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Impacts of salinity and freshwater inflow on oyster-reef communities in Southwest Florida

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Abstract – When assessing oyster-reef habitat in estuaries it is important to understand the influence of salinity on the spatial and temporal variability of associated organisms. How comparable is community structure among stations located at different points along the salinity gradients of estuaries or among tidal tributaries that experience different levels of freshwater inflow? Do assemblages vary seasonally in response to changing salinity and freshwater inflow? To address these questions, multivariate techniques were employed to analyze decapod crustacean and fish abundance data. Organisms were collected at three reefs along the salinity gradient of three estuaries: the Caloosahatchee River and estuary, Estero River and Bay, and Faka Union Canal and Bay. Additional collections were made from reefs located near the mouths of Estero Bay's five tidal tributaries. Samples were dominated by the decapods *Eurypanopeus depressus* and *Petrolisthes armatus*. Commonly occurring species included the decapods *Panopeus obesus*, *Alpheus heterochaelis* and *Rhithropanopeus harrisii* and the fishes *Gobiosoma robustum*, *Lophogobius cyprinoides* and *Gobiesox strumosus*. Analysis of similarities suggested differences among stations located along the salinity gradients of all three estuaries. Community structure also varied among stations located near the mouths of the tidal tributaries of Estero Bay. Multidimensional scaling identified community structure present at upper stations as distinct from that downstream and at high-flow tributaries as distinct from that near low-flow tributaries. Upper stations and stations near high-flow tributaries were typified by *E. depressus* and gobiid fishes. Downstream stations and stations near low-flow tributaries were typified by *E. depressus* and *P. armatus*. Percent dissimilarity was greatest when upper and lower stations were compared along the salinity gradient or when low salinity and high-salinity sites were compared among tributaries. Within-station sample variability tended to be higher upstream or in association with high-flow tributaries.

Key words: Oyster reef / Community / Salinity / Freshwater inflow / multivariate statistics / Atlantic Ocean

Résumé – Effets de la salinité et des arrivées d'eau douce sur les communautés récifales d'huîtres du sud-ouest de la Floride. Lors de l'évaluation des habitats de récifs d'huîtres, il est important de comprendre l'influence de la salinité sur la base de variabilités spatio-temporelles des organismes associés. Comment la structure des communautés peut être comparable entre stations situées à différents points d'un gradient de salinité des estuaires ou des cours d'eau soumis à l'influence de la marée, et qui sont donc soumis à différents niveaux d'arrivées d'eau douce ? Les assemblages varient-ils avec la saison au changement de salinité et des apports d'eau douce ? Pour répondre à ces questions, des méthodes statistiques multivariées sont utilisées pour analyser les données d'abondance de crustacés décapodes et de poissons. Les animaux sont récoltés sur trois récifs le long d'un gradient de salinité de trois estuaires : l'estuaire et le fleuve Caloosahatchee, de ceux de l'Estero et de la baie et du canal de Faka. Des prélèvements supplémentaires sont fait sur les récifs situés près de l'embouchure de 5 fleuves côtiers de la baie de l'Estero. Dans les échantillons, les crabes *Eurypanopeus depressus* et les crabes porcelaines vert *Petrolisthes armatus* sont les plus abondants. Les espèces les plus communément rencontrées incluent les Décapodes *Panopeus obesus* (crabes), *Alpheus heterochaelis* et *Rhithropanopeus harrisii* et les poissons *Gobiosoma robustum*, *Lophogobius cyprinoides* et *Gobiesox strumosus*. L'analyse des similarités laisse supposer des différences entre les stations situées le long de gradients de salinité des trois estuaires. La structure des communautés varie entre stations situées près de l'embouchure des fleuves de la baie de l'Estero. L'échelle multidimensionnelle permet d'identifier la structure de la communauté située au niveau des stations en amont, distincte de celle située en aval, ainsi que celle associée à d'importantes arrivées d'eau douce par rapport à celle de faibles arrivées d'eau douce. Les stations en amont et celles soumises à de fortes arrivées d'eau douce sont caractérisées par *E. depressus* et des poissons gobiidés. Les stations situées en aval et au niveau de faibles arrivées d'eau

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douce sont caractérisées par *E. depressus* et *P. armatus*. Les différences sont les plus grandes lorsque les stations les plus amont et les plus aval sont comparées. La variabilité des échantillons d'une même station tend à être plus élevée en amont ou en association avec d'importantes arrivées d'eau douce.

1 Introduction

Increasing human population and concomitant changes in land and water use alter the timing and amount of freshwater delivered to estuaries. Even though coastal counties represent 17% of the total land area of the U.S. (excluding Alaska) they account for 53% of the total population (Crossett et al. 2004). Regionally, Florida led the nation in coastal population growth (75%), normalized to percent change, from 1980 to 2003 (Crossett et al. 2004). This concentration of population along the coastline results in an intensification of environmental problems in coastal watersheds. Urbanization and development of coastal watersheds increase the area of impervious surfaces. As a result, runoff leaves the landscape more quickly and enters estuaries downstream in a pulse: peak flows are higher than under predevelopment conditions and the lag between rainfall and runoff is greatly reduced (Hopkinson and Vallino 1995). In Southwest Florida, where seasonal rainfall often determines the degree of freshwater inflow, tidal tributaries emptying into local estuaries are rendered even more flashy.

Freshwater inflow has been identified as a significant landscape process shaping community structure within estuaries (Mannino and Montagna 1997; Sklar and Browder 1998; Palmer et al. 2002). High levels of freshwater inflow can decrease the abundance of both estuarine residents and marine species that utilize estuaries as nursery areas (Garcia et al. 2004). Extreme fluctuations in salinity often elicit stress responses or emigration, resulting in a reduction of biodiversity (Sklar and Browder 1998). Altered freshwater delivery can greatly influence salinity distribution within an estuary both spatially, through the establishment of salinity gradients, and seasonally, through the relocation of isohalines. Biotic responses to these changes can restructure communities associated with affected habitats such as seagrasses (e.g., Matheson et al. 1999; Biber and Irlandi 2006) and oyster reefs (e.g., Maurer and Watling 1973; Tolley et al. 2005).

Because there is no commercial harvest for Eastern oyster *Crassostrea virginica* in Southwest Florida (i.e., beds are not classified for or are protected from shellfish harvesting), the ecosystem functions that oysters contribute to estuaries are a significant focus of research and a driving force behind restoration. One of these functions is the creation of complex three-dimensional habitat for commensal organisms (e.g., Wells 1961; Breitburg 1999; Coen et al. 1999; Posey et al. 1999). Many of these organisms are in turn forage for commercially and recreationally important species (Tolley et al. 2005). If relative habitat value is to be used as a measure of success for oyster-reef restoration projects, spatial variation in the communities of commensal organisms present is an important consideration. Furthermore, because seasonal cycles are determined as much by rainfall as by temperature in Southwest Florida, oyster-reef communities might be expected to vary significantly between wet and dry seasons.

The current study was conducted to investigate spatial and temporal influences of salinity and freshwater inflow on community structure of Southwest Florida oyster reefs. The estuaries selected for study are all undergoing major restoration efforts and/or changes in water management plans. Multivariate analysis was employed to characterize oyster-reef communities and to detect spatial and temporal differences among them.

2 Materials and methods

2.1 Study Location

Commensal decapods and fishes living among oyster reefs were sampled in three Southwest Florida estuaries: the Caloosahatchee River and estuary, Estero Bay and Faka-Union Canal and Bay. These estuaries are microtidal and the reefs they contain are intertidal and of limited vertical relief (< 1 m). The Caloosahatchee is highly altered and highly managed, possessing a watershed that was augmented considerably through a man-made connection with Lake Okeechobee established in the 19th century. The Caloosahatchee has been converted from a meandering river into a canal over much of its length and is impounded behind a series of control structures upstream. In its present configuration, the Caloosahatchee is subject to large regulatory releases of freshwater from Lake Okeechobee.

Estero Bay, lying 18 km to the south, was the State's first aquatic preserve. Though much of the lower estuary is protected, its principal tributaries – the Estero River and Imperial Rivers and Hendry, Mullock, and Spring Creeks – are increasingly subjected to development in the upper portions of their watersheds. Minimum water flows and levels are planned for this estuary to ensure that further changes in land and water use minimize ecological impact and protect existing water resources.

Farther southeast (90 km from Estero Bay) is the Faka Union Canal that empties into the Ten Thousand Islands adjacent to the western boundary of the Everglades National Park. Though the Faka Union is the least developed of these systems, its watershed is also highly augmented – the result of a failed real estate development in the 1960s that constructed 86 km of canals to drain freshwater wetlands. Restoration of freshwater inflow to the Ten Thousand Islands is pending through the state and federally sponsored Picayune Strand Restoration Project.

Seasons in Southwest Florida are determined as much by rainfall as by temperature. Seasonal rains are prevalent from mid-June through mid-October and, coupled with tropical weather systems, reduce salinities in local estuaries. In contrast, hypersaline conditions may occur in the downstream portion of these estuaries during the remainder of the year.

Table 1. Sampling locations and associated water quality. Water quality data are presented as mean with SD in parentheses. Longitudinal sampling was conducted along the salinity gradients of three estuaries, and transverse sampling was conducted near the mouths of five tidal tributaries emptying into a single estuary. Distance is measured from the river/tributary mouth and is positive upriver and negative toward the Gulf of Mexico.

