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Patterns of Distribution Along a Salinity Gradient in the Flatback Mud Crab *Eurypanopeus depressus*

JULIE VAN HORN AND S. GREGORY TOLLEY

To measure the effect of salinity on estuarine communities, spatial and temporal variations in population distribution were investigated in the flatback mud crab *Eurypanopeus depressus* (Smith, 1869), a dominant species on oyster reefs in southwest Florida. *Eurypanopeus depressus* were collected using lift nets (1 m²) deployed at three morphologically homologous stations along a salinity gradient in each of three estuaries. They were sampled monthly during three seasonally wet and three seasonally dry months. An analysis of abundance showed that although this species can survive extreme salinities, it is most common in moderate environments. Biomass is also highest at moderate salinities, though mean size is larger at low salinities. Few significant differences in these metrics between seasons were observed. These results suggest that although *E. depressus* is little affected by normal seasonal changes in salinity, salinity does play a role in its distribution. In light of these findings, changes in the freshwater flow regime of Southwest Florida estuaries as a result of land use changes resulting from human development have the potential to alter oyster-reef community structure.

In Southwest Florida, oysters are not harvested for direct human consumption, but they do provide vital ecosystem services. Among these is the provision of habitat for commensal organisms, many of which serve as prey for commercially and recreationally important species (Tolley et al., 2006a). Unfortunately, many reefs have been impacted by changes associated with human population growth and development: dredging, increased pollutant runoff, overfishing, and altered flow regimes (McPherson and Miller, 1987; Estevez, 2000). Altered freshwater inflow can affect the distribution and density of oysters and the commensal organisms that inhabit oyster reefs.

One way to assess the effectiveness of management decisions in the restoration process is to identify indicator species that are likely to respond quickly and obviously to ecosystem changes. Changes in their abundance or distribution may be related to changes in salinity or flow (Estevez, 2000). Kimmerer (2002) studied the northern San Francisco estuary and found that increased freshwater flow stimulated primary production, but effects did not continue further up trophic levels. Variation at higher trophic levels may be more closely tied to how particular physical perturbations in flow affect a species. Unfortunately, this cannot be generalized.

The flatback mud crab *Eurypanopeus depressus* is a dominant component of oyster-reef communities in southwest Florida (Tolley et al., 2005). Freshwater inflow has the ability to impact the

distribution of this species directly by restructuring the salinity regime and indirectly by impacting the oysters themselves, thus affecting habitat availability and quality. The spatial and temporal variation of *E. depressus* with reference to abiotic influences, particularly salinity, gives important insight into this species' environmental preferences. This study examined seasonal abiotic influences on the distribution, abundance, biomass, and size of *E. depressus* to assess the possible effects of altered freshwater inflow regimes on Southwest Florida oyster-reef communities.

MATERIALS AND METHODS

Study areas.—Data describing *Eurypanopeus depressus* distribution and abundance in relation to environmental conditions in the Caloosahatchee, Estero, and Faka Union estuaries in Southwest Florida were collected as a part of a study on the overall effect of salinity on oyster-reef habitat use (see Tolley et al., 2005, 2006a). The Caloosahatchee estuary has been converted from a meandering river to a straight channel in the upper portion by a man-made connection to Lake Okeechobee and receives periodic freshwater releases from the lake. It is altered by several water-control structures and its watershed has been highly augmented. To the south is Estero Bay, an aquatic preserve that nonetheless receives runoff from an increasingly developed watershed. The Faka Union estuary lies 90 km southeast of Estero Bay. It is not well developed but bears relics of an extensive canal system

