SPATIAL TRENDS IN COMMUNITY AND HEALTH-RELATED CHARACTERISTICS OF GALVESTON BAY OYSTER REEFS

A Thesis

bу

JUNGGEUN SONG

Submitted to the Office of Graduate Studies of Texas A&M University in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

May 1994

Major Subject: Oceanography

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ABSTRACT

Spatial Trends in Community and Health-Related Characteristics of Galveston Bay Oyster Reefs. (May 1994) Junggeun Song, B.S., Inha University Chair of Advisory Committee: Dr. Eric N. Powell

The spatial trends in the oyster community and healthrelated variables for Galveston Bay oyster reefs indicated that some other factors in addition to salinity are major structuring forces. Three different directional trends were found including one diametric to salinity. Cluster analyses, taking into account all measured variables, produced groupings primarily defined by salinity, and secondarily by region along the salinity gradient. Comparison of Perkinsus marinus analyses by the standard thioglycollate method and by the whole body count method showed that the standard method produced false negatives in many samples taken throughout the bay, probably due to low infection intensities associated with low salinity at the time of collection. Even after correcting for the false negatives, average Perkinsus marinus prevalence for the bay was unusually low (52.6%) compared to previous studies. Examination of different ovster size classes is important for the best estimate of P. marinus infection intensity and prevalence. Based on the variables directly related to oyster health and production, four

regions: the Redfish Bar area, the Yacht Club Reef area, the Dickinson Embayment, and the Houston Ship Channel, maintained the healthiest oyster populations in terms of density, biomass, and gonadal state. Sites at the extremes of the salinity range such as in Trinity Bay, upper East Bay, and West Bay were characterized by oyster populations in poorer condition.

DEDICATION

I would like to dedicate this thesis to my son, Brian Song, and to my wife, Carol Kwan. I love you with all my heart.

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INTRODUCTION

Oyster reefs are one of the most distinctive features in Galveston Bay. These reefs produce more than 75% of the Texas ovster harvest in most years (Hofstetter 1983) and provide a suitable habitat for a variety of associated fauna. Major factors affecting oyster production are salinity, temperature, food supply, disease, predation, and recruitment. The optimal salinity range for oysters is between 10 and 20 ppt (Butler 1954). Oysters at lower salinity can be plagued by freshwater kills and siltation whereas higher salinity exposes oysters to predation and disease (Ray 1987). The salinity regime in Galveston Bay is primarily determined by freshwater inflow from the Trinity River and the circulation pattern. Two important man-made structures, the Houston Ship Channel and the Texas City Dike, modify this circulation pattern. In contrast to Trinity Bay, where floodinduced fresh-water inflow directly affects oyster productivity, West Bay remains high in salinity even during flood periods because the Gulf water input from offshore and the Texas City Dike act as a barrier against lower-salinity inflow from the upper reaches of the bay.

Perkinsus marinus is a major parasite of Crassostrea virginica in the Gulf coast, being responsible for reduced growth, low fecundity (Mackin 1962), high mortality (Hofstetter 1977), and

This thesis follows the style and format of Journal of Shellfish Research.

changes in biochemical composition (Soniat and Koenig 1982). *P.* marinus infection intensity is a primary determinant of the health of oyster reefs. Since the parasite's growth is accelerated by high temperature and salinity (Mackin 1955), and since the salinity gradient is complex in the bay system, infection intensity and the effect of *P. marinus* in oyster populations can be expected to be locally variable throughout the bay.

Moreover, the effects of salinity may be offset or aggravated by other factors such as food availability and recruitment which may affect the population in a more complex way within or between different salinity ranges. Standing stocks of phytoplankton, the primary food source for oyster populations in the bay, have decreased over the last 20 years (Ward and Armstrong 1992), and oyster populations can decline rapidly in response to declining food supplies as reproductive activity declines and P. marinus infection increases (Powell et al. submitted a). Bathymetric features such as the Houston Ship Channel and its spoil banks also regulate the food availability as well as turbidity and current flow (Powell et al. submitted b), all of which affect both the parasite and its host. A flood, which kept salinity low on most reefs for several months prior to sampling for this study, offered an opportunity to estimate the effects of salinity and disease on population health.

The study was a component of a larger effort to define the aereal extent, relief and viability of Galveston Bay oyster reefs. This study provided the opportunity to determine the spatial trends in comunity and health-related parameters in Galveston Bay oyster populations.