Estuary	Station	Latitude (N)	Longitude (W)	Distance (km)	Salinity (psu)	Temperature (°C)	Dissolved oxygen (mg L^{-1})
Longitudinal Sampling							
Caloosahatchee River	Upper	26°30’54.46”	81°58’57.95”	5.0	15.41 (12.83)	29.02 (3.96)	
	Middle	26°30’47.26”	82°01’57.80”	–0.7	23.47 (9.79)	28.82 (4.02)	
	Lower	26°27’02.72”	82°04’48.49”	–9.0	30.36 (6.21)	28.64 (4.80)	
Estero River	Upper	26°26’08.04”	81°51’11.37”	1.0	26.48 (12.65)	28.00 (2.33)	
	Middle	26°25’44.36”	81°52’00.13”	–0.8	32.16 (7.86)	28.23 (2.24)	
	Lower	26°25’29.91”	81°52’15.36”	–1.5	34.06 (5.18)	27.93 (2.27)	
Faka-Union Canal	Upper	25°54’12.94”	81°30’39.21”	0.6	16.46 (16.67)	28.84 (0.85)	
	Middle	25°53’42.41”	81°31’09.82”	–0.8	20.76 (14.22)	29.64 (0.83)	
	Lower	25°52’53.42”	81°31’42.35”	–2.7	25.38 (10.59)	29.99 (1.00)	
Transverse Sampling							
Estero Bay	Estero	26°25’44.36”	81°52’00.13”	–0.8	22.58 (9.57)	28.46 (4.01)	5.55 (0.83)
	Hendry	26°28’00.02”	81°52’26.36”	0.8	9.32 (10.34)	28.93 (4.01)	5.25 (0.82)
	Imperial	26°20’35.89”	81°50’34.17”	–0.9	16.26 (13.67)	28.11 (3.02)	5.12 (1.39)
	Mullock	26°27’54.96”	81°51’52.33”	0.6	9.53 (11.57)	28.14 (2.99)	5.43 (0.60)
	Spring	26°22’48.49”	81°50’24.03”	0.0	26.35 (8.92)	29.00 (3.30)	5.93 (2.48)

2.2 Field sampling

In order to gauge the spatial variability of oyster-reef assemblages, two sampling schemes were employed: longitudinal, in which stations were oriented along the salinity gradient of an estuary; and transverse, in which stations were oriented perpendicular to the salinity gradient within an estuary. Longitudinal sampling aimed to establish whether variability in community structure was greater among estuaries than among stations experiencing different salinities within an estuary. In this sampling scheme, reef-resident fishes and decapods were collected at three stations along the salinity gradient of each of the three estuaries (6 sampling periods × 3 estuaries × 3 stations × 3 replicates). Sampling was conducted during three seasonally dry (mid-March through mid-June 2002) and three seasonally wet (mid-July through mid-October 2002) months to examine the influence of salinity on oyster-reef communities. Stations were selected at locations that were morphologically homologous among estuaries: an upper station located within the tidal river, a middle station located near the river mouth, and a lower station located downstream from the river mouth (Table 1). Transverse sampling sought to minimize among-estuary and among-station variability by focusing efforts on oyster reefs located near the mouths of tidal tributaries within a single estuary. Each tributary experienced different levels of freshwater inflow and therefore salinity. In the transverse sampling scheme, oyster reefs located near the mouths of the five tidal tributaries of Estero Bay – Estero and Imperial Rivers, and Hendry, Mullock, and Spring Creeks (Fig. 1, Table 1) – were sampled during six consecutive months (6 sampling periods × 1 estuary × 5 sites × 3 replicates) overlapping wet and dry seasons (April through September 2005). These sites were considered homologous.

For each sampling effort (station and month) triplicate lift nets (Crabtree and Dean 1982) were deployed intertidally, just above mean low water, on living oyster reefs for a duration of approximately 30 d. This contour typically contained the greatest living oyster densities as well as oyster clumps of greatest size. An area of bottom approximating the size of each lift net was cleared of any oyster shell prior to net deployment. Replicate nets at each location were placed 5 m apart from one another. Lift nets were selected to target small reef and facultative residents (Breitburg 1999). For more details on lift-net construction and deployment see Tolley et al. (2005), which reports on the univariate analysis of a portion of the data examined herein.

During longitudinal sampling, 1-m^2 lift nets were filled with 5 liters volume displacement of live oyster clusters collected from adjacent portions of the reef. Transverse sampling utilized 0.5-m^2 lift nets deployed with approximately 3 liters of live oyster clusters. In each sampling scheme, the volume of oyster clusters used was within the range of ambient densities. No effort was made to remove existing fauna from these oyster clusters. Upon retrieval of the nets, oysters were removed and associated fishes and decapods were extricated using forceps. Any target organisms remaining in the net were removed by hand or by sweeping the lift net with a small dip net. Organisms were transported on ice back to the laboratory for identification and all fishes and decapods were identified to the lowest taxon practical.

Salinity, temperature and dissolved oxygen were recorded upon lift-net deployment and retrieval (dissolved oxygen measurements were not included in the analysis of data collected during the longitudinal study due to technical difficulties associated with the probe). Provisional inflow data for each tidal tributary sampled in the transverse study were collected by

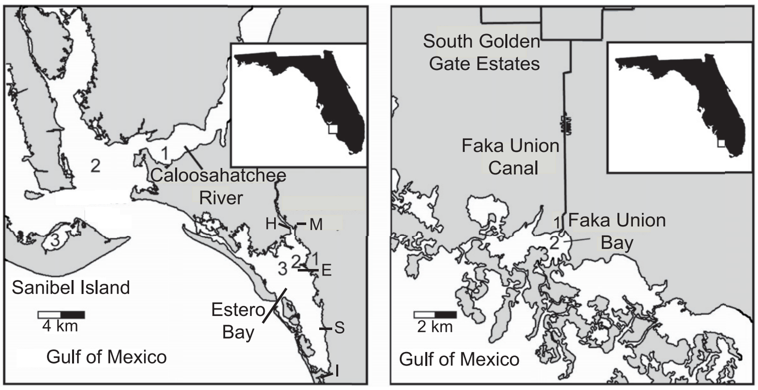

Fig. 1. Study area: Caloosahatchee and Estero estuaries on the left and Faka-Union estuary on the right. Longitudinal sampling sites are numbered sequentially from upstream to downstream (1 = upper, 2 = middle, 3 = lower) and transverse sampling sites (Estero Bay only) are as follows: E = Estero River, H = Hendry Creek, I = Imperial River, M = Mullock Creek, S = Spring Creek.

the U.S. Geological Survey and provided by the South Florida Water Management District. These daily flows were averaged to estimate monthly inflow (m^3 s^{-1}).

2.3 Statistical analysis

Multivariate analyses of samples (replicates) from different stations and different times (months) were performed using PRIMER (Plymouth Routines in Multivariate Ecological Research). Although the statistical routines used were nonparametric, all abundance data were square-root transformed prior to analysis to downweight the influence of the most common species (Clarke and Warwick 2001). Cases in which a species was represented by a single occurrence were considered sufficiently rare such that the species was omitted from further statistical analysis. Further data reduction was not considered as it has not been shown to alter the conclusions made using non-reduced data (Walters and Coen 2006).

Multidimensional scaling (MDS) was employed to search for natural groupings among samples. This statistical tool is based on Bray-Curtis similarity matrices and has been recommended for use in examining communities structured by environmental gradients (Clarke and Warwick 2001). MDS plots were not considered useful for interpretation if associated stress values were >0.2.

Analysis of similarities (ANOSIM), a nonparametric analog of analysis of variance, was used to test for *a priori* groupings of samples (Clarke 1993). When using ANOSIM, global tests were considered significant at $p \leq 0.05$, with p values being adjusted upwards using the Bonferroni correction for multiple comparisons. Pairwise tests between stations were interpreted primarily using the absolute value of the associated R statistic (i.e., a value approaching 1 indicates a difference between stations whereas an R close to 0 indicates no difference) as well as the adjusted p value (Clarke and Warwick 2001). Relative contributions of individual species to within group similarities as well as between-group dissimilarities were examined using similarity percentages (SIMPER).

Warwick and Clarke (1993) suggested that the degree of multivariate variability in ordination space among replicate samples could be used as a relative measure of environmental stress and introduced the concept of relative dispersion as a measure of this variability. Multivariate variability has since been interpreted as within-station heterogeneity (Levin et al. 2000), heterogeneity of community structure (Smith and Simpson 2002) and multivariate stability (Hoffmeyer 2004). Relative dispersion is indexed to a value of 1, with values greater than unity indicating above average variability among replicates and below unity indicating less than average variability (Somerfield and Clarke 1997), and was calculated for different stations in the current study to examine potential relationships between within-station variability and either salinity or freshwater inflow. Index of Multivariate Dispersion (IMD) (Warwick and Clarke 1993) was used in pairwise comparisons to test for between-station differences in the degree of within-station variability (dispersion). Values of IMD approaching 1 or -1 indicate differences in community assemblage between stations whereas values approaching 0 suggest no such difference.

Environmental data were examined using appropriate ANOVA. Homogeneity of variance was tested using the Levene statistic with significant differences ($p \leq 0.05$) being resolved using multiple comparison tests according to Day and Quinn (1989): Fisher's Least Significant Difference in cases of equal sample size and equal variance; Hochberg's GT2 method in cases of unequal sample size but equal variance; and the Games-Howell test in cases of unequal variance. Pearson's correlation coefficient was used to determine the degree of covariance between salinity and inflow as well as between relative dispersion and environmental parameters.

3 Results

3.1 Commensal organisms

Of the 26,177 specimens collected, decapod crustaceans dominated numerically regardless of estuary or sampling scheme (Tables 2 and 3). A total of 15 species of decapods were identified, with the flatback mud crab *Eurypanopeus depressus* and the green porcelain crab *Petrolisthes armatus* comprising 91% of the total organisms collected. The saltmarsh mud crab *Panopeus obesus* and the bigclaw snapping

Table 2. Decapod crustaceans and fishes collected during longitudinal sampling of three Southwest Florida estuaries reefs: Caloosahatchee River and Estuary (CAL), Estero River and Bay (EST), and Faka Union Canal and Bay (FUC). Organism size is presented as mean, with standard deviation in parentheses, and was measured as carapace length for shrimps, carapace width for crabs, and standard length for fishes.