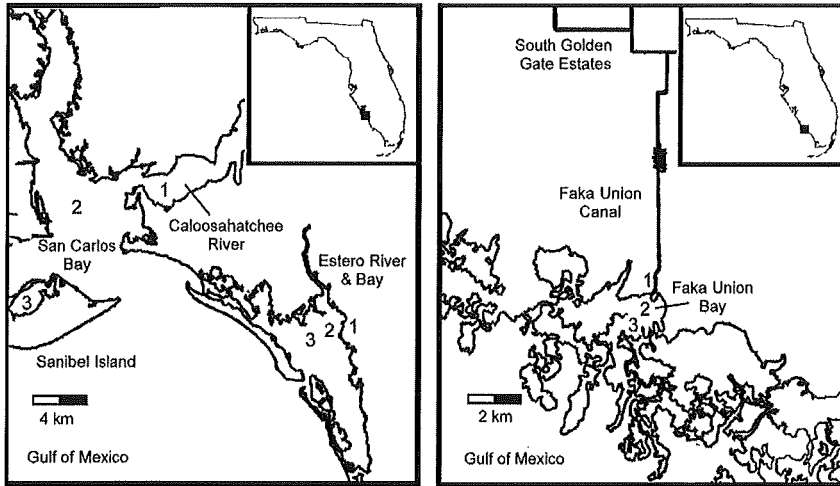


Fig. 1. Study area locations: Caloosahatchee and Estero estuaries on the left and Faka Union estuary on the right. Sampling stations are numbered from 1 (upper) to 3 (lower) (Tolley et al., 2005).

constructed in the 1960s to drain freshwater wetlands. These three estuaries are typical of many coastal areas in that they have all been altered by human development such as channelization, pollutant runoff, and/or the placement of dam and lock structures (McPherson and Miller, 1987). Such characteristics and the proximity of these estuaries to one another make them good candidates for a comparative study of their oyster-reef communities, particularly the distribution and abundance of *E. depressus*.

Sampling and statistical analysis.—*Eurypanopeus depressus* were collected using lift nets deployed in triplicate at three morphologically homologous stations along the salinity gradient of each estuary (Fig. 1). The upper station of each estuary was located within the tidal river, the middle station was located at the river mouth, and the lower station outside of the river mouth. Individuals were collected monthly during three seasonally wet (mid-July through mid-Oct.) and three seasonally dry months (mid-March through mid-June). Net retrieval was conducted during an ebb or low tide to minimize sampling bias due to tidal cycle. The 1-m² lift nets were placed intertidally, slightly above mean low water, and filled with a 5-liter volume displacement of live oyster clusters obtained from the nearby reef. Replicates were placed a minimum of 5 m apart. At the end of each 30-d sampling period, all organisms were removed from the oyster clusters and identified, enumerated, and measured to the nearest 0.1 mm carapace width. The first 10 crabs randomly encountered in each sample were also weighed to the nearest 0.01 g wet mass. Data from crabs that were both measured and weighed were

used to construct a length–weight regression for *E. depressus*. This length–weight regression was subsequently used to estimate biomass based upon the mean size of individuals collected in each sample (replicate). Salinity and water temperature were recorded at each site for each sampling effort (Tolley et al., 2005).

Abundance, biomass, and size response variables were investigated using analysis of variance (ANOVA) with estuary, season, and station as factors. One-way ANOVA was used to test for differences within estuaries for temperature, salinity, and weighted-mean salinity of capture. Where significant differences were detected, differences within factors were identified using multiple-comparisons procedures. After homogeneity of variance was tested using the Levine statistic, the appropriate procedure was performed: in the case of equal sample size and variance, Fisher's least significant difference was used; Hochberg's GT2 multiple comparison method was used where variances were equal but sample sizes were not; and the Games–Howell post hoc test was used in cases where variances were not equal regardless of sample size (Day and Quinn, 1989). Weighted-mean salinity of capture was calculated as the sum of the products of the number of crabs collected per sample and the salinity at the sampling site for each replicate divided by the total number of crabs in the sample for that station. Data are presented as mean \pm SD unless otherwise stated.

RESULTS

Environmental factors.—Significant differences were detected for salinity and temperature.