The present study includes the following objectives;

1. To evaluate two different methods of P. marinus prevalence.

2. To examine spatial trends of community-related attributes such as competitors, predators, endobionts, and epibionts.

3. To examine spatial trends of health-related attributes such as size-frequency composition, *P. marinus* prevalence and infection intensity, and gonadal state.

4. To evaluate the effects of flood-induced low salinity on the population and community structure of oyster reefs.

5. To evaluate the condition of oyster populations at the level of community and the individual.

LITERATURE REVIEW

Since the first description of P. marinus by Mackin et al. (1950), numerous studies have shown the protozoan to be the most destructive parasite of oysters in the Gulf of Mexico, and to be widely distributed throughout the Gulf coast. Many studies of the parasite have focused on Galveston Bay, the major harvest area of Texas oysters (Hofstetter 1983). Salinity and temperature are the most important factors affecting the distribution, incidence and infection intensity of the parasite. Higher salinity and temperature are preferred by the parasite. According to Hofstetter (1977), the highest infection intensity occurred at salinities between 21 and 25 ppt and some decline in infection intensity occurred at salinities of 26 to 30 ppt but this was likely due to increased adult mortality at higher salinity. P. marinus requires salinities above 12 to 15 ppt for its proliferative development. Even though lower salinities alone reduce infection intensity, they do not eliminate the parasite from oysters. According to Fisher et al. (1992), temperature was more influential than salinity in controlling P. marinus intensity and oyster mortality, although both environmental factors are undoubtedly important.

The transmission of the parasite has been explained in three ways; (a) proximity transfer which was tested by placing both healthy and infected oysters at varying distances from one another (Andrews 1965, 1967), (b) transfer by feeding, in which

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minced tissues of infected oyster were included in ambient water (Ray 1954), and (c) transfer of the parasite by oyster ectoparasites, *Boonea impressa* (White *et al.* 1987).

The development of the fluid thioglycollate technique (Ray 1966), together with Mackin's numerical scale (Mackin 1962), provided a standard assay method for the prevalence and infection intensity of the parasite. The standard method based on the examination of a piece of mantle or rectal tissue, however, is not fully quantitative, and often fails to reveal the infection if infection intensity is very low.

Several modifications of Ray's standard method have been made to solve these two drawbacks. Gauthier & Fisher (1990) evaluated the disease intensity by counting hypnospores of P. marinus collected from oyster hemolymph incubated in thioglycollate medium. Since hemolymph can be collected without sacrificing oysters, this method can be useful for time-series experiments. Choi *et al.* (1989) used whole oyster tissue incubated in thioglycollate medium instead of a small piece of mantle tissue, and dissolved the tissues with sodium hydroxide. Both methods provided more quantitative and accurate measurements than the standard examination of mantle tissue. Also, attempts have been made to identify and quantify the parasite using polyclonal antibodies from hypnospores (Choi *et al.* 1991).

Oysters develop a layer of creamy-white gonad on the surface of the body in early spring, and spawn from late spring to early fall. Since reproduction requires considerable energy, a change in reproductive effort (the fraction of net production allocated to reproduction) can be closely related to the effects of changes in environmental conditions such as temperature, food availability, salinity, and parasitism (Hofmann *et al.* in press).

Since it is difficult to separate the gonad from other parts of the oyster body mass, several different methods have been used to evaluate reproductive condition and reproductive effort in oysters. Histological sectioning has been used to determine the state of gonadal development using a semi-quantitative scale (Kennedy and Krantz 1982, Morales-Alamo and Mann 1989). Gonadal index, calculated from gonadal thickness and the diameter of the adductor muscle, was used to estimate gonadal condition (Soniat and Ray 1985, Soniat *et al.* 1989). Even though the oyster size is also considered, the index is not very accurate because of the uneven thickness of the gonadal layer in section. An immunological approach was developed by Choi *et al.* (1993) to quantitatively measure reproductive effort in oysters. This method uses polyclonal antibodies against oyster egg and sperm.

Very few community-based studies have been carried out on oyster reefs in the Galveston Bay system. Soniat *et al.* (1989) evaluated mortality and condition in Galveston Bay oysters from sixteen sites. Hofstetter (1977, 1983) reported general oyster population trends including the effects of flooding, oyster disease, and the oyster fishery.