Species	Common Name	Number Collected			Size (mm)
		CAL	EST	FUC	
Decapods					
Farfantepenaeus sp.	penaeid shrimp	24	1	5	24.4 (10.6)
Palaemonetes pugio	daggerblade grass shrimp	7	6	0	14.4 (4.8)
Palaemonetes vulgaris	marsh grass shrimp	36	0	0	18.8 (7.6)
Alpheus heterochaelis	bigclaw snapping shrimp	107	49	41	19.8 (6.1)
Petrolisthes armatus	green porcelain crab	1343	3595	5136	5.2 (1.8)
Libinia dubia	longnose spider crab	3	0	7	16.5 (5.8)
Portunas gibbesii	iridescent swimming crab	1	0	1	15.5 (0.0)
Eurypanopeus depressus	flatback mud crab	3442	2525	3040	9.2 (3.7)
Hexapanopeus angustifrons	smooth mud crab	0	0	2	6.2 (0.8)
Menippe mercenaria	Florida stone crab	19	11	0	19.7 (8.3)
Panopeus lacustris	knotfinger mud crab	11	5	14	20.4 (10.0)
Panopeus obesus	saltmarsh mud crab	75	155	203	17.8 (7.7)
Panopeus simpsoni	oystershell mud crab	14	18	4	16.4 (7.1)
Rhithropanopeus harrisii	Harris mud crab	1	0	6	6.7 (1.0)
Fishes					
Opsanus beta	gulf toadfish	46	27	14	53.0 (21.6)
Gobiesox strumosus	skilletfish	59	14	42	28.4 (7.8)
Cyprinodon variegatus	sheepshead minnow	0	4	0	54.8 (8.6)
Anarchopterus criniger	fringed pipefish	1	0	0	13.4
Lutjanus griseus	gray snapper	0	5	4	68.3 (14.9)
Lutjanus synagris	lane snapper	0	3	0	29.8 (16.6)
Eucinostomus sp.	mojarra	16	22	32	19.0 (10.2)
Archosargus probatocephalus	sheepshead	1	4	4	52.2 (11.3)
Lagodon rhomboides	pinfish	5	9	4	46.4 (13.9)
Bairdiella chrysoura	silver perch	13	0	0	17.7 (2.0)
Chasmodes saburrae	Florida blenny	62	2	9	36.3 (8.6)
Hypsoblennius hentz	feather blenny	6	0	0	42.2 (12.4)
Lupinoblennius nicholsi	highfin blenny	2	1	1	27.8 (13.7)
Bathygobius soporator	frillfin goby	3	0	3	44.4 (9.7)
Gobiosoma bosc	naked goby	2	4	7	25.8 (2.9)
Gobiosoma robustum	code goby	177	3	49	21.1 (4.5)
Lophogobius cyprinoides	crested goby	0	112	11	36.4 (10.1)
Sphoeroides nephelus	southern puffer	1	0	0	62.4

shrimp *Alpheus heterochaelis* were also found commonly on oyster reefs in all three estuaries and the Harris mud crab *Rhithropanopeus harrisii* was found frequently at two low-salinity sites during transverse sampling of Estero Bay. Fishes were slightly more diverse with 19 species represented but were, in general, much less abundant (4% of the total) than decapods. The gobies *Gobiosoma robustum* and *Lophogobius cyprinoides* and the skilletfish *Gobiesox strumosus* were the most abundant fishes sampled in all three estuaries (Table 2). Other fishes occurring frequently included gulf toadfish *Opsanus beta*, Florida blenny *Chasmodes saburrae*, and juvenile mojarras *Eucinostomus* sp.

3.2 Spatial and temporal patterns

3.2.1 Longitudinal study

Although multidimensional scaling failed to indicate any clear segregation of oyster-reef assemblages by estuary, the results of two-way crossed ANOSIM (estuary x station) indicated variation among estuaries (global $R = 0.416$, $p < 0.001$) and among stations across estuaries (global $R = 0.644$, $P < 0.001$). Subsequent pair-wise comparisons suggested that the Caloosahatchee assemblage overlapped but was clearly separable from assemblages present in the other two estuaries, which were in turn barely separable from one another (Caloosahatchee, Estero: R = 0.583, $p < 0.01$); Caloosahatchee, Faka Union: $R = 0.482$, $p < 0.01$; Estero, Faka Union: $R = 0.229$, $p < 0.01$). Regarding differences among stations, upper stations were distinct from those downstream (Upper, Middle: $R = 0.826$, $p < 0.01$; Upper, Lower: $R = 0.913$, $p < 0.01$); in contrast, middle and lower stations were barely separable ($R = 0.384$, $p < 0.01$).

Two-way crossed analysis of similarity (season x station) indicated significant variation in oyster-reef assemblages within each estuary. Assemblages in the Caloosahatchee were spatially distinct from one another (global $R = 0.824$, $p < 0.001$) with the upper station being well separated from both the middle and lower stations (upper, middle: $R = 0.868$,

Table 3. Decapod crustaceans and fishes collected during transverse sampling of Estero Bay oyster reefs: Estero River (EST), Hendry Creek (HEN), Imperial River (IMP), Mullock Creek (MUL) and Spring Creek (SPR).

		Number Collected				
Species	Common Name	EST	HEN	IMP	MUL	SPR
Decapods						
Farfantepenaeus sp.	penaeid shrimp	2	0	1	0	3
Palaemonetes vulgaris	marsh grass shrimp	1	0	0	0	0
Alpheus heterochaelis	bigclaw snapping shrimp	79	0	6	0	67
Petrolisthes armatus	green porcelain crab	450	0	0	0	508
Callinectes sapidus	blue crab	0	0	1	3	0
Eurypanopeus depressus	flatback mud crab	1380	418	495	302	1198
Menippe mercenaria	Florida stone crab	14	0	0	0	10
Panopeus spp.	mud crabs	6	7	6	2	23
Panopeus lacustris	knotfinger mud crab	1	1	0	0	1
Panopeus obesus	saltmarsh mud crab	4	0	1	0	8
Panopeus simpsoni	oystershell mud crab	5	3	7	1	17
Rhithropanopeus harrisii	Harris mud crab	1	32	4	119	0
Fishes						
Opsanus beta	gulf toadfish	10	2	2	1	3
Gobiesox strumosus	skilletfish	0	11	64	7	3
Lutjanus griseus	gray snapper	0	0	0	0	1
Archosargus probatocephalus	sheepshead	0	2	0	3	6
Lagodon rhomboides	pinfish	0	3	1	0	1
Chasmodes saburrae	Florida blenny	3	0	1	0	7
Hypsoblennius hentz	feather blenny	3	0	1	0	2
Bathygobius soporator	frillfin goby	3	3	1	0	5
Gobiosoma bosc	naked goby	2	6	18	7	3
Gobiosoma robustum	code goby	3	0	3	1	13
Lophogobius cyprinoides	crested goby	5	19	0	56	13
Achirus lineatus	lined sole	1	0	0	0	0

$p < 0.01$); upper, lower: $R = 0.972$, $p < 0.01$) and with the middle and lower stations overlapping but clearly separable ($R = 0.679$, $p < 0.01$). Assemblages in the Estero and Faka Union overlapped but were still clearly separable (Estero: global $R = 0.692$, $p < 0.001$; Faka Union: global $R = 0.661$, $p < 0.001$). In the Estero, upper station samples were distinct from those collected downstream (upper, middle: $R = 0.977$, $p < 0.01$; upper, lower: R = 0.996, $p < 0.01$), but samples from middle and lower stations exhibited considerable overlap without clear separation ($R = 0.389$, $p < 0.01$). In the Faka Union, samples from the upper station were well separated from those from middle and lower stations (upper, middle: $R = 0.770$, $p < 0.01$; upper, lower: $R = 0.839$, $p < 0.01$), and although middle and lower stations overlapped they were still clearly separable ($R = 0.685$, $p < 0.01$). Significant between-season variation among oyster-reef assemblages was also detected within each estuary (Caloosahatchee: global $R = 0.422$, $p < 0.001$; Estero: global $R = 0.389$, $p < 0.001$; Faka Union: global $R = 0.310$, $p < 0.001$); however, the low associated R values suggest considerable overlap in community structure between seasons.

To further investigate potential seasonal differences, data were segregated by season and reexamined using MDS and ANOSIM. Multidimensional scaling revealed that Caloosahatchee samples grouped according to station regardless of season; samples collected from the upper station in both the Estero and Faka Union were clearly distinct from samples taken downstream, but the separation in ordination space was greatest for samples collected during wet months.

One-way ANOSIM indicated that Caloosahatchee samples segregated by station during both seasons (dry: global $R = 0.818$, $p < 0.001$; wet: global $R = 0.830$, $p < 0.001$). During the dry season all three stations were well separable (upper, middle: $R = 0.776$, $p < 0.01$; upper, lower: $R = 0.978$, $p < 0.01$; middle, lower: $R = 0.822$, $p < 0.01$) (Fig. 2). During wet months the upper station was distinct from those downstream (upper, middle: $R = 0.973$, $p < 0.01$; upper, lower: $R = 0.966$, $p < 0.01$), and although middle and lower stations overlapped they were still separable ($R = 0.519$. $p < 0.01$) (Fig. 2). Estero samples overlapped in ordination space but were still clearly separable (dry: global $R = 0.708$, $p < 0.001$; wet: global $R = 0.673$, $p < 0.001$): during dry months the upper station was quite distinct from those downstream (upper, middle: $R = 0.953$, $p < 0.01$; upper, lower: $R = 0.994$, $p < 0.01$), and although middle and lower stations overlapped, they were separable ($R = 0.519$, $p < 0.01$) (Fig. 3); during wet months the upper station was again distinct from stations downstream (upper, middle: $R = 1.000$, $p < 0.01$; upper, lower: $R = 1.000$, $p < 0.01$) but middle and lower stations were not separable ($R = 0.208$) (Fig. 3). In the Faka Union, separation was less distinct during the dry season (global $R = 0.560$, $p < 0.001$) compared to wet months (global $R = 0.761$, $p < 0.001$). Although dry season samples overlapped, they were separable (upper, middle: $R = 0.598$,