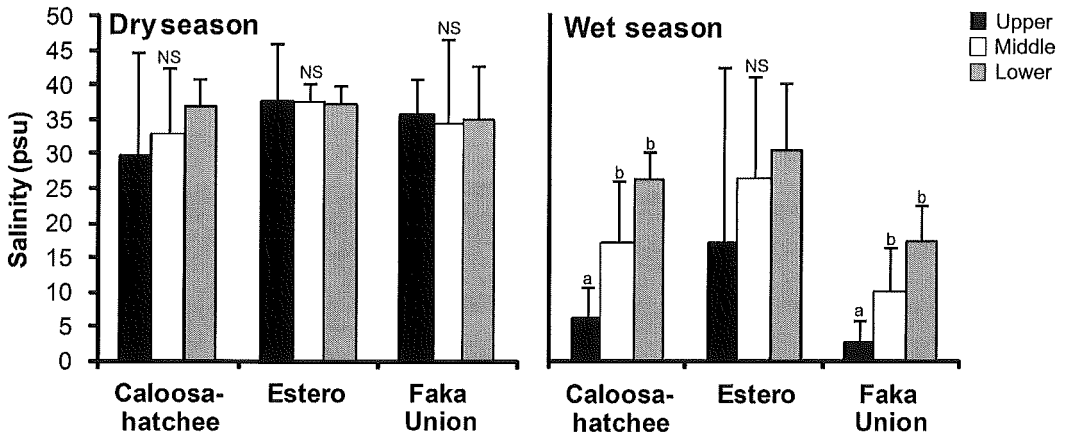


Fig. 2. Spatial and seasonal differences in salinity on oyster reefs. Bars are means with 95% confidence intervals. Differences in salinity among stations within estuaries are indicated by different letters.

Salinity was always greater in the dry season and at the lower station during wet months, with the difference in salinity between stations being greatest during the wet season (Fig. 2). Wet-season salinity was lowest in the Faka Union estuary and highest in Estero. Salinity increased downstream for all estuaries, but the differences between stations were only significant during the wet season in the Caloosahatchee and Faka Union estuaries (Fig. 2). Salinity was significantly greater in the dry season for all estuaries [$F(1,54) = 294.3, P < 0.001$]. In the Caloosahatchee, mean dry season salinity was 33.1 ± 5.0 practical salinity units (psu) vs 16.0 ± 8.9 psu in the wet season. Similarly, for the Estero, mean dry season salinity was 37.0 ± 2.1 psu whereas mean salinity in the wet season was 24.1 ± 8.4 psu. The Faka Union demonstrated the greatest differences in salinity with a mean dry-season salinity of 35.0 ± 3.2 psu and a mean wet-season salinity of 9.5 ± 6.6 psu.

Although mean temperature was higher during the wet season for all three estuaries, this difference was only significant for the Caloosahatchee ($F_{13} = 5.477, P = 0.037$). No other seasonal differences in temperature among stations or estuaries were detected.

Abundance, biomass and size.—Significant spatial differences in *E. depressus* abundance were detected. Although multifactor ANOVA identified a significant effect of estuary on abundance, post hoc testing (Games-Howell) failed to identify any differences. Abundance also varied significantly among stations [$F(2,160) = 41.784, P < 0.001$] with higher abundance typical at the middle stations (Fig. 3). No differences in the abundance of individuals ≤ 5 mm carapace width, representing new recruits to the reef, were detected. Although the Faka Union and Estero estuaries had lowest abundances at the

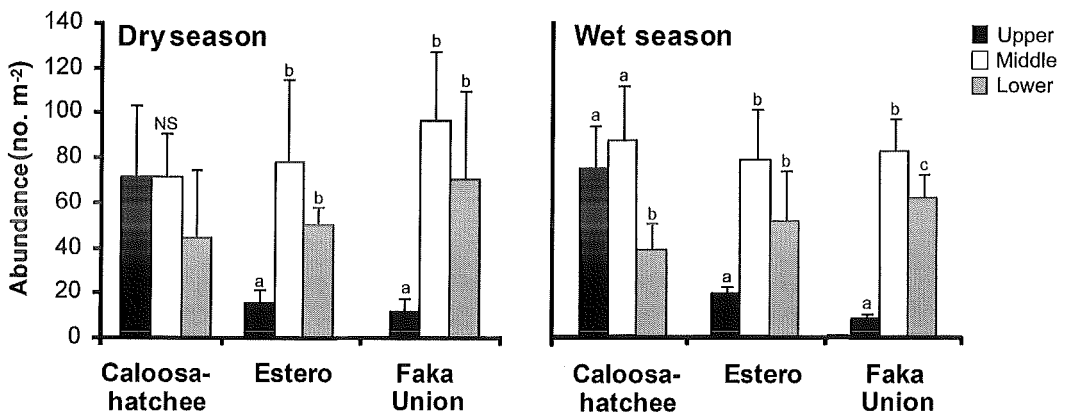


Fig. 3. Spatial and seasonal differences in abundance of *Eurypanopeus depressus*. Bars are means with 95% confidence intervals. Differences in abundance among stations within estuaries are indicated by different letters.

TABLE 1. Comparison of *Eurypanopeus depressus* weighted-mean salinity (practical salinity units) of capture data between seasons. Data are mean values for each estuary with SD in parentheses. Asterisks mark significant effects.

