicola Bay, Florida. Their model used salinities and flows from the hydrodynamic model to predict oyster mortality in the bay. Percent of bottom covered with suitable cultch, mean summer water salinity, abundance of living oysters, historic mean water salinity, frequency of killing floods, and substrate firmness were chosen as variables in the previous models (Coke 1983, Soniat & Brody 1988). As previously mentioned, water flows within the Caloosahatchee estuary are managed for flood control. High temperatures and low salinities in the summer time alternate with high salinities and low temperatures in the winter time and contrast with other natural systems in the Gulf of Mexico, as well as in the Chesapeake Bay, where higher temperatures and salinities coincide within a given season. Because salinity, temperature, flow, and distribution of oysters serve as proxies for most of the variables in previous models (suitable cultch, mean water salinity, historic mean salinity, frequency of killing flood, and substrate availability), salinity, temperature, substrate, and high flow frequency have been chosen as the particular requirements for determining habitat suitability for the eastern oyster in the Caloosahatchee estuary. Table 1 lists scientific literature indicating specific requirements and data from local monitoring programs, along with their source, for both adults and larval oysters. For the purpose of alternative selection for the C43 West Basin Reservoir Project, substrate has been turned off, or removed from the model. This is because depth within model boundaries does not exceed 3 m, except for within navigation channels, which are not available areas for oyster settlement or growth and because including substrate in the model application limits restoration benefits to areas where oysters are already present, as that is the only hard substrate data available to the model. The addition of hard substrate to areas with high habitat suitability will be included as part of the restoration plan. Specific temperature, salinity, and flow values used for generating HSI results are presented in Figure 2.

**HSI Formula**

Below is the formula used to calculate the HSI for the eastern oyster in the Caloosahatchee estuary:

$$\text{Eastern Oyster LarvalComponentIndex} = (\text{Salinity}^{w1} * \text{Temperature}^{w2} * \text{Flow}^{w3})$$

$$\text{Eastern Oyster AdultComponentIndex} = (\text{Salinity}^{w4} * \text{Temperature}^{w5} * \text{Substrate}^{w6})$$

$$\text{HSI}_{\text{May–November}} = \text{MIN} (\text{LarvaeComponentIndex}, \text{AdultComponentIndex})$$

$$\text{HSI}_{\text{December–April}} = (\text{AdultComponentIndex})$$

where *w* is a weight between 0 and 1 assigned to each variable and the substrate component can be turned on or off in the model depending on the users need.

The oyster model was programmed in Microsoft Visual Basic using ESRI ArcObjects geographic information system (GIS) libraries to model habitat response spatially within a grid system that encompasses the spatial extent of the estuary. Each modeled grid cell is ~45 m<sup>2</sup>. As a result, the model describes a response surface of habitat suitability values that vary spatially

according to environmental conditions at specific locations (grid cells) in the estuary, and temporally according to patterns in environmental variables. Additionally, the GIS provides the ability to create visual aids to facilitate the decision making process.

Input data for the model came from multiple sources. The South Florida Water Management Model (SFWMM) coupled with an estuary-salinity regression model provided salinity data. The SFWMM simulates major components of the hydrologic cycle and estimates regional scale hydrologic responses (MacVicar et al. 1984, Hydrologic Realities, Inc. 2005), supplying flow from the S-79 water control structure. The regression model uses this flow data to produce grids of salinity values for different flow alternatives. Previous projects (Avineon 2003, Hansen & Perry 2003, Tetra Tech Inc. 2004) provided substrate, bathymetry, and temperature data.

**Modeling Scenarios**

Four hydrologic scenarios have been evaluated for the C-43 West Reservoir Project: (1) a preferred flow frequency for the

**TABLE 1.**  
**Habitat requirements for the eastern oyster.**

Variable	Value	Source
Oyster Larvae: Salinity	Limits: 5‰ and 35‰ Optimal: 10‰ to 30‰ Peak: 20‰ to 22‰ Settlement peak: 25‰ to 29‰ In Caloosahatchee most favorable: 15‰ to 25‰	Calabrese and Davis (1970). Carriker (1951). Castagna and Chanley (1973). Chatry et al. (1983). Davis (1958). Hopkins (1931). Menzel et al. (1966). Savarese et al. (2004). Savarese et al. (2003). Volety et al. (2003).
Oyster Larvae: Temperature	Optimal: 20°C to 30°C With peaks at the higher end	Loosanoff and Davis (1963). Stanley and Sellers (1986).
Oyster Adult: Temperature	Optimal: 20°C to 30°C Can tolerate: 1°C to 49°C Stop feeding: 6°C to 7°C Physiological functions cease: 42°C	Cake (1983). Copeland and Hoese (1966). Galtsoff (1964). Stanley and Sellers (1986). Stenzel (1971).
Oyster Adult: Salinity	Optimal: 10‰ to 20‰ Normal range: 10‰ to 30‰  Can tolerate: 5‰ to 40‰	Butler (1954). Eleuterius (1977). Galtsoff (1964). Gunter and Geyer (1955). Stenzel (1971).
Oyster Larvae and Adult: Depth	Optimal: 0.5–3 m	Volety et al. (2003).
Oyster Larvae and Adult: Substrate	Oyster shells, calcareous remains of other molluscs, wooden material, rocks, gravel, and solid refuse	Butler (1954). Galtsoff (1964). Hedgepeth (1953). Lunz (1958). MacKenzie (1977). MacKenzie (1981). MacKenzie (1983).
Oyster Larvae: Flow	Optimal: 500–2500 cfs (14.15–70.79 cm) in the Caloosahatchee River resulting in salinities above 5–10 ppt. Flows >4,000 cfs (113.26 cm) will restrict larval settlement	Shumway (1996). Wilson et al. (2005)  Volety et al. (2003).
		Volety (2003 et al.).Wilson et al. (2005)

Caloosahatchee estuary based on a hydrologic target set to provide an optimum inflow range that includes natural variation in salinity to insure a diverse composition of estuarine biota (Table 2) (Chamberlain & Doering 1998a, Chamberlain & Doering 1998b, Doering & Chamberlain 1999, Doering & Chamberlain 2000, Doering et al. 1999, Doering et al. 2001, Doering et al. 2002, Chamberlain et al. 2003); (2) an existing conditions scenario based on hydrology, water demands and land use in the year 2000; (3) a future conditions without the implementation of any Comprehensive Everglades Restoration Plan projects, using predicted 2050 hydrology, water demands, and land use; and (4) a future conditions (year 2050) with the Comprehensive Everglades Restoration fully implemented

(United States Army Corps of Engineers and South Florida Water Management District 1999).