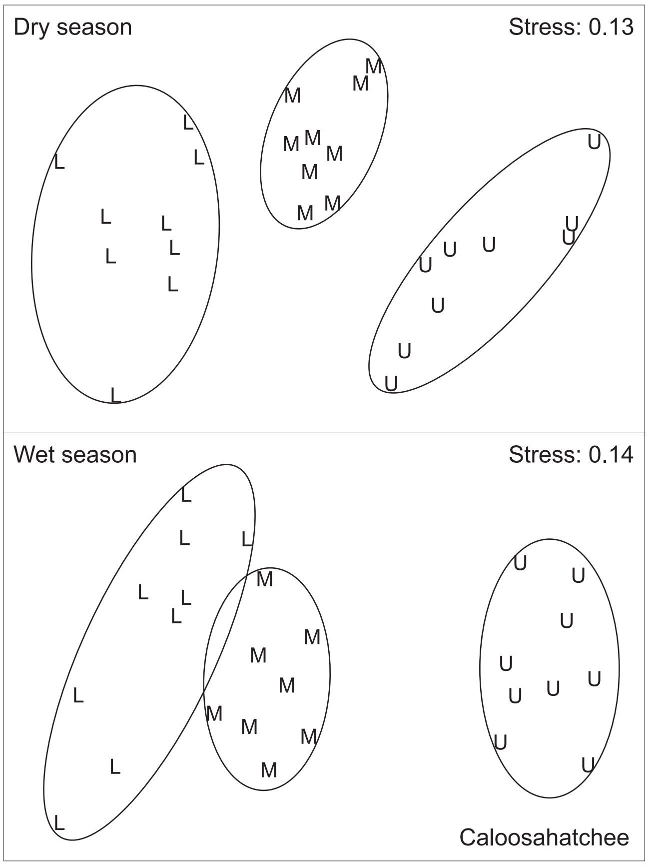

Fig. 2. Multidimensional scaling of samples collected along the salinity gradient of the Caloosahatchee (U = upper, M = Middle, L = Lower) segregated by season. Samples from the upper station are clearly separable from those collected downstream.

$p < 0.01$; upper, lower: $R = 0.694$, $p < 0.01$; middle, lower: $R = 0.521$, $p < 0.01$) (Fig. 4). In contrast, wet season samples were clearly separable (upper, middle: $R = 0.941$, $p < 0.01$; upper, lower: $R = 0.984$, $p < 0.01$; middle, lower: $R = 0.849$, $p < 0.01$) (Fig. 4).

3.2.2 Transverse study

Multidimensional scaling revealed sample segregation by site, with samples from Estero River and Spring Creek forming a tight group in ordination space and being segregated from samples from Hendry and Mullock Creeks and from the Imperial River (Fig. 5). Samples from these latter sites also grouped together in ordination space but much more loosely than Estero and Spring samples. Analysis of similarities (global $R = 0.652$, $p < 0.001$) and pairwise comparisons supported this interpretation, with greater similarities (lower R values) calculated for Estero River and Spring Creek samples (Estero, Spring: $R = 0.053$, ns) as well as for Hendry and Mullock Creek and Imperial River samples (Hendry, Imperial: $R = 0.245$, $p < 0.01$; Hendry, Mullock: $R = 0.120$, ns; Imperial, Mullock: $R = 0.423$, $p < 0.01$). Greatest dissimilarity was calculated for pairwise comparisons between these two groups (Estero, Hendry: $R = 0.955$, $p < 0.01$; Estero, Imperial: $R = 0.913$, $p < 0.01$; Estero, Mullock: $R = 0.901$, $p < 0.01$; Hendry, Spring: $R = 0.984$. $p < 0.01$; Imperial, Spring: $R = 0.935$, $p < 0.01$; and Mullock, Spring: $R = 0.914$, $p < 0.01$).

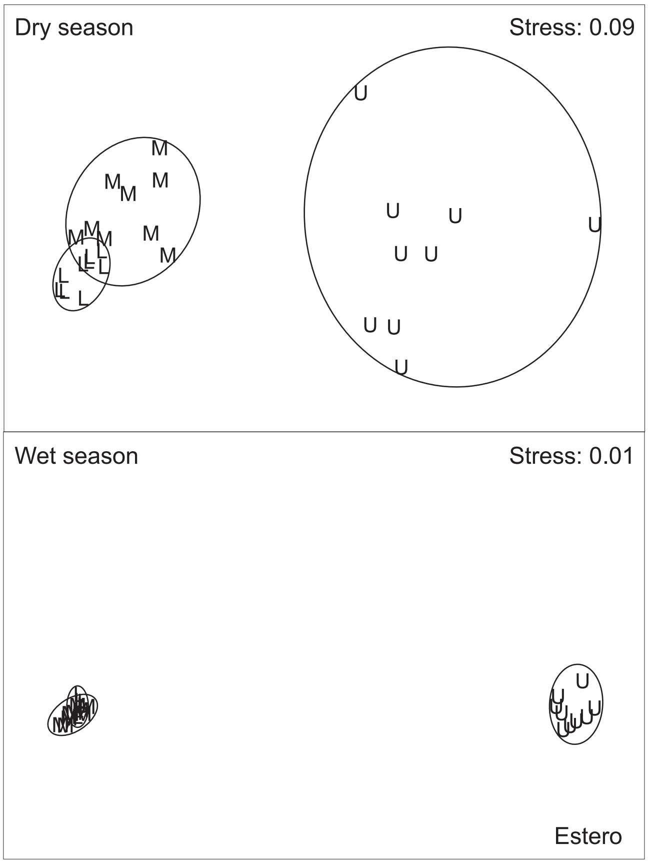

Fig. 3. Multidimensional scaling of samples collected along the salinity gradient of the Estero (U = upper, M = Middle, L = Lower) segregated by season. Samples from the upper station are clearly separable from and exhibit greater scatter in ordination space than those collected downstream.

3.3 Environmental factors

3.3.1 Longitudinal comparison

Significant main effects on salinity were detected using a three-way factorial ANOVA: 3 estuaries × 2 seasons × 3 stations. Mean salinity was higher in Estero (30.90 ± 1.32‰) compared to either the Caloosahatchee (24.28 ± 1.42‰) or Faka Union (20.87 ± 1.32‰) (F[2,51] = 14.6, $p < 0.001$); salinity was higher during the dry season (33.73 ± 1.14‰) compared to wet months (16.96 ± 1.08‰) (F[1,51] = 114.5, $p < 0.001$); and salinity was significantly reduced at the upper stations (19.99 ± 1.36‰) compared to the lower (30.20 ± 1.36‰) (F[2,51] = 14.2, $p < 0.001$). (Salinities at the middle stations averaged 25.85 ± 1.36 but were not deemed significantly different from those of the other stations.) Upon examination of interaction effects it was clear that salinity was higher during the dry season regardless of system (Fig. 6). Furthermore, salinity increased significantly downstream in the

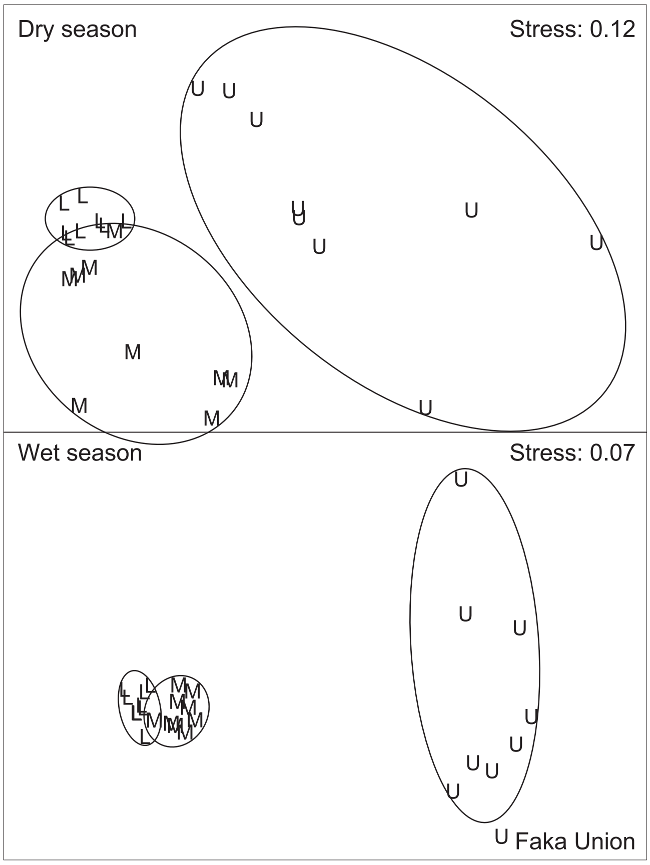

Fig. 4. Multidimensional scaling of samples collected along the salinity gradient of the Faka Union (U = upper, M = Middle, L = Lower) segregated by season. Samples from the upper station are clearly separable from and exhibit greater scatter in ordination space than those collected downstream.

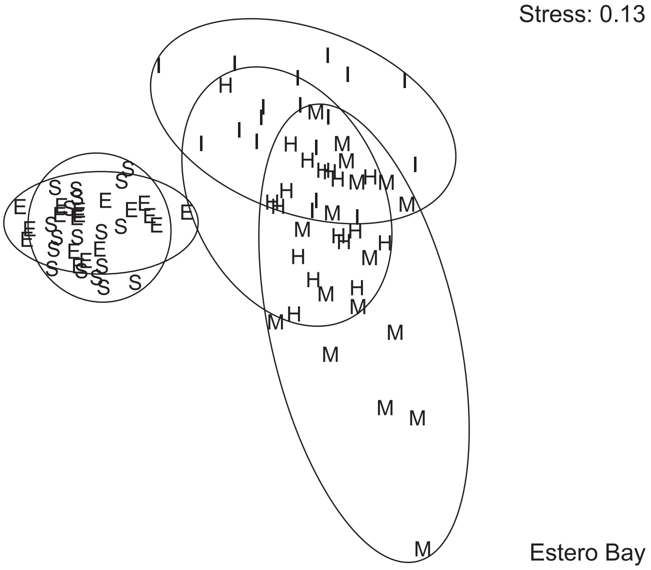

Fig. 5. Multidimensional scaling of samples collected near the mouths of Estero Bay tributaries (E = Estero River, H = Hendry Creek, I = Imperial River, M = Mullock Creek, S = Spring Creek). Samples from low freshwater inflow/higher salinity sites group together and are tightly packed compared to samples from low salinity and/or higher inflow sites.