Estuary	Season		F statistic	P value	df
	Dry	Wet			
Caloosahatchee	33.2 (3.8)	15.4 (8.6)	10.800	0.030*	5
Estero	37.4 (0.8)	23.4 (7.5)	10.310	0.033*	5
Faka Union	34.2 (1.2)	9.2 (7.2)	34.722	0.040*	5

upper station, the Caloosahatchee had the lowest abundances at the downstream location.

The overall weighted mean salinity of capture was 24.3 ± 11.4 psu, 30.4 ± 9.0 psu, and 21.7 ± 14.4 psu for the Caloosahatchee, Estero, and Faka Union estuaries, respectively. This measure was not significantly different among estuaries or stations, or between seasons, but within each estuary, weighted-mean salinity of capture was significantly higher during the dry season (Table 1).

Biomass patterns closely followed abundance (Fig. 4). In the Estero estuary, the upper station had significantly lower biomass than the middle station (Hochberg's GT2). In the Faka Union, biomass was significantly lower at the upper station than at the lower station, which was significantly lower than at the middle station (Hochberg's GT2) (Fig. 4). In the Caloosahatchee estuary, biomass was not significantly different among any of the stations. As was the case for abundance, biomass was generally highest at the middle station regardless of season (Fig. 4). Biomass was only marginally higher in Caloosahatchee during the wet season [$F(1,17) = 4.286$, $P = 0.055$].

Some spatial patterns in size were detected (Fig. 5). Crabs were significantly larger at the upper station for the Estero and Faka Union

estuaries ($P \leq 0.001$), although for the Caloosahatchee crabs were significantly ($P \leq 0.001$) larger at the lower station (Games-Howell) (Fig. 5). Games-Howell testing did not distinguish between the upper and middle stations for the Caloosahatchee or between the lower and middle stations for the Estero and the Faka Union estuaries. This pattern existed in both wet and dry seasons (Fig. 5).

DISCUSSION

The flatback mud crab *Eurypanopeus depressus* is a common inhabitant of oyster reefs from the northeastern United States to Texas (Garcés, 1987) and is often the dominant member of the macrofauna in these ecosystems (Tolley et al., 2005). The success of this species is linked closely with the existence of oyster reefs, so examining how its population distribution changes seasonally across a salinity gradient may provide clues to how oyster-reef communities may be affected by changes in freshwater inflow.

Differences in salinity existed, both seasonally and spatially, that could be related to degree and type of watershed alteration. Estero Bay is a shallow estuary fed by small tributaries that operates as a lagoon during much of the year. The Caloosahatchee and Faka Union estuaries

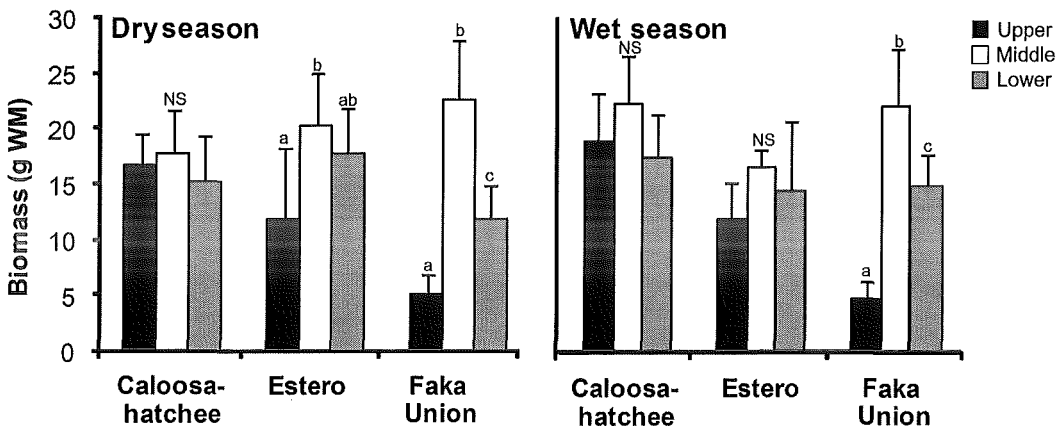


Fig. 4. Spatial and seasonal differences in biomass of *Eurypanopeus depressus*. Bars are means with 95% confidence intervals. Differences in biomass among stations within estuaries are indicated by different letters.