METHODS

Field Sampling and Laboratory Analysis

Samples were collected from 51 oyster reefs in the Galveston Bay system including Trinity Bay, East Bay, and West Bay in April and May 1992 (Table 1). The sampled reefs were selected based on salinity regime, previous studies, use by the oyster fishery, and proximity to the Houston Ship Channel. Sites were chosen from the recent oyster reef survey of Galveston Bay (Powell *et al.* submitted b) and their GPS positions recorded. A 12-toothed Louisiana-style dredge with 68 cm mouth was used and one to four hauls were taken from each site. Distance dredged was determined using a precision range finder.

Total shell volume collected from each site was estimated from displacement volume. The longest axis of the ten largest clumps was measured. All oysters collected were counted and their length measured. Forty live oysters were selected from three size classes: juveniles less than 50 mm, submarket-sized adults between 50 and 76 mm and market-sized adults larger than 76 mm. Wet weight of the live oysters was recorded and their dry weight was estimated using the conversion factor of Choi *et al.* (1993). All significant predators such as oyster drills and crabs were identified and measured. Axial length was measured for oyster drills and carapace width for the crabs. Selected common epibionts and endobionts were recorded. Mussels were counted

TABLE 1.

Summary of sites sampled.

Site	Site Abbreviation	Date	Latitude	Longitude	No. of Hauls	Sampled Area (m ²)	Shell Volume (i)	Temperature (°C)	Salinity (ppt)
April Fools Reef	APRIL	16/04/92	29° 28.87'	94° 55.00'	з	150.7	5.5	25.0	9
Buoy 53/55	B5355	28/04/92	29° 30.06'	94° 52.35'	2	118.4	12.0	22.0	5
Buoy 73/75	B7375	27/04/92	29° 35.89'	94° 56.65'	2	98.3	21.0	22.5	3
Bart's Pass Reef	BARTS	27/04/92	29° 32.25'	94° 48.00'	1	39.5	9.0	22.5	0
Big Beezley Reef	BBEEZ	26/04/92	29° 39.47'	94° 52.81'	2	111.2	7.0	24.0	з
Bull Hill	BHILL	21/04/92	29° 28.38'	94° 44.81'	2	114.8	7.5	23.0	2
Bull Shoals	BSHOA	03/05/92	29° 29.42'	94° 47.28'	3	157.1	8.0	24.0	8
Buoy 59	BUO59	28/04/92	29° 31.55'	94° 53.54'	3	177.2	6.0	22.0	5
Buoy 63	BUO63	28/04/92	29° 32.38'	94° 54.17'	3	183.7	14.5	22.0	5
Confederate Reef	CONFE	13/04/92	29° 15.83	94° 54.59'	2	91.8	10.5	24.0	14
Dickinson Reef	DIKIN	16/04/92	29° 27.86	94° 55.28'	2	91.8	5.5	25.0	10
Dollar Reef	DOLLA	15/04/92	29° 26.40'	94° 52.50'	4	196.6	2.5	23.8	8
Dow Reef	DOWRE	26/04/92	29° 39.08'	94° 54.37'	4	200.2	0.5	24.0	4
East Redfish Reef	EREDF	29/04/92	29° 30.23'	94° 49.25'	1	35.9	8.0	22.3	2
South Redfish Reef (east)	ESRED	29/04/92	29° 29.52'	94° 49.70'	1	58.8	11.0	22.3	2
Fisher Reef	FISHE	26/04/92	29° 40.31'	94° 51.35'	3	131.3	0.8	24.0	з
Four Bit Reef	FOBIT	03/05/92	29° 27.74'	94° 50.66'	2	101.9	13.0	24.0	13
Frenchy's Reef	FRENC	20/04/92	29° 31.32'	94° 35.87'	2	118.4	4.0	22.5	4
Gale's Reef	GALES	22/04/92	29° 30.73'	94° 40.51'	4	196.6	4.0	23.5	5
Gaspipe Reef	GPIPE	26/04/92	29° 30.80'	94° 47.50'	1	39.5	10.0	21.5	0
Half Moon Reef	HMOON	15/04/92	29° 23.99'	94° 50.99'	2	95.4	3.5	22.0	17
Lost Beezley Reef	LBEEZ	02/05/92	29° 28.63'	94° 48.99'	2	78.9	11.0	24.0	10
Levee Reef	LEVEE	15/04/92	29° 26.57'	94° 53.86'	3	160.7	2.5	24.5	7
Middle Reef	MIDDL	21/04/92	29° 30.18'	94° 39.38'	з	177.2	6.0	23.5	4
Morgan Point Reef	MORPT	20/04/92	29° 39.60'	94° 58.59'	4	229.6	1.3	23.5	4

TABLE 1. Continued.