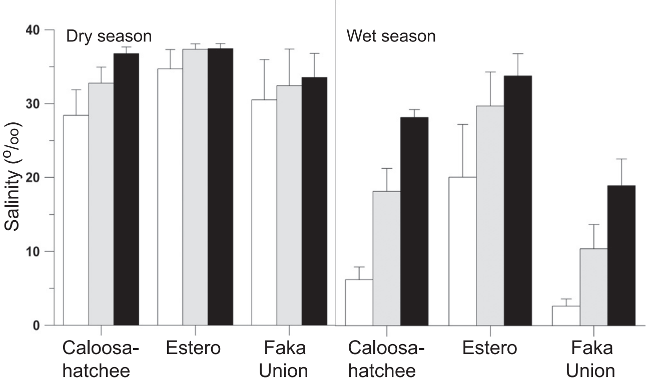

Fig. 6. Spatio-temporal differences in salinity at oyster reefs located along the salinity gradient of three Southwest Florida estuaries. Bars represent untransformed means and standard errors (stations: open = upper, hatched = middle, solid = lower).

Caloosahatchee and was higher at the lower station than at the upper station in Faka Union; however, these patterns were significant only during the wet season (Fig. 6). No among-station differences in salinity were detected in the Estero.

Water temperature measured during the longitudinal study was higher during the wet season (29.03 ± 0.60 °C) compared to dry months (27.25 ± 0.52 °C) (F[1,54] = 14.7, $p < 0.001$). No system, station, or interaction effects were detected.

Relative dispersion tended to increase upstream. Results of pairwise comparisons using the Index of Multivariate Dispersion suggested that within-station variability increased progressively upstream in Estero during the dry season and was greater at the upper station compared to those downstream during wet months (Table 4). In the Faka Union, among-sample variability increased progressively upstream regardless of season (Table 4). No clear trends were apparent in the Caloosahatchee: although the upper station was characterized by a greater degree of among-sample variability than the middle station during both seasons, this difference was only deemed to be significant for dry months (Table 4). Furthermore, among-sample variability was also high at the lower station during both seasons (Table 4).

3.3.2 Transverse study

One-way ANOVA revealed significant variation in salinity among sampling sites in Estero Bay (F[4,30] = 3.41, $p \leq 0.05$) with Estero River (22.91 ± 3.30‰) and Spring Creek (26.20 ± 3.07‰) values being significantly higher than those measured for Hendry (9.60 ± 3.28‰) and Mullock Creeks (9.97 ± 4.07‰). Salinities for the Imperial River site were intermediate (16.15 ± 5.25‰) and indistinguishable from values measured at the other sites. No significant among-site differences were detected for either water temperature (22.13–33.45 °C) or dissolved oxygen (3.0 - 9.67 mg L^{-1}). Mean freshwater inflow ($m^3 s^{-1}$) calculated for the entire sampling period was substantially higher for Mullock Creek (11.79 ± 15.75 $m^3 s^{-1}$) and the Imperial River (6.34 ± 5.98 $m^3 s^{-1}$) compared to the Estero River (1.84 ± 2.17 $m^3 s^{-1}$) and to Hendry (0.20 ± 0.39 $m^3 s^{-1}$) and Spring (0.45 ± 0.58 $m^3 s^{-1}$) Creeks.

Table 4. Relative dispersion (i.e., within-station multivariate variability) associated with oyster-reef communities at different locations along the salinity gradient of three estuaries (longitudinal sampling) or near the mouths of tidal tributaries within a single estuary (transverse sampling). Index of Multivariate Dispersion (IMD) was used in pairwise comparisons to identify differences in the degree of sample variability between stations.

Estuary	Season / Inflow	Station	Relative Dispersion	Pairwise Comparisons	IMD
Longitudinal Sampling					
Caloosahatchee	Dry	Upper	1.207	U, M	0.543
		Middle	0.601	U, L	0.085
		Lower	1.191	M, L	–0.664
	Wet	Upper	0.906	U, M	0.036
		Middle	0.873	U, L	–0.292
		Lower	1.193	M, L	–0.319
Estero	Dry	Upper	1.583	U, M	0.778
		Middle	0.990	U, L	0.986
		Lower	0.427	M, L	0.748
	Wet	Upper	1.432	U, M	0.716
		Middle	0.709	U, L	0.819
		Lower	0.661	M, L	0.011
Faka Union	Dry	Upper	1.536	U, M	0.671
		Middle	1.043	U, L	0.951
		Lower	0.422	M, L	0.801
	Wet	Upper	1.641	U, M	0.966
		Middle	0.831	U, L	0.975
		Lower	0.528	M, L	0.455
Transverse Sampling					
Estero	Low	Estero	0.731	EST, HEN	–0.401
	Low*	Hendry	1.117	EST, IMP	–0.505
	Low	Spring	0.721	EST, MUL	–0.438
	High	Imperial	1.242	EST, SPR	–0.023
	High	Mullock	1.214	HEN, IMP	–0.154
				HEN, MUL	–0.136
				HEN, SPR	0.446
				IMP, MUL	–0.016
				IMP, SPR	0.538
				MUL, SPR	0.458

* Although Hendry Creek receives little freshwater inflow, the lower portion of the watershed can experience reduced salinities due to the influence of the neighboring Mullock Creek.

Monthly salinity and freshwater inflow data were well correlated; however, data from Hendry Creek presented several outliers. The Hendry Creek site is notable in that though the creek itself receives little freshwater inflow, oyster reefs located at its mouth experience reduced salinities. This effect is due to the influence of freshwater discharge from the adjacent Mullock Creek and its tributary Ten-Mile Canal, discharge which backs up into the mouth of Hendry Creek creating low salinity conditions there during the rainy season. When Hendry Creek was removed from consideration, salinity was highly correlated with freshwater inflow with 95% of the variation in the data explained by the model (Fig. 7).

Correlation analysis using monthly data revealed a significant inverse relationship between relative dispersion and mean salinity of collection ($r = -0.54$, $p < 0.01$, $n = 30$) (Fig. 8a). The relationship between relative dispersion and inflow calculated for all stations was marginal ($p = 0.08$); however, when data from Hendry Creek were removed from consideration, relative dispersion varied positively with inflow ($r = 0.54$, $p < 0.01$, $n = 24$) (Fig. 8b). No relationship was detected between relative dispersion and either temperature or dissolved oxygen.

3.4 Community indicators

3.4.1 Longitudinal study

Similarity and dissimilarity percentages (SIMPER) were used to identify species within each estuary that typified a station or that could be used to discriminate among stations (Tables 5 and 6). In general, total similarity increased downstream suggesting that assemblages downstream were more

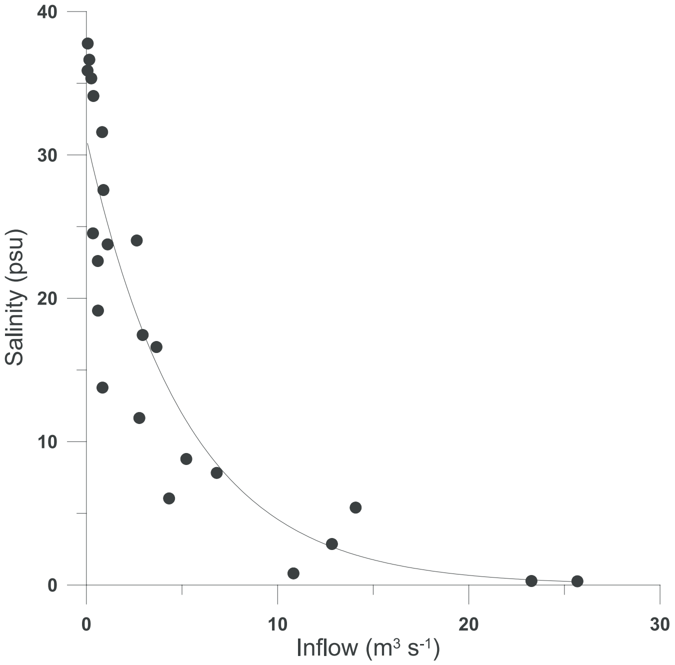

Fig. 7. Correlation between monthly salinity recorded at stations near the mouths of the five tidal tributaries of Estero Bay and inflow measured upstream ($r = -0.95$, $p < 0.001$, $n = 24$). Data from Hendry Creek were excluded because of the influence of the neighboring Mullock Creek on recorded salinities there.

distinct than those upstream (Table 5). Species typifying the upper station in the Caloosahatchee included *Eurypanopeus depressus* and *Gobiosoma robustum*; although *Gobiesox strumosus* was typical during dry months, this was not the case during the wet season (Table 5). In the Estero, the upper station was typified by *E. depressus* and *Lophogobius cyprinoides*; again, *G. strumosus* was typical of this station only during the dry season (Table 5). In the Faka Union, *E. depressus* typified the upper station but *L. cyprinoides* was typical only during the wet season. Both *Petrolisthes armatus* and *Panopeus obesus* typified the site during dry months.

Eurypanopeus depressus and *Petrolisthes armatus* were typical of both middle and lower stations in all three estuaries, regardless of season, but their relative roles were reversed with the euryhaline *E. depressus* usually being more abundant at the middle station and the marine stenohaline *P. armatus* being more abundant at the lower station.

The greatest among-station dissimilarity usually occurred between upper and lower stations regardless of estuary and season, and the least dissimilarity was consistently found between middle and lower stations (Table 6). Discriminating species included *Petrolisthes armatus*, which was normally absent upstream and could therefore be used to distinguish the upper station from those downstream and *Gobiosoma robustum* (Caloosahatchee) and *Panopeus obesus* (Estero and Faka Union), which could be used to distinguish assemblages at the middle and lower stations (Table 6). The latter two species were found in greater abundances at lower compared to middle stations.