In addition, running simulations for a normal rainfall year (1996) illustrates the role of substrate limitation for oysters in the Caloosahatchee estuary. Runs were made with and without the substrate component of the model turned on. Under the with-substrate scenario, the model utilizes the existing substrate, where the removal of substrate as a metric in the model assumes no substrate limitation.

**RESULTS**

Figures 3, 4, 5, and 6 show the HSI results for various scenarios described earlier. Models display results as an average

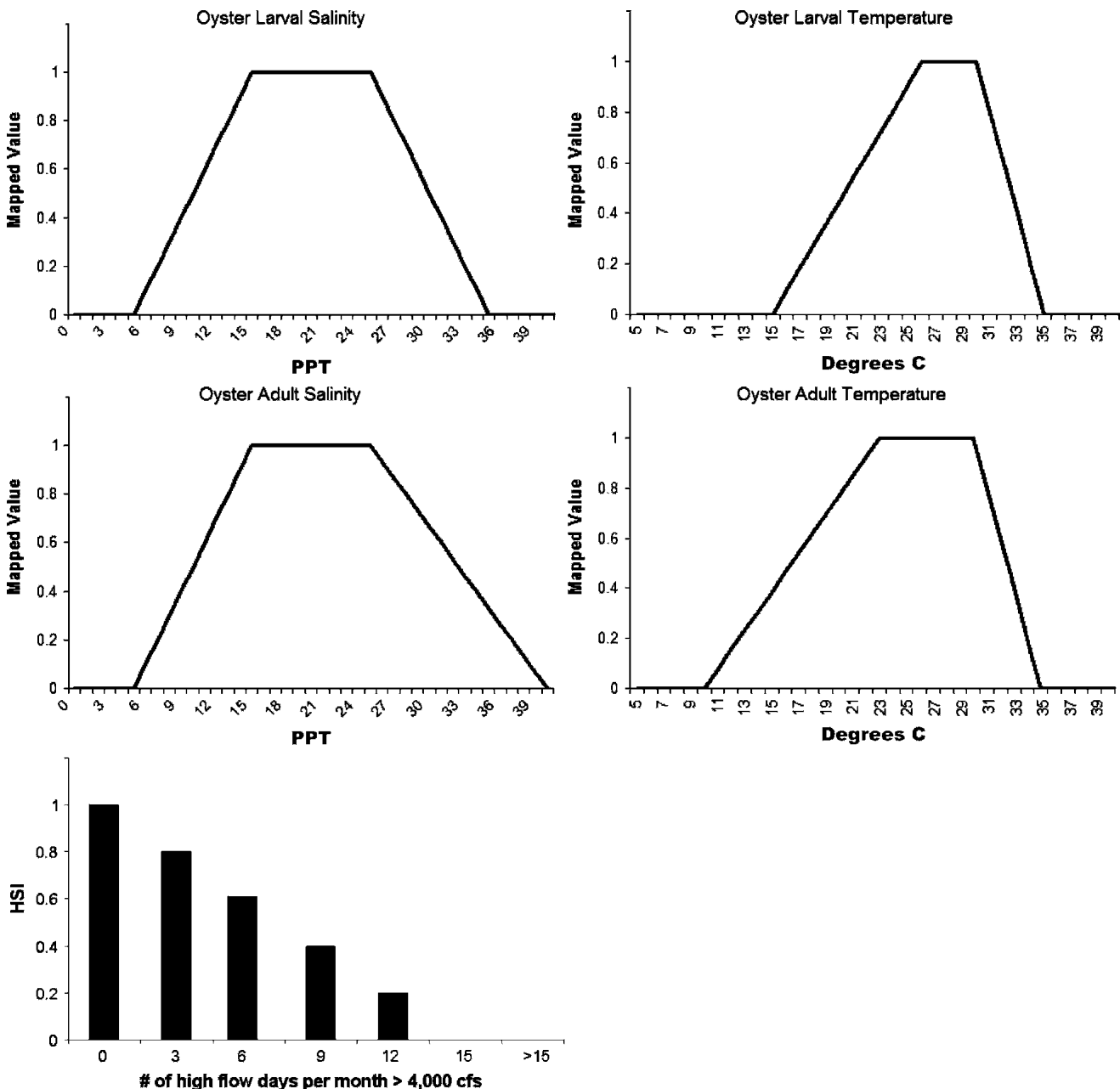


Figure 2. Suitability index diagrams created for the eastern oyster using data from Table 1 (adjusted for local conditions by expert opinion and recent research).

TABLE 2.

**Preferred flow regimen for the Caloosahatchee estuary based on a hydrologic target based on an optimum inflow range that includes natural variation in salinity to insure a diverse composition of estuarine biota (Chamberlain & Doering 1998a, 1998b, Doering & Chamberlain 1999, 2000, Doering et al. 1999, 2001, 2002, Chamberlain et al. 2003). The frequency distribution of flows from Lake Okeechobee (S-79 lock and dam) is without tidal basin contribution.**

Discharge Range in cubic meters per second (cms) from S-79	Percent Distribution of Flows from S-79
0–12.75	0.0%
12.75–14.16	42.8%
14.16–22.65	31.7%
22.65–42.48	19.2%
42.48–79.29	5.6%
79.29–127.43	0.7%
>127.43	0.0%

yearly HSI computed from monthly HSI values. Models also have capability of displaying results as average yearly habitat units (results not shown). For the purpose of this paper, we used average HSI values for the year.

**Preferred Flow**

The model predicts that establishment of preferred flows (Table 2) will result in HSI values of 0.5–1 in the majority of the study area (Fig. 3). This is especially favorable during wet years when high regulatory releases as well as watershed runoff is likely to occur, resulting in favorable salinities in the estuary.