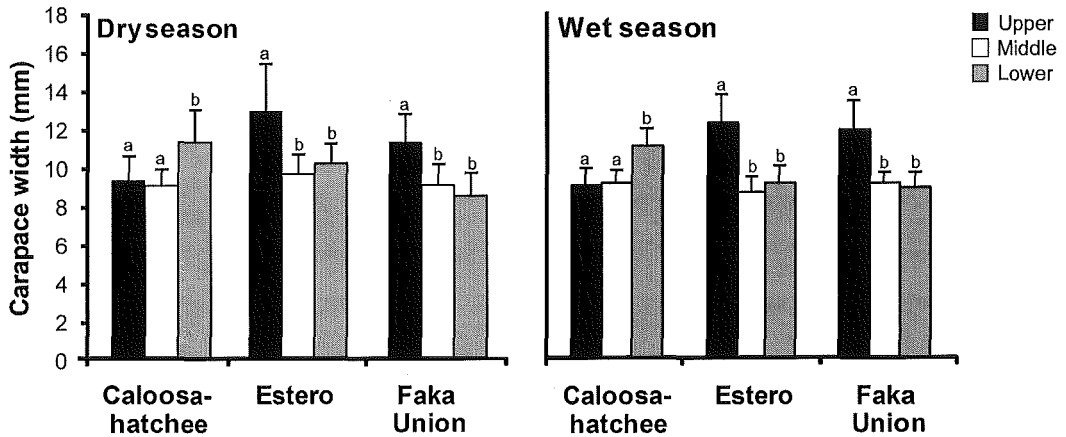


Fig. 5. Spatial and seasonal differences in size of *Eurypanopeus depressus*. Bars are means with 95% confidence intervals. Differences in size among stations within estuaries are indicated by different letters.

both have highly augmented watersheds and both receive regulated freshwater flow through lock and/or dam structures. The Estero Bay estuary's mean salinity (30.5 ± 8.9 psu) was significantly higher than that of the Caloosahatchee (24.6 ± 11.2 psu) and Faka Union estuaries (22.2 ± 14.0) [$F(2,54)=21.1$, $P<0.001$]. In addition, seasonal mean salinities differed, suggesting differing impacts of seasonal rains possibly as a result of watershed alteration. Although upstream stations had larger seasonal salinity variation than downstream stations, salinity differences among stations were only significant in the Caloosahatchee and Faka Union estuaries during the wet season when the salinity gradient was fully expressed. The heavily altered Faka Union estuary had the largest seasonal difference in salinity, ranging from 35.0 ± 3.2 psu in the dry season to 9.5 ± 6.6 psu in the wet season, and Estero Bay had the smallest difference (from 37.0 ± 2.1 psu to 24.1 ± 8.0 psu respectively). These results suggest that, in addition to watershed size, watershed alteration enhances the effects of seasonal rains on salinity, but because statistical tests did not detect any significant difference with season for *E. depressus* population metrics, the effects on this oyster-reef inhabitant are still not clear.

Because few of the metrics examined reflected significant changes as a result of seasonal rains, the data suggest that this species is not highly affected by freshwater inflow, although changes in freshwater inflow certainly may result in population responses. Increased nutrients in the tidal river during the wet season may fuel primary production and increase the detrital food source of *E. depressus*, leading to increased abundance. Lower-salinity waters also tend to have fewer predators (Kimmerer, 2002), and

rhizocephalan parasites have been found to be more predominant in some xanthid crabs in higher salinity environments, although this was not the case for *E. depressus* in southwest Florida (Tolley et al., 2006b).

Biomass was greater, but only marginally so, in the wet season in the Caloosahatchee and could correlate with body changes related to preparation for breeding. In support of this, McDonald (1982) collected ovigerous *E. depressus* during the summer months in South Carolina that correspond to the wet season in Southwest Florida. The current study also revealed that larger numbers of new recruits are found at the middle and lower stations in the Estero and Faka Union estuaries during the wet season. More data are needed to clarify these results as no significant differences were detected.