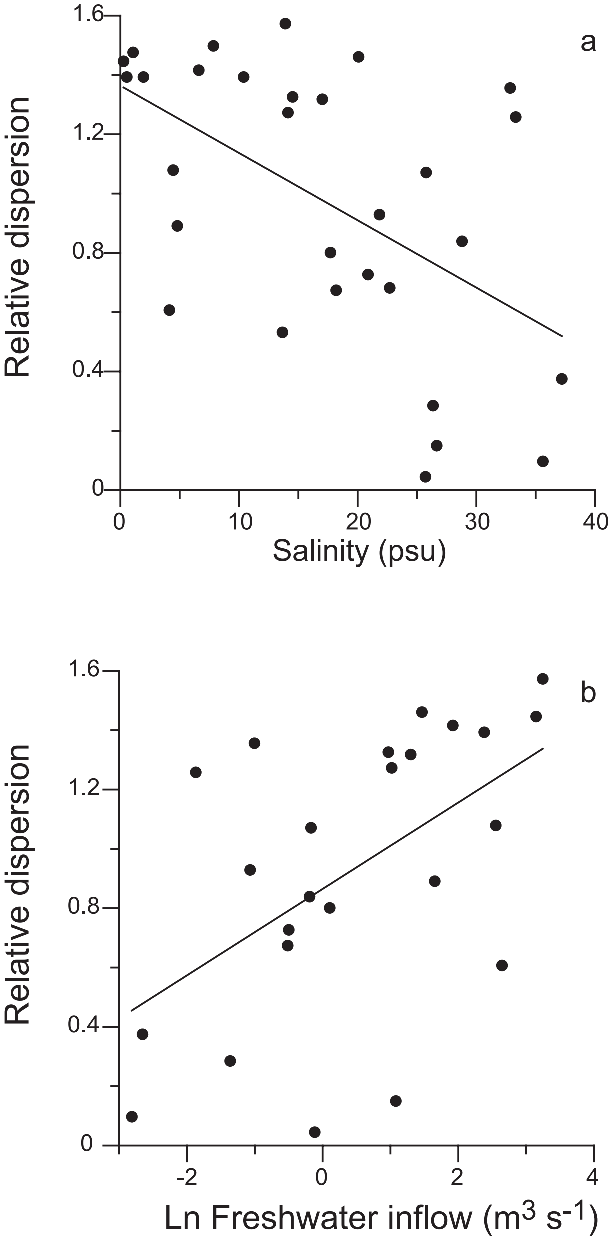

Fig. 8. Correlations between relative dispersion and (a) salinity of capture ($r = -0.54$, $p < 0.01$, $n = 30$) and (b) freshwater inflow measured upstream ($r = 0.54$, $p \leq 0.01$, $n = 24$). Dispersion was calculated using monthly samples collected near the mouths of the five tidal tributaries of Estero Bay.

3.4.2 Transverse study

Total similarity among samples (SIMPER) was greater for Estero River and Spring Creek sites than for Hendry Creek, Imperial River, or Mullock Creek sites (Table 7). Species typifying these sites included *Eurypanopeus depressus* (all sites), *Petrolisthes armatus* (Estero River and Spring Creek sites), *Lophogobius cyprinoides* and *Rhithropanopeus harrisii* (Hendry and Mullock Creeks) and *Gobiesox strumosus* and *Gobiosoma bosc* (Imperial River) (Table 7).

Table 5. Species contributions to similarity percentages of oyster-reef communities in three Southwest Florida estuaries. Only those species accounting for 90% of the cumulative similarity are included. Abundance is presented as individuals m^{-2}.

Estuary	Season	Station	Total similarity	Species	Average abundance	Average similarity	Contribution %	Cumulative %
Caloosahatchee	Dry	Upper	61.4	*E. depressus*	50.4	38.0	61.8	61.8
				G. robustum	5.4	13.4	21.7	83.5
				G. strumosus	1.4	4.7	7.7	91.2
		Middle	74.3	*E. depressus*	68.2	27.9	37.6	37.6
				P. armatus	11.1	17.3	23.3	60.9
				P. obesus	4.1	13.4	18.0	78.9
				G. robustum	1.7	4.2	5.7	84.6
				G. strumosus	1.4	4.1	5.5	90.1
		Lower	70.2	*P. armatus*	28.0	13.6	19.4	19.4
				E. depressus	23.1	13.4	19.1	38.5
				A. heterochaelis	4.3	8.1	11.5	50.0
				O. beta	2.3	7.2	10.3	60.3
				G. robustum	6.1	6.4	9.1	69.4
				P. obesus	2.6	5.8	8.2	77.6
				M. mercenaria	1.8	3.1	4.4	82.0
				C. saburrae	0.9	2.7	3.8	85.8
				P. lacustris	0.9	2.5	3.6	89.4
				G. strumosus	1.2	1.9	2.7	92.1
	Wet	Upper	68.5	*E. depressus*	100.7	44.7	65.2	65.2
				G. robustum	3.3	17.8	26.0	91.2
		Middle	74.5	*E. depressus*	99.6	25.2	33.9	33.9
				P. armatus	29.5	18.4	24.7	58.6
				C. saburrae	3.0	9.0	12.2	70.8
				P. obesus	1.6	6.6	8.8	79.6
				G. strumosus	1.2	6.1	8.2	87.8
				A. heterochaelis	1.4	2.9	3.9	91.7
		Lower	71.3	*P. armatus*	97.2	25.0	35.0	35.0
				E. depressus	61.8	22.8	32.0	67.0
				P. obesus	2.6	7.8	10.9	77.9
				A. heterochaelis	3.6	5.9	8.3	86.2
				G. robustum	2.6	4.2	5.9	92.1
Estero	Dry	Upper	60.7	*E. depressus*	14.9	26.2	43.2	43.2
				L. cyprinoides	4.2	14.8	24.4	67.6
				G. strumosus	0.8	8.0	13.2	80.8
				P. obesus	1.9	6.4	10.5	91.3
		Middle	74.1	*E. depressus*	50.4	33.0	44.5	44.5
				P. armatus	39.0	28.2	38.0	82.5
				O. beta	1.0	5.1	6.9	89.4
				A. heterochaelis	0.9	3.6	4.9	94.3
		Lower	83.3	*P. armatus*	92.8	33.4	40.2	40.2
				E. depressus	50.7	29.1	34.9	75.1
				P. obesus	7.6	16.8	20.2	95.3
	Wet	Upper	65.8	*E. depressus*	20.7	34.9	53.1	53.1
				L. cyprinoides	8.2	24.6	37.3	90.4
		Middle	79.2	*P. armatus*	191.0	34.0	43.0	43.0
				E. depressus	114.4	31.0	39.2	82.2
				P. obesus	2.2	11.6	14.6	96.8
		Lower	79.2	*P. armatus*	130.7	35.1	44.4	44.4
				E. depressus	66.2	28.5	36.0	80.4
				P. obesus	5.2	13.4	17.0	97.4
Faka Union	Dry	Upper	44.6	*E. depressus*	7.4	26.9	60.3	60.3
				P. armatus	5.9	7.0	15.8	76.1
				P. obesus	1.1	5.0	11.2	87.3
				G. robustum	0.6	2.0	4.4	91.7
		Middle	61.4	*E. depressus*	75.3	30.9	50.3	50.3
				P. armatus	61.6	19.9	32.3	82.6
				G. strumosus	2.4	2.9	4.7	87.3
				L. dubia	0.6	1.7	2.7	90.0
		Lower	82.4	*P. armatus*	138.8	34.7	42.2	42.2
				E. depressus	43.8	26.5	32.2	74.4
				P. obesus	14.2	20.4	24.8	99.2
	Wet	Upper	50.6	*E. depressus*	12.0	31.1	61.4	61.4
				L. cyprinoides	0.7	8.0	15.8	77.2
				G. robustum	2.1	3.3	6.4	83.6
				G. strumosus	0.7	2.5	5.0	88.6
				O. beta	0.3	1.8	3.6	92.2
		Middle	72.2	*E. depressus*	107.9	34.7	48.0	48.0
				P. armatus	62.6	28.8	39.9	87.9
				P. obesus	1.2	2.9	4.0	91.9
		Lower	81.4	*P. armatus*	301.9	36.0	44.2	44.2
				E. depressus	91.3	26.3	32.3	76.5
				P. obesus	8.0	13.8	16.9	93.4

Table 6. Dissimilarity among stations of oyster-reef commensals in Southwest Florida estuaries. Station: U = upper, M = middle, L = lower. Abundance is presented as individuals m^{-2}. Only those species accounting for 50% of the cumulative dissimilarity are included.