**Current Conditions**

The model predicts that, in wet years, HSI values are between 0–0.5 in most of the study area (Fig. 3). Under current conditions, high regulatory discharges occur during May to

October in the Caloosahatchee River, reducing the salinities as well as flushing the larvae downstream. However, in normal to dry years, conditions are favorable with HSI values between 0.5–1 in the study area.

**2050 without CERP**

The model predicts that HSI values and habitat suitability in the Caloosahatchee estuary without implementation of CERP (and resulting water management practices) are similar to those of current conditions (see earlier) with poor HSI values during the wet years and relatively favorable HSI values during dry and normal years (Fig. 4).

**2050 with CERP**

The model predicts that HSI values in the Caloosahatchee estuary with CERP implementation (and resulting flow patterns) mimic those of preferred flow regimen during normal and dry years (HSI values between 0.5–1), but with lower values (0.25–0.75) during a wet year compared with those of preferred flow regimen under similar conditions (Fig.3). Figure 6 compares the HSI values for year 2050 with and without the CERP for a six-year period of rainfall (1995–2000).

**Role of Substrate**

When simulations were run to examine the yearly HSI values for oysters in the Caloosahatchee Estuary under normal rain conditions, with existing substrate as a parameter, HSI values were extremely low (0–0.25) in most areas, with limited areas showing HSI values between 0.5–0.75. When substrate was removed as a factor (implying that substrate was not a limiting factor), most of the HSI values in the estuarine portion of the Caloosahatchee River ranged between 0.5–1 (Fig. 5).

Results from the HSI model indicate that preferred flow frequency distribution and future conditions with implementation of the Comprehensive Everglades Restoration Plan have higher HSI values than existing conditions or the future without the Comprehensive Everglades Restoration Plan.

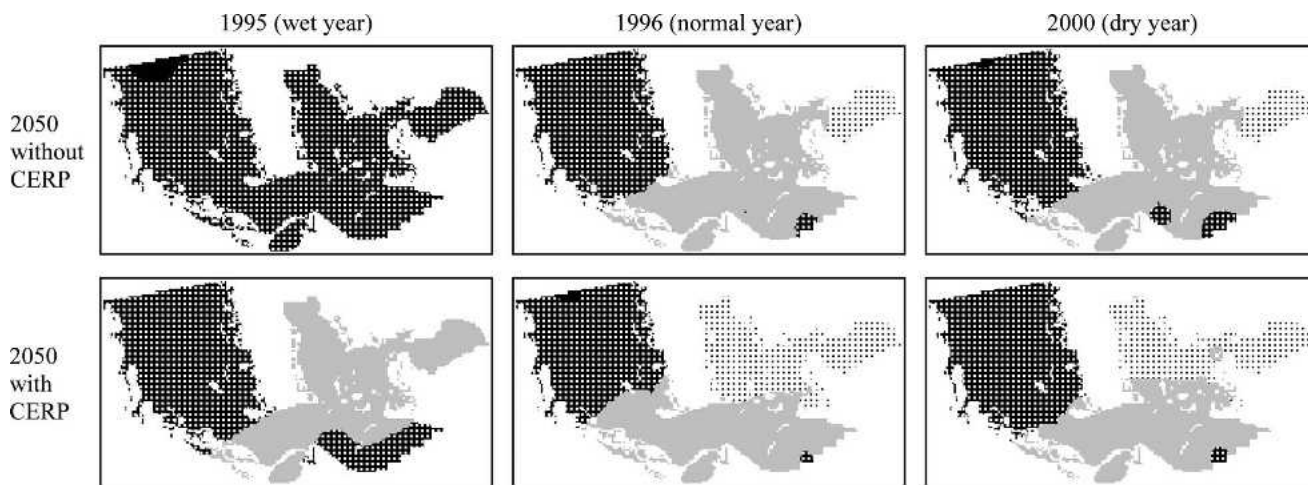


Figure 3. HSI values for the eastern oyster in the Caloosahatchee estuary under current conditions of flow (based on 2000 hydrology and land use) compared with preferred flow frequency (Table 2) for wet (1995), dry (2000), and normal (1996) rain fall years.

■ 0.00–0.25, ▨ 0.25–0.50, □ 0.50–0.75, ▤ 0.75–1.00.

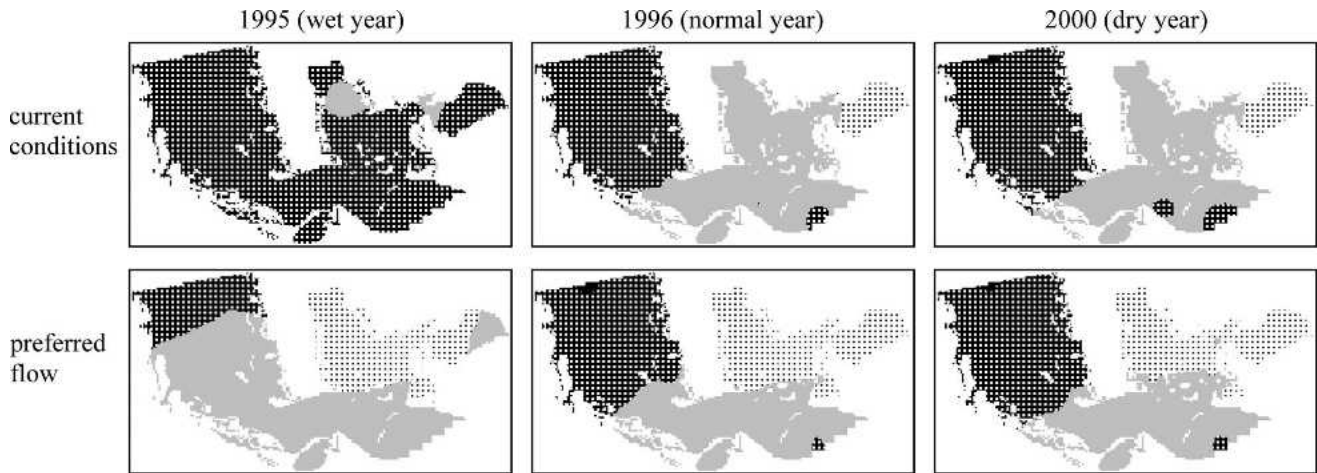


Figure 4. HSI values for the eastern oyster in the Caloosahatchee Estuary using 2050 without the Comprehensive Everglades Restoration hydrology and land use conditions compared with 2050 with complete implementation of the Comprehensive Everglades Restoration hydrology and land use conditions. ■ 0.00–0.25, ▨ 0.25–0.50, ◻ 0.50–0.75, ▩ 0.75–1.00.