Some patterns in *E. depressus* populations were observed along the salinity gradient. Abundance and biomass were greatest at the moderate-salinity middle stations, where salinity averaged 26.0 ± 11.0 psu. Garcés (1987) found the range of salinity tolerance for *E. depressus* to be between 5 and 45 psu. Hulathduwa et al. (2007) found the 28-d 50% Lethal Concentration (LC50) of *E. depressus* to be 0.2 psu and the energy budget, measured as scope for growth, to be positive at salinities as low as 7.5 psu. However, the scope for growth at 7.5 psu was only 20% as high as at 17.5 psu.

Hall et al. (1992) reported that individuals of a species tend to be most successful in the middle of their range of environmental tolerance, although this tolerance window can be quite wide in temperate and tropical species (Pörtner, 2002).

Biomass was lowest upstream regardless of season in the Estero and Faka Union estuaries. This could be a result of reduced oyster densities, and thus reduced habitat, at upstream

locations (Tolley et al., 2005). Although the mean salinity at the upstream stations was 21.0 ± 14.6 psu and within the tolerance range of *E. depressus*, crabs adapted to 7.5 psu expend 37% more energy on aerobic respiration than crabs adapted to 17.5 or 25 psu (Hulathduwa et al., 2007) leaving less energy to support growth and reproduction.

Larger crabs tended to be more prevalent at the stations upstream. Recruitment could account for the small size of *E. depressus* at the middle and lower stations but, because no differences in the number of recruits among stations were found, more information is needed to support this explanation. Osmoregulatory ability may also vary according to age or size. Ontogenetic trends in osmoregulation have been demonstrated in the lobster *Homarus americanus*, the shrimp *Penaeus japonicus* (Charmantier et al., 1988), and many other crustaceans (see review, Péqueux, 1995). In most cases metamorphosis marks the beginning of the adult-type osmoregulation, although in the shrimp *P. japonicus*, the efficiency of osmoregulation is not established until days or weeks after metamorphosis (Charmantier et al., 1988; Charmantier, 1998). Studies of the development of ion-transporting epithelia in the gills of *E. depressus* in different ontogenetic stages or size classes would help clarify the importance of ontogeny in salinity tolerance and the resulting distribution along salinity gradients.

The availability of appropriate substrate can be as important as salinity in determining the distribution of estuarine organisms (Felder, 1978) and the rate of freshwater inflow helps determine the dynamic location of productive habitat in an estuary (Browder and Moore, 1981). Although estuarine productivity generally increases with freshwater inflow, the relationship is rarely linear and differs according to estuary and species (Browder and Moore, 1981). Further research into the effects of salinity on species distribution and abundance and how hydrology affects productivity is needed to fully address the effects of variable freshwater flow on *E. depressus* populations.

Oyster density may play a role in *E. depressus* population distribution. Oyster densities in the three estuaries in this study have been previously reported (Tolley et al., 2005) and the only estuary for which oyster density and *E. depressus* population density could be related was the Faka Union estuary. Unlike the Estero and Faka Union estuaries, the Caloosahatchee had low oyster density at the lower station (Tolley et al., 2005), which may account for the differences in abundance and biomass seen in this estuary

compared to the other two. Otherwise, there appears to be little if any relationship between *E. depressus* population density and oyster density. Similarly, differences in oyster density did not affect crab abundance for xanthid crabs on Alabama reefs (May, 1974).

A fundamental question of ecology addresses what determines a species' distribution. A survey of how a species is distributed and the character of the population along its range will help answer this question. The finding that seasonal changes had little effect on abundance, size, and biomass of *E. depressus* in three Florida estuaries lends strength to the conclusion that this crab is a cosmopolitan, euryhaline species able to succeed at a wide range of temperatures and salinities. Based on the distribution of *E. depressus* larvae collected monthly in Estero Bay (Tolley et al., 2007), this species likely reproduces year-round, which may help explain the lack of strong seasonal signals because there are always larvae available for recruiting to the reefs. Other researchers have confirmed the euryhaline and widespread distribution of *E. depressus*: they have been found living in a range of salinities from 4 to 52 psu in estuarine oyster beds from Massachusetts to Texas (Garcés, 1987; Shirley and McKenney, 1987).

Southwest Florida's estuaries have undergone significant alterations, the results of which span physical, chemical, geological, and biological realms. Changes in salinity and freshwater inflow have been occurring as a result of oyster-reef destruction, coastal development, and channel dredging and locking (Estevez, 2000). Tracking the responses of organisms to changes in habitat quality brought about by these actions gives clues to how we can better compare the costs of recreational and economic needs with those of the natural environment.

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