Estuary	Season	Station	Total dissimilarity	Species	Average abundance		Average dissimilarity	Contribution %	Cumulative %
					Group 1	Group 2			
Caloosahatchee	Dry	U-M	49.5	*P. armatus*	0.0	11.1	11.0	22.3	22.3
				P. obesus	0.0	4.1	8.6	17.4	39.7
				G. robustum	5.4	1.7	4.7	9.6	49.3
				A. heterochaelis	1.0	1.8	4.2	8.4	57.7
		U-L	58.0	*P. armatus*	0.0	28.0	10.3	17.7	17.7
				P. obesus	0.0	2.6	5.1	8.7	26.4
				A. heterochaelis	1.0	4.3	4.2	7.3	33.7
				O. beta	0.7	2.3	4.0	7.0	40.7
				M. mercenaria	0.0	1.8	3.7	6.3	47.0
				P. lacustris	0.0	0.9	3.0	5.2	52.2
		M-L	38.9	*M. mercenaria*	0.0	1.8	3.2	8.3	8.3
				G. robustum	1.7	6.1	3.2	8.1	16.4
				A. heterochaelis	1.8	4.3	3.0	7.8	24.2
				E. depressus	68.2	23.1	2.7	7.0	31.2
				C. saburrae	1.1	0.9	2.7	7.0	38.2
				P. lacustris	0.0	0.9	2.7	6.9	45.1
				O. beta	1.1	2.3	2.7	6.8	51.9
	Wet	U-M	51.3	*P. armatus*	0.0	29.5	12.5	24.3	24.3
				C. saburrae	0.2	3.0	6.0	11.7	36.0
				G. robustum	3.3	0.9	5.1	9.9	45.9
				P. obesus	0.1	1.6	4.8	9.4	55.3
		U-L	52.2	*P. armatus*	0.0	97.2	17.2	33.0	33.0
				P. obesus	0.1	2.6	5.7	10.9	43.9
				A. heterochaelis	0.9	3.6	4.8	9.2	53.1
		M-L	31.4	*P. armatus*	29.5	97.2	3.4	10.8	10.8
				G. robustum	0.9	2.6	3.3	10.6	21.4
				A. heterochaelis	1.4	3.6	3.1	9.9	31.3
				C. saburrae	3.0	1.9	3.1	9.8	41.1
				G. strumosus	1.2	1.2	3.0	9.4	50.5
Estero	Dry	U-M	57.6	*P. armatus*	0.1	39.0	15.8	27.4	27.4
				L. cyprinoides	4.2	0.0	8.8	15.2	42.6
				O. beta	1.2	1.0	4.9	8.6	51.2
		U-L	61.8	*P. armatus*	0.1	92.8	18.9	30.6	30.6
				L. cyprinoides	4.2	0.0	8.1	13.1	43.7
				P. obesus	1.9	7.6	5.3	8.5	52.2
		M-L	29.9	*P. obesus*	1.3	7.6	6.0	20.0	20.0
				P. armatus	39.0	92.8	4.2	14.2	34.2
				O. beta	1.0	0.0	4.2	14.2	48.4
				A. heterochaelis	0.9	0.6	3.7	12.5	60.9
	Wet	U-M	62.0	*P. armatus*	0.9	191.0	21.3	34.4	34.4
				L. cyprinoides	8.2	0.0	10.2	16.5	50.9
		U-L	62.0	*P. armatus*	0.9	130.7	20.4	32.9	32.9
				L. cyprinoides	8.2	0.0	10.5	17.0	49.9
				P. obesus	0.3	5.2	7.5	12.1	62.0
		M-L	21.9	*A. heterochaelis*	2.1	0.5	3.2	14.9	14.9
				Eucinostomus sp.	1.1	2.3	3.2	14.6	29.5
				E. depressus	114.4	66.2	2.3	10.4	39.9
				M. mercenaria	0.0	0.7	2.0	9.0	48.9
				P. armatus	191.0	130.7	1.9	8.6	57.5
Faka Union	Dry	U-M	55.3	*P. armatus*	5.9	61.6	11.1	20.1	20.1
				E. depressus	7.4	75.3	9.2	16.6	36.7
				G. strumosus	0.9	2.4	4.6	8.4	45.1
				P. obesus	1.1	0.6	4.2	7.7	52.8
		U-L	55.0	*P. armatus*	5.9	138.8	17.1	31.1	31.1
				P. obesus	1.1	14.2	8.9	16.2	47.3
				E. depressus	7.4	43.8	6.5	11.8	59.1
		M-L	39.4	*P. obesus*	0.6	14.2	8.3	21.1	21.1
				P. armatus	61.6	138.8	6.4	16.4	37.5
				G. strumosus	2.4	0.0	3.7	9.4	46.9
				G. robustum	1.2	0.1	2.7	6.9	53.8
	Wet	U-M	67.3	*P. armatus*	0.0	62.6	19.6	29.0	29.0
				E. depressus	12.0	107.9	9.8	14.6	43.6
				L. cyprinoides	0.7	0.0	4.8	7.1	50.7
		U-L	72.2	*P. armatus*	0.0	301.9	25.4	35.2	35.2
				P. obesus	0.0	8.0	10.1	13.9	49.1
				E. depressus	12.0	91.3	7.6	10.4	59.5
		M-L	31.1	*P. armatus*	62.6	301.9	6.8	22.0	22.0
				P. obesus	1.2	8.0	5.2	16.8	38.8
				A. heterochaelis	0.4	2.2	3.7	11.8	50.6

Table 7. Species contributions to similarity percentages of oyster-reef communities in Estero Bay. Abundance is presented as individuals 0.5 m^{-2}. Only those species accounting for 90% of the total similarity are included.

Station	Total	Species	Average abundance	Average similarity	Contribution %	Cumulative %
Estero	67.0	*E. depressus*	76.7	29.4	43.8	43.8
		P. armatus	25.1	21.5	32.1	75.9
		A. heterochaelis	4.4	8.8	13.1	89.0
		M. mercenaria	0.8	2.0	3.0	92.0
Hendry	57.8	*E. depressus*	24.2	44.5	77.1	77.1
		L. cyprinoides	1.1	5.7	9.8	86.9
		R. harrisii	1.8	2.2	3.8	90.7
Imperial	59.3	*E. depressus*	27.5	38.6	65.1	65.1
		G. strumosus	3.6	14.5	24.5	89.6
		G. bosc	1.0	3.3	5.6	95.2
Mullock	60.8	*E. depressus*	17.8	33.4	55.0	55.0
		L. cyprinoides	3.3	17.6	28.9	83.9
		R. harrisii	7.0	7.6	12.4	96.3
Spring	81.4	*E. depressus*	66.6	25.9	39.7	39.7
		P. armatus	28.2	20.5	31.5	71.2
		A. heterochaelis	3.7	8.0	12.3	83.5
		Panopeus spp.	1.3	3.0	4.5	88.0
		P. simpsoni	0.9	1.7	2.6	90.6

Greatest dissimilarity occurred when samples from Estero River or Spring Creek – the two high salinity sites – were compared with those from any of the other sites (Table 8). Comparison of Estero River and Spring Creek samples yielded the lowest degree of dissimilarity (34.5).

4 Discussion

The results of this study suggest that assemblages of fishes and decapod crustaceans inhabiting Southwest Florida oyster reefs are shaped partly by salinity, with distinct communities occurring at different locations along the salinity gradient of individual estuaries as well as at the mouths of tidal tributaries experiencing different levels of freshwater inflow. Even though differences in community structure are greatest during wet months, when the salinity gradient is more fully expressed, these differences are also apparent in the dry season. In the analysis of samples collected along the salinity gradients of all three estuaries, the greatest among-station segregation occurred between upper stations and those downstream, which tended to group together and exhibit considerable overlap in ordination space. Salinity gradients have previously been identified as important spatial determinants of community structure in fishes and macroinvertebrates. Weinstein et al. (1980), examining marine nekton in coastal marsh habitats, Ysebaert and Herman (2002), examining benthic macrofauna, and Jaureguizar et al. (2004), examining fish communities, all concluded that the estuarine salinity gradient present played an important role in shaping community structure. More specifically, Gorzelany (1986) noted a "nearshore/offshore trend" in oyster reef communities, with samples collected from nearshore stations in different estuaries being more similar to one another than were samples collected from nearshore and offshore stations within the same estuary: this trend was attributed to observed differences in salinity. In contrast, the influence of salinity may be less important than depth and sediment characteristics (i.e., silt-clay content, total organic carbon, and xenobiotic contaminants) in structuring benthic infaunal communities (McRae et al. 1998).

In a comparison of oyster reefs occurring near the mouths of Estero Bay's tidal tributaries, assemblages of fishes and decapods at sites associated with lower freshwater inflow and higher salinities (Estero River, Spring Creek) were distinct from those experiencing higher freshwater inflow and/or lower salinities (Hendry and Mullock Creeks, Imperial River). Tsou and Matheson (2002) suggested that cyclical patterns in community structure observed in the Suwannee River estuary were related in part to seasonality in river discharge, and studies have documented changes in estuarine communities resulting from increased rainfall associated with El Niño events (Garcia et al. 2004) and tropical weather systems (Boesch et al. 1976).

Eby and Crowder (2004) explained spatial variation in community structure of estuarine nekton in terms of gradients in dissolved oxygen. Lenihan et al. (2001) noted that hypoxic or anoxic conditions were not only responsible for increased mortality of crustaceans inhabiting oyster reefs of limited vertical relief but also for an influx of fishes onto reefs of high vertical relief to escape oxygen stress. Both of these effects would alter oyster-reef community structure. Dissolved oxygen data were not analyzed from the longitudinal study and no significant among-site variation in dissolved oxygen concentration was detected in the transverse data; it is therefore unclear from this study what role oxygen might play in structuring communities occurring on shallow, intertidal oyster reefs in Southwest Florida.

Salinity is an important factor influencing the physiology of estuarine organisms; therefore, changes in isohaline position can restructure the assemblages of organisms present (Sklar and Browder 1998). Ritter et al. (2005) proposed that salinity tolerance was primarily responsible for species replacement and succession following high inflow events in the

Table 8. Dissimilarity among stations of oyster-reef commensals in Estero Bay. Stations: EST = Estero River, HEN = Hendry Creek, IMP = Imperial River, MUL = Mullock Creek, and SPR = Spring Creek. Abundance is presented as individuals 0.5 m^{-2}. Only those species accounting for 50% of the cumulative dissimilarity are included.