DISCUSSION

The United States Fish and Wildlife Service (USFWS) originally developed species-specific HSI models to evaluate environmental impact and project planning studies (Schamberger & Farmer 1978, United States Fish & Wildlife Service 1981), including one for the eastern oyster (Cake 1983). This HSI was later modified and adapted for use in the Galveston Bay by simplifying the model structure and better accounting for local stressors of importance (high salinity, disease, and parasitism on oysters) (Soniati & Brody 1988).

HSIs and other habitat assessment models have become common tools to examine effects of habitat changes on specific species resulting from land use changes, watershed alteration, mitigation, and restoration (USFWS 1981, Soniat & Brody 1988, Turner et al. 1995, Mladenoff et al. 1997, Elliott et al. 1999, Curnutt et al. 2000, Livingston et al. 2000, Larson et al. 2003, Tarboton et al. 2004). As a component of a larger forecasting model, the current study developed a HSI for the eastern oyster to examine the ecological effects of a series of restoration alternatives proposed for the C43 West Basin Reservoir project. The model takes into account primary environmental conditions (salinity, flow, and substrate) in the Caloosahatchee estuary and simulates effects of these on oysters. Because oysters are physiologically adapted to local conditions and their responses vary geographically with variations in seasonal temperature, food availability, seasonal salin-

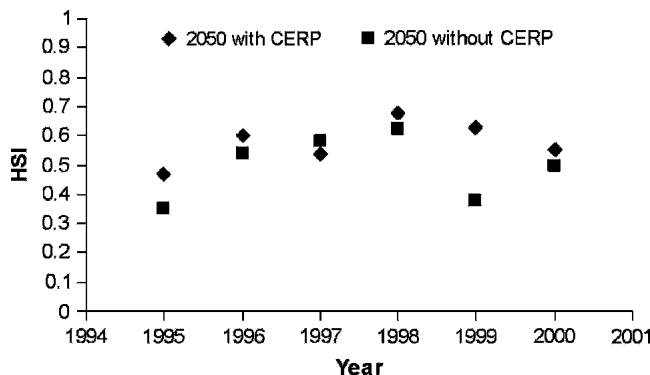
ity patterns, disease, and predation; it is not easy to adapt existing HSI models to estuaries in Southwest Florida. For example, high salinity conditions prevail in the estuary during summer and early fall in the western Gulf of Mexico estuaries, whereas low salinity conditions are experienced by oysters inhabiting estuaries along the eastern Gulf of Mexico (Volety et al. 2003). In addition, temperature for spawning and duration of spawning varies geographically in oysters. Therefore, suitable ranges for environmental metrics should be specific to the study area to optimize model sensitivity and accuracy (e.g., Layher & Maughan 1985).

Because of the nature of the Caloosahatchee estuary, flow is an essential criterion for identifying and delineating habitat suitability. During the wet season, high flow events resulting from excess rainfall and regulatory releases from Lake Okeechobee can flush larvae from the estuary to the high salinity downstream locations (Volety et al. 2003) and/or into the Gulf of Mexico where substrate is limited, preventing larval settlement. This flushing can be more detrimental to oyster population than lower salinities resulting from excess freshwater entering the estuary. Whereas the previous models considered frequency of killing floods (salinity), flow is not considered in other existing HSI models for the eastern oyster (Cake 1983, Soniat & Brody 1988).

Model results show that under the four different hydrology and land use scenarios examined, the preferred flow frequency



Figure 5. HSI values for the Caloosahatchee Estuary under the preferred flow regimen for model runs with and without substrate. ■ 0.00–0.25, ▨ 0.25–0.50, ◻ 0.50–0.75, ▩ 0.75–1.00.



**Figure 6.** Average yearly HSI scores for year 2050 with and without the implementation of the Comprehensive Everglades Restoration Plan. For this model run, substrate is not limiting.

and the 2050 with restoration (CERP) conditions produce higher HSI values than existing conditions (2000) and 2050 without restoration. The preferred flow frequency and the 2050 with restoration (CERP) conditions produce similar results during a normal and dry year and the existing conditions (2000) and 2050 without restoration produce similar results in all three rainfall years (wet, dry, and normal). The C43 West Basin Reservoir project, the most substantial project currently scheduled to occur in the study area, will capture high flows in the wet season and store water to provide a minimum flow to the estuary during the dry season. By capturing flow, number and magnitude of detrimental high flow events to the estuary will be greatly reduced. This is especially important during spawning season. By holding the water and making it available for a minimum flow in the dry season, the extent of high salinity areas in the estuary will also be reduced, reducing oyster predation and disease. In addition, results show that during a wet year, even with the proposed restoration (CERP) fully implemented, habitat suitability is suboptimal when compared with the preferred flow conditions (Figs. 3 and 5). This suggests that the current restoration plan (CERP) is not enough to achieve wet season flows into the estuary that will result in optimal habitat quality for oysters. The Southwest Florida Feasibility Study (SWFFS), initiated by CERP, will address additional water resource needs in Southwest Florida, including additional water storage in the Caloosahatchee Basin. It should be strongly noted that the preferred flow regimen (Table 2) into the estuary cannot be accomplished without full implementation of CERP, including the SWFFS.

Modeling results also indicate that under the current flow regimen and existing conditions in the Caloosahatchee estuary, the estuary is severely substrate-limited in areas otherwise optimal for oysters, resulting in poor HSI values (0–0.25) in those areas (Fig. 6). An additional value of the model is that it can be used to identify areas where substrate should be restored to achieve maximum colonization by oyster larvae, thus reducing uncertainty associated with restoration of oyster reefs.