Site	Site Abbreviation	Date	Latitude	Longitude	No. of Hauls	Sampled Area (m ²)	Shell Volume (i)	Temperature (°C)	Salinity (ppt)
Green's Cut Shell	MWBAY	14/04/92	29° 15.25'	94° 59.20'	2	95.4	5.0	25.5	13
Carancahua Reef (north)	NCARA	14/04/92	29° 13.45'	95° 00.81'	з	164.3	1.5	26.0	14
North Deer Island Reef	NDEER	13/04/92	29° 16.63'	94° 55.09'	2	101.9	5.5	24.5	14
Hanna Reef (north)	NHANN	02/05/92	29° 28.83'	94° 43.49'	4	216.7	7.0	23.3	6
North Redfish Reef	NREDF	29/04/92	29° 30.25'	94° 51.49'	1	58.8	10.0	22.0	4
Pelican Island Reef	PELIS	12/04/92	29° 20.40'	94° 52.94'	2	114.1	1.3	24.5	14
Pepper Grove Reef	PEPGR	22/04/92	29° 29.05'	94° 39.29'	4	144.2	5.0	22.6	4
Possum Pass Reef	POSSU	28/04/92	29° 31.55'	94° 48.32'	з	160.7	6.0	22.3	o
Red Bluff Reef	RBLUF	25/04/92	29° 36.16'	94° 58.42'	2	88.3	8.5	23.8	3
Richard's Reef	RICHA	26/04/92	29° 31.42'	94° 44.36'	2	91.8	6.0	21.5	1
San Leon Reef	SANLE	20/04/92	29° 30.40'	94° 56.33'	4	247.5	4.5	23.8	7
Carancahua Reef (south)	SCARA	14/04/92	29° 12.91'	95° 00.02'	з	173.6	3.0	24.8	14
Scott Reef	SCOTT	20/04/92	29° 34.45'	94° 59.41'	2	104.8	2.9	23.8	6
South Deer Island Reef	SDEER	14/04/92	29° 15.79'	94° 55.86'	2	104.8	11.5	26.0	13
Hanna Reef (south)	SHANN	02/05/92	29° 27.97'	94° 42.38'	4	216.7	4.0	23.0	
Shell Island Reef	SHEIS	14/04/92	29° 11.43'	95° 01.02'	з	177.2	4.0	26.0	14
Stephenson Reef	STEPH	22/04/92	29° 32.03'	94° 41.12'	4	196.6	2.5	23.5	3
Tern Reef	TERNR	27/04/92	29° 36.42'	94° 50.93'	1	56.0	6.0	22.5	2
Todd's Dump	TODDS	16/04/92	29° 29.99'	94° 53.59'	4	219.6	3.0	24.5	8
Trinity Reef	TRINI	25/04/92	29° 41.33'	94° 50.44'	4	180.1	3.0	23.3	3
Vingt-et-un Reef	VINGT	27/04/92	29° 33.91'	94° 46.94'	1	39.5	4.0	22.5	0
Whitehead Reef	WHEAD	22/04/92	29° 31.28'	94° 42.94'	4	210.2	2.7	23.5	3
South Redfish Reef (west)	WSRED	29/04/92	29° 29.58'	94° 51.25'	1	39.5	10.5	22.5	5
Yacht Club Reef	YACHT	25/04/92	29° 37.30'	94° 59.55'	1	35.9	8.0	23.5	2

and their anterior-posterior length measured. Algae, barnacles and bryozoans were estimated by percent areal coverage. Polychaetes were removed by dissolving the oyster shell in a decalcifying solution which contained 0.7 g/l EDTA tetrasodium salt, 8 mg/l sodium potassium tartrate, 99.2 ml/l HCL and 0.14 g/l sodium tartrate (Gittings *et al.* 1984), and weighed. Condition index was estimated from dry weight and mantle cavity volume measured by displacement before and after shucking. Condition of each oyster was rated immediately after opening using a condition code rating. Sex was determined by examining a smear slide.