Station	Total dissimilarity	Species	Average abundance		Average dissimilarity	Contribution %	Cumulative %
			Group 1	Group 2			
EST-HEN	63.0	*P. armatus*	25.1	0.0	15.6	24.7	24.7
		A. heterochaelis	4.4	0.0	8.2	13.1	37.8
		E. depressus	76.7	24.2	4.9	7.8	45.6
		L. cyprinoides	0.3	1.1	4.4	7.0	52.6
EST-IMP	62.7	*P. armatus*	25.1	0.0	15.1	24.0	24.0
		G. strumosus	0.0	3.6	7.6	12.2	36.2
		A. heterochaelis	4.4	0.3	6.9	11.0	47.2
		E. depressus	76.7	27.5	5.0	8.0	55.2
HEN-IMP	47.7	*G. strumosus*	0.6	3.6	8.8	18.5	18.5
		L. cyprinoides	1.1	0.0	6.0	12.6	31.1
		G. bosc	0.4	1.0	5.4	11.3	42.4
		R. harrisii	1.8	0.2	5.1	10.8	53.2
EST-MUL	69.1	*P. armatus*	25.1	0.0	15.3	22.2	22.2
		A. heterochaelis	4.4	0.0	8.1	11.8	34.0
		L. cyprinoides	0.3	3.3	7.4	10.6	44.6
		E. depressus	79.7	17.8	6.9	9.9	54.5
HEN-MUL	43.6	*R. harrisii*	1.8	7.0	9.5	21.8	21.8
		L. cyprinoides	1.1	3.3	7.7	17.6	39.4
		G. strumosus	0.6	0.4	4.7	10.9	50.3
IMP-MUL	55.5	*L. cyprinoides*	0.0	3.3	11.3	20.3	20.3
		G. strumosus	3.6	0.4	9.2	16.5	36.8
		R. harrisii	0.2	7.0	9.0	16.1	52.9
EST-SPR	34.5	*A. heterochaelis*	4.4	3.7	3.2	9.2	9.2
		Panopeus spp.	0.4	1.3	3.2	9.2	18.4
		M. mercenaria	0.8	0.6	2.9	8.3	26.7
		P. simpsoni	0.3	0.9	2.7	7.9	34.6
		O. beta	0.6	0.2	2.4	7.1	41.7
		L. cyprinoides	0.3	0.7	2.4	6.9	48.6
		G. robustum	0.2	0.7	2.2	6.4	55.0
HEN-SPR	63.3	*P. armatus*	0.0	28.2	15.0	23.7	23.7
		A. heterochaelis	0.0	3.7	7.5	11.8	35.5
		E. depressus	24.2	66.6	4.2	6.7	42.2
		Panopeus spp.	0.4	1.3	4.1	6.5	48.7
		L. cyprinoides	1.1	0.7	4.0	6.3	55.0
IMP-SPR	63.4	*P. armatus*	0.0	28.2	14.6	22.9	22.9
		G. strumosus	3.6	0.2	6.3	9.9	32.8
		A. heterochaelis	0.3	3.7	6.2	9.8	42.6
		E. depressus	27.5	66.6	4.3	6.8	49.4
		Panopeus spp.	0.3	1.3	4.1	6.4	55.8
MUL-SPR	68.6	*P. armatus*	0.0	28.2	14.8	21.5	21.5
		A. heterochaelis	0.0	3.7	7.4	10.7	32.2
		E. depressus	17.8	66.6	6.0	8.8	41.0
		R. harrisii	7.0	0.0	6.0	8.7	49.7
		L. cyprinoides	3.3	0.7	5.6	8.2	57.9

Rincon Bayou, Texas, and Wells (1961) suggested that reduced salinities limit the upstream distribution of the majority of species found in association with oyster reefs. Though many estuarine species are broadly euryhaline, their distributions may be limited. *Rhithropanopeus harrisii* occurs primarily in the upper reaches of the estuary (Ryan 1956) and was found primarily during the wet season either upstream or at low salinity sites in the current study. In contrast, Shumway (1983) noted that though *Panopeus herbstii* is tolerant of reduced salinities it primarily occurs at higher salinities. No *P. herbstii* were collected as part of the current study; however the congener *P. obesus* exhibited a similar distribution with densities increasing downstream. A dominant resident of Southwest Florida oyster reefs is the porcellanid *Petrolisthes armatus*, a stenohaline species with limited tolerance to reduced salinities (Shumway 1983). This species was only rarely found at the upper stations during longitudinal sampling, and only in limited numbers when it did occur there, and was absent from low salinity sites during transverse sampling of Estero Bay.

Increased energetic costs and declines in performance resulting from reduced salinities have been reported for estuarine species (e.g., Pérez-Pinzón and Lutz 1991; McGaw and Reiber 1998; Anger et al. 2000). Any avoidance of low salinity habitats due to such penalties would be expected to affect community structure both spatially and temporally, when the sites are impacted by pulses of freshwater. Previous work examining salinity tolerance of *Eurypanopeus depressus*, *Rhithropanopeus harrisii*, and *Panopeus herbstii* (a congener of the *Panopeus* species collected in the current study) suggests that the dominant xanthids present on Southwest Florida oyster reefs are hyperosmotic regulators at reduced salinities and osmoconformers at higher salinities. This switch in osmoregulation occurs at estimated salinities of 15‰, 27‰, and 28‰for *R. harrisii* (Reisser and Forward 1991), *E. depressus* (Shirley and McKenney 1981) and *P. herbstii* (Blasco and Forward 1988), respectively. Furthermore, oxygen consumption rates increase with decreasing salinities for the xanthids *P. herbstii* (Dimock and Groves 1975; Shumway 1983) and *E. depressus* (Walls 2006) and for the porcellanid *Petrolisthes armatus* (Shumway 1983). Even if adult oyster-reef residents are able to tolerate reduced salinities, potential impacts exist for developing larvae. Costlow et al. (1962) reported both decreased survival and increased period of larval development for *P. herbstii* zoea reared at reduced salinities. Any reduction in larval survival resulting directly or indirectly from reduced salinities would impact recruitment of larvae to oyster reefs, potentially altering community structure.

Increased freshwater inflow might also act indirectly to influence oyster-reef communities by altering the nature of the oyster-reef habitat itself. May (1972) noted significant oyster mortality in the field when salinity dropped below 2‰ for a period of weeks, and La Peyre et al. (2003) reported that cumulative mortality in the laboratory was higher during the summer for oysters exposed to freshets (0–1‰) compared to control oysters (20‰). May (1972) further noted reduced oyster densities on reefs in upper Mobile Bay, which is subjected to severe freshets, compared to those downstream, and Tolley et al. (2005) reported reduced oyster densities at lower salinity sites upstream in two Southwest Florida estuaries that experience high seasonal freshwater inflow. In contrast, Bergquist et al. (2006) reported that percent cover and oyster density were negatively correlated with salinity in the Suwannee River and suggested that increased predation and incidence of parasitism associated with higher salinities were responsible. Thus, depending on the estuary, the development of oyster-reef habitat is likely best at sites experiencing intermediate salinities where oyster growth and survival are optimal. These results suggest that reduced salinities, occurring upstream or as a result of high freshwater inflow, have the potential to alter the habitat value of oyster reefs for commensal organisms by increasing oyster mortality and reducing oyster density. Such changes would not only affect microhabitat within oyster clusters (e.g., availability of oyster boxes) but also increase the patchiness of oyster reef habitat.

Biotic factors may work together with salinity to shape spatial and seasonal distributions of some species. As noted previously, *Rhithropanopeus harrisii* is a euryhaline xanthid normally found in waters of reduced salinity. This species is host to the rhizocephalan parasite *Loxothylacus panopaei*, which can inhibit host reproduction through sterilization and feminization. Reisser and Forward (1991) proposed that "salinity tolerance of parasite larvae controlled the parasite's distribution" and that host crabs might find reproductive refuge at salinities < 10 or > 15‰. Walker and Clare (1994) provided additional evidence supporting a low-salinity refuge from parasite infestation but their work did not support the hypothesized refuge at > 15‰. These studies suggest that the distribution of *R. harrisii* in the upper reaches of the estuary may in part be an adaptive response to higher rates of parasite infestation and ultimately to reduced reproductive potential occurring in more saline waters downstream.

Variation in multivariate structure itself has been suggested as an indicator of environmental stress. Warwick and Clarke (1993), in a meta-analysis of environmental impact studies, found that samples from impacted sites exhibited greater among-replicate differences (relative dispersion) than those from control sites; Warwick et al. (1997) attributed between-site differences in community structure to the presence of a reef-building mussel, which they proposed was acting to stress the associated nematode assemblage; Hoffmeyer (2004) noted a difference in multivariate structure among samples collected ten years apart and credited the increased multivariate variability or "decrease in community stability" to environmental disturbance occurring subsequent to the initial sampling; Levin et al. (2000) found increased multivariate variability in samples of macrobenthos collected below the oxygen minimum zone in the Arabian Sea; and Boyd et al. (2004) reported "greater variability in community composition" associated with samples taken from areas that had been intensely dredged. Other investigators have found no such link between multivariate variability and environmental stress or disturbance (Chapman et al. 1995; Kaiser and Spencer 1996; Vopel and Thiel 2001; Chou et al. 2002; Kreutzweiser et al. 2005).

In the present study, multidimensional scaling indicated increased variation, at least seasonally, among samples associated with oyster-reef communities experiencing low salinities and/or high-freshwater inflow. Supporting this interpretation, relative dispersion was significantly greater at upper stations compared to those downstream in the longitudinal analysis of the Estero and Faka Union estuaries. Furthermore, relative dispersion calculated for samples collected at the mouths of each of the tidal tributaries emptying into Estero Bay was inversely correlated with mean salinity and positively related to freshwater inflow.

Patterns of variability in multivariate structure suggest that reduced salinities might act not only to shape oyster-reef communities but also to stress communities at sites that experience high levels of freshwater inflow. It is not clear by which mechanism(s) multivariate variability may increase in response to higher levels of freshwater inflow, but several possibilities exist. First, Levin et al. (2000) proposed that reduced macrofaunal densities below the oxygen minimum zone may explain the higher relative dispersion calculated for samples collected there. Organism density in the current study was lower upstream in all three estuaries (see also Tolley et al. 2005) and near the mouths of tidal tributaries in Estero Bay that experience high freshwater inflow. Second, lower salinity may favor species exhibiting inherently greater variance to mean ratios representing more highly aggregated spatial distributions. Variance to mean ratios were calculated for oyster-reef organisms collected in Estero Bay: of the seven species exhibiting variance to mean ratios > 1, four were found predominantly at low salinity/high inflow sites (*R. harrisii*, *G. strumosus*, *G. bosc*, *L. cyprinoides*) and one, though found more abundantly at higher salinity sites, was common at stations experiencing reduced salinities (*E. depressus*). Last, Eggleston et al. (1999) found that "estuarine macrofauna respond to habitat heterogeneity at relatively small spatial scales (0.25-1 m^2)" and cautioned that high among-sample variability characteristic of many studies on oyster-reef commensals may partly be a function of sampling scale. Although heterogeneity of oyster habitat within lift nets (i.e., relative spacing and volume of oyster clusters) was manipulated to be similar among stations in the present study, fragmentation of surrounding oyster habitat in response to increased freshwater inflow and any concomitant changes in the patchiness of associated organisms could result in variable recruitment between natural oyster habitat and the sampling gear. Both habitat cover and configuration are known to influence organism abundance (Villard et al. 1999; Hovel 2003), and Eggleston et al. (1999) suggested that macrofauna may be particularly sensitive to fragmentation of oyster shell habitat compared to seagrass or a mixture of oyster shell and seagrass.

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