The forecasting model for the C43 West Basin Reservoir Project incorporates the oyster HSI model with habitat suitability models for other species. There are several advantages of this type of forecasting tool. The HSI models are easily developed using scientific literature, local knowledge, and field data. This tailors the models to local conditions allowing them to depict results that are more accurate by accounting for

physiological adaptations to local environments. Incorporation of the HSIs into a GIS interface makes overall interpretation of results easier for managers by providing visual aids and allowing them to display details for any specific location within the estuary. Additionally, HSI results easily feed into a multi-criteria decision analysis model, the final step in the forecasting process.

When using forecasting models, it is important to remember that output provided by HSIs depends on the quality of data put into the HSI model. In the current HSI model, geographic range specific, peer-reviewed scientific data, in concert with data from local monitoring programs that use published procedures and have QA/QC procedures, minimized uncertainty (Volety et al. 2003). Whereas the current simplified HSI model has several advantages stated earlier, the model is not comprehensive and has certain limitations. For example, whereas temperature, salinity, flow, and substrate are included in the model, and serve to estimate indirectly, effects of disease, predation, and reproduction, their specific role and contribution to habitat suitability are not examined. However, when such information becomes available, it can be incorporated into the model provided their input is deemed critical to decision making. Substrate availability was examined by using existing oyster reefs and mangrove roots that support visible growth of oyster clusters and that provide hard substrate for spat settlement. Because other hard substrate such as boat docks and rip-rap are not examined, the substrate availability may be slightly underestimated in this model. However, given the size of the estuarine portion of the Caloosahatchee River, contribution of these structures towards suitable substrate is negligible. In addition, HSIs only provide information about quality of their habitat at a fixed time point and not take into account population dynamics of organisms modeled, nor do they take into account the spatial and temporal changes of species-habitat relations (Turner et al. 1995). For example, in the case of the oyster HSI model, the model does not predict if oyster larval settlement is actually occurring; it only examines suitability of the habitat for settlement and at any given point in time. Whether settlement is actually occurring is beyond the scope of this model. Additionally, actual oyster population densities are dependent on what has happened in the estuary in previous years, if settlement conditions are poor one year, the following year there may be a decrease in the population of spawning females and in turn a decrease in larvae for settlement. This may not be apparent in the model results, which strictly looks at average monthly and yearly habitat conditions and is where scientific opinion becomes necessary in model interpretation (Barnes et al. 2006).

Also, it should be cautioned that resource managers should not depend on HSI models alone for selection of restoration or management alternatives, but should also incorporate HSIs with monitoring and research plans. This should be accompanied by efforts to verify the model and calibrate it as new data become available (Barnes & Mazzotti 2005).

In summary, previously developed oyster HSI models (Cake 1983, Soniat & Brody 1988) were optimized for use in the Caloosahatchee estuary and augmented by incorporating GIS for visual display. Modeling efforts by Livingston et al. (2000) plotted the results of freshwater input on the mortality of oysters using GIS. In the current study, whereas the model is optimized for use in the Caloosahatchee estuary, it can be applied to other



estuaries by adjusting variable values to mimic local conditions. This model will enhance decision making by resource managers by providing a tool that is based on real scientific data rather than using informal judgments or professional opinion and is easily exportable for use in other estuaries in Florida and other Gulf States with minor modifications.

#### ACKNOWLEDGMENTS

The authors thank Janet Starnes for her support, along with the anonymous reviewers for their helpful suggestions. The project was supported by the South Florida Water Management District, United States Geological Survey, and the United States Army Corps of Engineers.