Prevalence and infection intensity of P. marinus was assessed using the culture method of Ray (1966). Mantle tissue was removed from each oyster and incubated in thioglycollate medium for two weeks. After staining with Lugol's iodine, the tissue was examined under the microscope and infection intensity based on the number of P. marinus hypnospores present using Mackin's (1962) numerical scale modified by Craig et al. (1989). Prevalence was calculated as percent infected. Since there were many false negatives, a subset of the false negatives was examined using the method of Choi et al. (1989). A whole tissue of each adult-sized oyster was homogenized using a Brinkmann Polytron tissue homogenizer at level 3 for 2 minutes. The homogenized tissue was incubated in thioglycollate medium as described previously. After two weeks, the volume of the mixture was recorded. A thirty ml subsample was obtained and centrifuged at 6000 RPM for 10 minutes. The pellet was mixed with 30 ml of 2 M NaOH and

incubated at 50 °C in a water bath for 1 hr. After incubation, the mixture was centrifuged and the pellet rinsed with phosphatebuffered saline three times. The volume of the pellet was recorded. A hundred μ l subsample was taken from the pellet and mixed with Lugol's solution. The number of hypnospores was counted ten times using a hemacytometer under a microscope. The amount of gonad present in individual female oysters was assessed quantitatively by single ring immunodiffusion assay following the method of Choi *et al.* (1993) as described in detail by Choi and Powell (in press). A Gonadal-Somatic Index (GSI) was calculated as mg dry wt egg per mg dry wt somatic tissue.

Statistics

The primary data used for cluster analysis are maximum clump size (mean in mm), oyster biomass (g m⁻²), juvenile oyster density (individual m⁻²), submarket-sized oyster density (individual m⁻²), market-sized oyster density (individual m⁻²), prevalence of *P. marinus* (%), mean infection intensity of *P. marinus* (mean of Mackin's numerical scale), mussel density (individual m⁻²), crab density (individual m⁻²), shell volume (1 m⁻²), boxes (individual m⁻²), condition index (mean of g dry wt. ml⁻¹), egg quantity (mean of mg individual⁻¹), GSI (mean of mg dry wt egg mg dry wt somatic tissue⁻¹), polychaetes (mean of total wt oyster⁻¹), barnacles (mean of % coverage), bryozoans (mean of % coverage), algae (mean of % coverage). Raw data were normalized to m^{-2} , where appropriate, using the area covered by the dredge. All data categories were internally standardized to parts per thousand and log-transformed (Boesch 1977). The cluster program used an unweighted pair-group algorithm with Euclidean distance as the similarity index.

The spatial distribution of each variable was examined using a spatial autocorrelation method described by Cliff and Ord (1973). We used Moran's I as the test statistic,

$$I = (n / W) \frac{ \sum_{i=1}^{n} \sum_{j=1}^{n} w_{ij} z_i z_j }{ \sum_{i=1}^{n} \sum_{j=1}^{n} z_i^2 }$$

and

$$W = \sum_{\substack{i=1 \\ i \neq j}}^{n} \sum_{\substack{j=1 \\ j=1}}^{n} w_{ij}; z_i = x_i - \overline{x};$$

where n= number of samples; x_i = datum of sample i; and w_{ij} = a weighting measure as described below.

Moran's I is sensitive to the location of extreme departures from the mean $(x_i - \bar{x})$. In a patchy population, adjacent samples would both tend to be much above or below the mean more frequently than would be expected by chance. Cliff and Ord (1973) showed, for samples that are spatially randomly distributed, that the expected value of I is $-(n-1)^{-1}$ (about 0 in this study). The use of this technique depends upon the choice of a weighting system (w_{ij}) which is a mathematical expression of the spatial relationship between the sampled sites. Following Wilson *et al.* (1992), a Gabriel-connected graph was constructed (Gabriel and Sokal 1969) for the sites. In this case, two sites (\overline{AB}) were considered connected if no third site (C) existed that formed an obtuse angle when connected between the other two (angle ACB). Sokal and Oden (1978) discussed occasions eliciting modifications in a Gabriel graph. In this case, all pairs linked by overland connections were deleted.

The change in spatial relationship among samples at varying distances can be used to identify the scale of spatial variation. The change in spatial relationship was examined using two approaches; distance using correlograms (plots of sample similarity versus distance between samples), and compass direction (Sokal et al. 1987). Distances were calculated along the Gabriel network by Marble's (1967) method. Correlograms for directional spatial autocorrelation were generated from north northeast (22.5°) to south (180°) in 22.5° intervals. For each interval, a weight was calculated for each Gabriel pair as the fractional deviation of the angle between the site pairs from the preferred angle for that interval, calculated as $sin(\alpha)$. Only site pairs directly linked in the Gabriel network without intervening sites were included in the analysis, so the resulting correlogram considers only those sites very near to each other in spatial arrangement.