#### LITERATURE CITED

- Andrews, J. D. 1988. Epizootiology of the disease caused by oyster pathogen, *Perkinsus marinus*, and its effects on the oyster industry. *Am. Fish. Soc. Special Publication* 18:47–63.
- Avineon. 2003. Seagrass mapping project final report contract PC P2201325 submitted to the South Florida Water Management District, West Palm Beach, Florida.
- Barnes, T. K. 2005. Caloosahatchee Estuary conceptual ecological model. *Wetlands* 25:884–897.
- Barnes, T. K. & F. J. Mazzotti. 2005. Using conceptual models to select ecological indicators for monitoring restoration and management of estuarine ecosystems. In: S. A. Bortone, editor. *Estuarine indicators*. Boca Raton, Florida: CRC Press. pp. 493–502.
- Barnes, T. K., F. J. Mazzotti, L. Pearlstine & A. Volety. 2006. Ecological evaluation in coastal southwestern Florida: a policy decision model for the blue crab (*Callinectes sapidus*). *Florida Scientist* 69:140–151.
- Burreson, E. M. & L. M. Ragone-Calvo. 1996. Epizootiology of *Perkinsus marinus* disease of oysters in Chesapeake Bay with emphasis on data since 1985. *J. Shellfish Res.* 15:17–34.
- Butler, P. A. 1949. Gametogenesis in the oyster under depressed salinity. *Biol. Bull.* 96:263–269.
- Butler, P. A. 1952. Growth and mortality rates in sibling and unrelated oyster populations. *Proc. Annu. Gulf Caribb. Fish. Inst.* 4:71.
- Butler, P. A. 1954. Summary of our knowledge of the oyster in the Gulf of Mexico. *U.S. Fish Wildl. Serv. Bull.* 89:479–489.
- Cake, E. W., Jr. 1983. Habitat suitability index models: Gulf of Mexico Eastern oyster. U.S. Fish Wildl. Ser.FWS/OBS-82/10.57. 37 pp.
- Calabrese, A. & H. S. Davis. 1970. Tolerances and requirements of bivalve molluscs. *Helgol. Wiss. Meeresunters.* 20:553–564.
- Chamberlain, R. H. & P. H. Doering. 1998a. Freshwater inflow to the Caloosahatchee Estuary and the resource-based method for evaluation. In: S. F. Treat, editor. *Proceedings of the Charlotte Harbor public conference and technical symposium*. Charlotte Harbor Estuary Program, North Fort Myers, Florida. Technical Report No. 98-02. pp. 88–91.
- Chamberlain, R. H. & P. H. Doering. 1998b. Preliminary estimate of optimum freshwater inflow to the Caloosahatchee Estuary: a resource based approach. In: S. F. Treat, editor. *Proceedings of the Charlotte Harbor public conference and technical symposium*. Charlotte Harbor Estuary Program. North Fort Myers, FL, USA. Technical Report No. 98-02. pp. 111–120.
- Chamberlain, R. H., P. H. Doering, K. M. Haunert & D. Crean. 2003. Impacts of freshwater inflows on the distribution of zooplankton and ichthyoplankton in the Caloosahatchee Estuary, Florida. In: *Technical Documentation to support development of minimum flows and levels for the Caloosahatchee River and Estuary*. Draft January 2003 status update report Appendices. South Florida Water Management District. West Palm Beach, Florida. Appendix pages C1–C20.
- Chanley, P. E. 1958. Survival of some juvenile bivalves in water of low salinity. *Proc. Natl. Shellfish Assoc.* 48:52–65.
- Chu, F. L. E. & 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. *Dis. Aquat. Organ.* 28:61–68.
- Copeland, B. J. & H. D. Hoese. 1966. Growth and mortality of the Eastern oyster, *Crassostrea virginica*, in high salinity shallow bay in central Texas. *Publ. Inst. Mar. Sci. Univ. Tex.* 11:149–158.
- Carriker, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monogr.* 21:19–38.
- Castagna, M. & P. Chanley. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. *Malacologia* 12:47–96.
- Chatry, M., R. J. Dugas & K. A. Easley. 1983. Optimum salinity regime for oyster production on Louisiana's state seed grounds. *Contrib. Mar. Sci.* 26:81–94.
- Coen, L. D., M. W. Luckenbach & D. L. Breitberg. 1999a. 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., D. M. Knott, E. L. Wenner, N. H. Hadley, A. H. Ringwood & M. Y. Bobo. 1999b. Intertidal oyster reef studies in South Carolina: design, sampling and experimental focus for evaluating habitat value and function. In: M. W. Luckenbach, R. Mann & J. A. Wesson, editors. *Oyster Reef habitat restoration: a synopsis and synthesis of approaches*. pp. 133–158.
- Curnuett, J. L., J. Comiskey, M. P. Nott & L. J. Gross. 2000. Landscape-based spatially explicit species index models for Everglades restoration. *Ecol. Appl.* 10:1849–1860.
- Davis, H. C. 1958. Survival and growth of clam and oyster larvae at different salinities. *Biol. Bull.* 114:296–307.
- Davis, S. M. & J. C. Ogden. 1994. *Toward ecosystem restoration*. In: S. M. Davis & J. C. Ogden, editors. *Everglades, the ecosystem and its restoration*. Boca Raton, Florida: St. Lucie Press. pp. 769–796.
- Doering, P. H. & R. H. Chamberlain. 1999. The Caloosahatchee Estuary: what freshwater flow regime will protect and enhance submerged grass beds, and other biotic resources? Poster presented at the South Florida Restoration Forum, Boca Raton, Florida.
- Doering, P. H. & R. H. Chamberlain. 2000. Experimental studies on the salinity tolerance of Turtle Grass, *Thalassia testudinum*. In: S. A. Bortone, editor. *Seagrasses: monitoring, ecology, physiology, and management*. Boca Raton, Florida: CRC Press LLC. pp. 81–98.
- Doering, P. H., R. H. Chamberlain, K. M. Donohue & A. D. Steinman. 1999. Effect of salinity on the growth of *Vallisneria americana* Michx. from the Caloosahatchee Estuary, Florida. *Florida Scientist* 62:89–105.
- Doering, P. H., R. H. Chamberlain & J. M. McMunigal. 2001. Effects of simulated saltwater intrusion on the growth and survival of Wild Celery, *Vallisneria americana*, from the Caloosahatchee Estuary (South Florida). *Estuaries* 24:894–903.
- Doering, P. H., R. H. Chamberlain & D. E. Haunert. 2002. Using submerged aquatic vegetation to establish minimum and maximum freshwater inflows to the Caloosahatchee Estuary, Florida. *Estuaries* 25:1343–1354.
- Eleuterius, C. K. 1977. Location of the Mississippi Sound oyster reefs as related to salinity of bottom waters during 1973–1975. *Gulf Res. Rep.* 6:17–23.

- Elliott, C. R. N., M. J. Dunbar, I. Gowing & M. C. Acreman. 1999. A habitat assessment approach to the management of groundwater dominated rivers. *Hydrol. Process.* 13:459–475.
- Fore, P. L. & T. W. Schmidt. 1973. Biology of juvenile and adult snook, *Centropomus undecimalis*, in the Ten Thousand Islands, Florida. In: M. R. Carter, L. A. Burns, T. R. Cavinder, K. R. Dugger, P. L. Fore, D. B. Hicks, H. L. Revells & T. W. Schmidt, editors. Ecosystems analysis of the Big Cypress swamp and estuaries. U.S. Environmental Protection Agency, Surveillance and Analysis Division, Athens, Georgia. pp. XVI 1–18.
- Galtsoff, P. S. 1964. The eastern oyster: *Crassostrea virginica* Gmelin. Fishery Bulletin. U.S. Fish and Wildlife. Service Publication 64:480.
- Gilmore, R. G., C. J. Donohoe & D. W. Cooke. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook, *Centropomus undecimalis* (Bloch). *Florida Scientist* 46:306–313.
- Gunter, G. & R. A. Geyer. 1955. Studies of fouling organisms in the northwestern Gulf of Mexico. *Publ. Inst. Mar. Sci. Univ. Tex.* 4:114–116.
- Hansen, M. and G. Perry. 2003. Estero Bay to Charlotte Harbor bathymetric survey USGS final report contract C-13105-WO01 submitted to the South Florida Water Management District, West Palm Beach, Florida.
- Harris, B. A., K. D. Haddad, K. A. Steidinger & J. A. Huff. 1983. Assessment of fisheries habitat: Charlotte Harbor and Lake Worth, Florida. Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida.
- Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwest Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Mar. Sci. Univ. Tex.* 3:107–224.
- Hopkins, A. E. 1931. Factors influencing the spawning and settling of oysters in Galveston Bay, Texas. *Bull. U.S. Bur. Fish.* 47: 57–83.
- Hopkins, S. H. 1962. Distribution of species of *Cliona* (boring sponge) on the eastern shore of Virginia in relation to salinity. *Chesapeake Science.* 3:121–124.
- Hydrologic Realities, Inc. 2005. Documentation of the South Florida water management model, Report to the South Florida water management district and the Interagency Modeling Center. November 2005. <http://www.sfwmd.gov>.
- Ingle, R. M. & C. E. Dawson, Jr. 1953. A survey of the Cedar Key area. State of Florida Board of Conservation. *Technical Series* 9:1–27.
- Ingle, R. M. & F. G. W. Smith. 1956. Oyster culture in Florida. Florida Board of Conservation, Educational Series 5. 25 pp.
- Klopatek, J. M. & J. M. Kitchings. 1985. A regional technique to address land use changes and animal habitats. *Environ. Conserv.* 12:343–354.
- La Peyre, M. K., A. D. Nickens, A. K. Volety, S. G. Tolley & J. F. La Peyre. 2003. Environmental significance of freshets in reducing *Perkinsus marinus* infections in eastern oysters (*Crassostrea virginica*): potential management implications. *Mar. Ecol. Prog. Ser.* 248:165–176.
- Larson, M. A., W. D. Dijk, F. R. Thompson, III & J. J. Millsbaugh. 2003. Landscape-level habitat suitability models for twelve wildlife species in Southern Missouri. General Technical Report NC\_233. St. Paul, MN: U.S. Dept of Agriculture, Forest Service, North Central Research Station. 51 pp.
- Layher, W. G. & O. E. Maughan. 1985. Spotted bass habitat evaluation using an unweighted geometric mean to determine HSI values. *Proc. Okla. Acad. Sci.* 65:11–17.
- Light, S. S. & J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. In: S. M. Davis & J. C. Ogden, editors. Everglades, the ecosystem and its restoration. Boca Raton, Florida: St. Lucie Press. pp. 47–84.
- Livingston, R. J., F. G. Lewis, G. C. Woodsum, X.-F. Niu, B. Galperin, W. Huang, J. D. Christensen, M. E. Monacao, T. A. Battista, C. J. Klein & R. L. Howell, IV & G. L. Ray. 2000. Modelling oyster population response to variation in freshwater input. *Estuar. Coas. Shelf Sci.* 50:655–672.
- Loosanoff, V. L. 1932. Observations on propagation of oysters in James and Corrotoman Rivers and the seaside of Virginia. Virginia Commission on Fisheries, Newport News, Virginia. pp. 1–45.
- Loosanoff, V. L. 1945. Effects of sea water of reduced salinities upon starfish, *A. forbesi*, of Long Island Sound. *Trans. Conn. Acad. Arts and Sciences* 36:813–835.
- Loosanoff, V. L. 1953a. Behavior of oysters in waters of low salinity. Proceedings of the National Shellfisheries Association. (1952). pp. 135–151.
- Loosanoff, V. L. 1953b. Lack of relation between age of oysters or clams and quality of their spawn. *Serv. Fish. Bull.* 4:1–2.
- Loosanoff, V. L. 1956. Two obscure oyster enemies in New England waters. *Science* 123:1119–1120.
- Loosanoff, V. L. & H. C. Davis. 1963. Rearing of bivalve mollusks. *Adv. Mar. Biol.* 1:1–136.
- Lunz, G. R. 1958. Unused oyster shell in South Carolina suitable for seed oyster production. *Proc. Nat. Shellfish. Assoc.* 48:44–51.
- MacKenzie, C. L., Jr. 1970. Causes of oyster spat mortality, conditions of oyster setting beds, and recommendations for oyster bed management. *Proc. Nat. Shellfish. Assoc.* 60:59–67.
- MacKenzie, C. L., Jr. 1977. Development of an aquaculture program for rehabilitation of damaged oyster reefs in Mississippi. *Mar. Fish. Rev.* 39:1–13.
- MacKenzie, C. L., Jr. 1981. Biotic potential and environmental resistance in the Eastern oyster (*Crassostrea virginica*) in Long Island Sound. *Aquaculture* 22:229–268.
- MacKenzie, C. L., Jr. 1983. To increase oyster production in the Northeast United States. *Mar. Fish. Rev.* 45:1–22.
- MacVicar, T., T. Van Lent & A. Castro. 1984. South Florida water management model documentation report, Technical Publication 84-3, South Florida Water Management District, West Palm Beach, Florida.
- Manzi, J. J. 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinera* (Say) (Prosobranchia: Muricidae). *Biol. Bull.* 138:35–46.
- Marshall, A. R. 1958. A survey of the snook fishery of Florida, with studies of the biology of the principal species, *Centropomus undecimalis* (Bloch). Florida State Board of Conservation, Technical Series No. 22. 39 pp.
- McDonald, J. 1982. Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Brachyura: Xanthidae). *Mar. Ecol. Prog. Ser.* 8:173–180.
- McIvor, C. C., J. A. Ley & R. D. Bjork. 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: a review. Pages 117–146. In: S. M. Davis & J. C. Ogden, Everglades, The ecosystem and its restoration. Boca Raton, Florida: St. Lucie Press.
- McMichael, R. H., Jr. & K. M. Peters. 1989. Early life history of spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Estuaries* 12:98–110.
- Meyer, D. L. 1994. Habitat partitioning between the xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus* on intertidal oyster reefs (*Crassostrea virginica*) in southeastern North Carolina. *Estuaries* 17:674–679.
- Mladenoff, D. J., R. C. Haight, T. A. Sickley & A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems. A spatial landscape projection of wolf population recovery. *Bio-science* 47:21–31.
- Newell, R. I. E. 1988. Ecological changes in Chesapeake bay: are they the result of overharvesting the eastern oyster (*Crassostrea virginica*)? In: M. Lynch, editor. Understanding the estuary: advances in Chesapeake Bay research. Gloucester Point,

- VA: Chesapeake Research Consortium Publication 129. pp. 536–546.
- Newell, R. I. E. & C. J. Langdon. 1996. Mechanisms and physiology of larval and adult feeding. In: V. S. Kennedy, R. I. E. Newell & A. F. Eble, editors. The Eastern Oyster, *Crassostrea virginica*. College Park, Maryland: Maryland Sea Grant College Publication. pp. 185–229.
- Ogden, J. C., S. M. Davis, T. K. Barnes, K. J. Jacobs & J. H. Gentile. 2005a. Total System conceptual ecological model. *Wetlands* 25:955–979.
- Ogden, J. C., S. M. Davis, K. J. Jacobs, T. K. Barnes & H. E. Fling. 2005b. The use of conceptual ecological models to guide ecosystem restoration in South Florida. *Wetlands* 25:795–809.
- Peters, K. M. 1981. Reproductive biology and developmental osteology of the Florida blenny, *Chasmodes saburrae* (Perciformes: Blenniidae). *Northeast Gulf Science* 4:79–98.
- Peters, K. M. & R. H. McMichael, Jr. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Estuaries* 10:92–107.
- Savarese, M., A. K. Volety & S. G. Tolley. 2004. Oyster health and habitat quality in Fakahatchee estuary: establishing a baseline performance for ten thousand island estuarine restoration. Final Report Submitted to the South Florida Water Management District, Big Cypress Basin. 42 pp.
- Savarese, M., A. K. Volety & S. G. Tolley. 2003. Influence of watershed alteration on oyster health and oyster-reef habitat: management implications for the Faka-Union and Estero Bays. Final Report (Award # C-13252) submitted to the South Florida Water Management District. 86 pp.
- Schamberger, M. & A. Farmer. 1978. The habitat evaluation procedures: their application in project planning and impact evaluation. Transactions of North American Wildlife Natural Resources Conference 43. pp. 274–283.
- Science Coordination Team. 2003. The role of flow in the Everglades ridge and slough landscape. South Florida Ecosystem Restoration Task Force, Miami, Florida. <http://www.sfrestore.org>.
- Shumway, S. E. 1996. Natural environmental factors. pp. 467–513. In: V. S. Kennedy, R. I. E. Newell & A. F. Eble, editors. The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant College Publication, College Park, Maryland.
- Soniat, T. M. 1996. Epizootiology of *Perkinsus marinus* disease of eastern oysters in the Gulf of Mexico. *J. Shellfish Res.* 15:35–43.
- Soniat, T. M. & M. S. Brody. 1988. Field validation of a habitat suitability index model for the American oyster. *Estuaries* 11:87–95.
- Stanley, J. G. and M. A. Sellers 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)—Eastern oyster. Report No. Biological-82 (11.64). National Wetlands Research Center, Slidell, LA, Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.
- Stenzel, H. B. 1971. Oysters. Treatise on invertebrate paleontology. Part N. *Bivalvia* 3:953–1224.
- Tabb, D. C. & R. B. Manning. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. *Bull. Mar. Sci. Gulf Caribb* 11:552–649.
- Tarboton, K. C., M. M. Irizarry-Ortiz, D. P. Loucks, S. M. Davis & J. T. Obeysekera. 2004. Habitat suitability indices for evaluation water management alternatives. South Florida Water Management District Office of Modeling Technical Report, West Palm Beach, Florida.
- Tetra Tech, Inc and Janicki Environmental, Inc. 2004. Compilation, evaluation, and archiving of existing water quality data for Southwest Florida. Final Report May 5, 2004 submitted to and US Army Corp of Engineers Jacksonville District, Jacksonville, Florida. Contact No. DACW 17-02-D-0009.
- Tolley, S. G. & A. K. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *J. Shellfish Res.* 24:1007–1012.
- Tolley, S. G., A. K. Volety, M. Savarese, L. D. Walls, C. Linardich & E. M. Everham. 2006. Impacts of salinity and freshwater inflow on oyster-reef communities in Southwest Florida. *Aquat. Living Resour.* 19:371–387.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loed & K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecol. Appl.* 5:12–16.
- United States Army, Corps of Engineers and South Florida Water Management District. 1999. Central and Southern Florida Project Comprehensive Review Study Final Integrated Feasibility Report and Programmatic Environmental Impact Statement April 1999. U.S. Army Corp of Engineers, Jacksonville District, Jacksonville, Florida.
- United States Fish & Wildlife Service. 1981. Standards for the development of habitat suitability index models. 103 ESM, U.S. Fish and Wildlife Service, Division of Ecological Services. Washington, DC.
- Volety, A. K. 1995. A study of the histozoic oyster parasite, *Perkinsus marinus*: I. Disease processes in American Oysters; II. Biochemistry of *P. marinus*. Ph.D. Dissertation, College of William and Mary, Williamsburg. 208 pp.
- Volety, A. K. & M. Savarese. 2001. Oysters as indicators of ecosystem health: determining the impacts of watershed alterations and implications for restoration. Final Report submitted to National Life Foundation, South Florida Water Management District (Big Cypress Basin), and Florida Gulf Coast University Foundation. 104 pp.
- Volety, A. K., S. G. Tolley & J. T. 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 #C12412-A1) submitted to the South Florida Water management District, West Palm Beach, Florida. 111 pp.
- Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monogr.* 31:239–266.
- Wilber, D. H. 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, FL. *Estuar. Coast. Shelf Sci.* 35:179–190.
- Wilber, D. H. & R. Bass. 1998. Effect of Colorado River diversion on Matagorda Bay epifauna. *Estuar. Coast. Shelf Sci.* 47:309–318.
- Wilson, C., L. Scotto, J. Scarpa, A. Volety, S. Laramore & D. Haurert. 2005. Survey of water quality, oyster reproduction and oyster health status in the St. Lucie Estuary. *J. Shellfish Res.* 24:157–165.
- Woodburn, K. D. 1965. Clams and oysters in Charlotte County and vicinity. Florida Board of Conservation, no. 62-12. 29 pp.
- Yoe, C. E. & K. D. Orth. 1996. Planning Manual, IWR Report 96-R-21. U.S. Army Corp of Engineers, Water Resources Support Center, Alexandria, Virginia.