RESULTS

Primary Data

Salinity was low, ranging from 0 to 17 ppt (Table 1) and usually below 10 ppt, over most of the bay during the sampling period. Relatively high salinity was recorded in all West Bay sites where the salinity regime remains high all year. High salinity was also observed at a few sites right above Bolivar Peninsula, where the intrusion of high-salinity water from the Gulf of Mexico starts. Trinity Bay sites showed lowest salinities and the direct effect of the Trinity river input was obvious down to Smith Point where salinity remained near 0 ppt. The salinity arose to 13 ppt south of the Redfish Bar area at Bull Shoals, Four Bit Reef, Lost Beezley Reef and Mattie B. Reef. Salinity increased across the Houston Ship Channel from the Trinity Bay sites through Todds Dump to Scott and San Leon Reefs in the Clear Lake area.

A higher shell volume per m^2 dredged was obtained in the Redfish Bar area, the Clear Lake area and along the Houston Ship Channel than elsewhere. These areas contributed 68% of the total shell collected in the entire bay (Table 2, Fig. 1). All sites along the West side of the Houston Ship Channel from Morgan's Point to Half Moon Reef yielded a relatively low shell volume except for Yacht Club Reef, Red Bluff Reef and Dickinson Reef. Low volumes were also obtained at the extremes of the salinity gradient in lower West Bay, upper East Bay and upper Trinity Bay. The largest

Summary of community and health-related variables.

	Condition	P. marinus	Infection	Egg	Gonadal-	Shell	Crab	Mussel	Clump	Oyster	Total Oyster
	Index	Prevalence	Intensity	Quantity	Somatic Index	Volume	Density	Density	Size	Biomass	Density
EAST BAY											
Bull Hill	13.160	75.0	0.248	127.245	0.051	0.065	0.096	2.065	121	9.679	1.063
Frenchy's Reef	15.349	50.0	0.165	159.621	0.082	0.034	0.042	0.845	147	0.442	0.051
Gale's Reef	14.194	35.3	0.116	295.349	0.116	0.020	0.020	2.869	116	1.043	0.183
Lone Tree Reet	12.292	52.5	0.173	58.013	0.018	0.040	0.328	1.561	89	2.354	0.363
Mattie B. Reef	10.138	70.0	0.231	593.694	0.244	0.088	0.136	0.425	114	11.603	2.083
Middle Reef	12.779	75.0	0.275	105.495	0.034	0.034	0.017	0.277	142	1.516	0.226
Hanna Reef (north)	13.088	47.5	0.157	454.091	0.187	0.032	0.162	1.735	109	5.045	0.794
Pepper Grove Reef	12.115	56.7	0.210	43.073	0.012	0.035	0.007	0.388	116	4.089	0.257
Richard's Reef	9.789	42.5	0.140	67.903	0.036	0.065	0.338	13.475	124	7.414	1.754
Hanna Reef (south)	14.315	82.5	0.348	524.611	0.231	0.019	0.097	1.504	94	2,209	0.438
Stephenson Reef	11.882	48.1	0.159	175.946	0.110	0.013	0.046	0.254	101	0.876	0.137
Whitehead Reef	12.929	25.8	0.085	45.757	0.026	0.013	0.024	0.871	110	1.302	0.257
AVERAGE	12.669	55.1	0.192	220.900	0.096	0.038	0.109	2.189	115	3,964	0.634
HOUSTON SHIP CHANNEL											
Buoy 53/55	12.946	62.5	0.215	204.131	0.062	0.101	0.051	0.068	114	8.328	1.140
Buoy 59	12.857	42.5	0.140	437.684	0.128	0.034	0.062	0.051	116	5.043	1.163
Buoy 63	11.449	65.0	0.273	485.122	0.130	0.079	0.011	0.103	164	6.675	1.486
Buoy 73/75	9,246	77.5	0.650	328.018	0.134	0.214	0.102	1.078	133	15.824	4 435
Morgan Point Reef	12.094	46.7	0.188	30.522	0.013	0.006	0.000	0.070	111	0.822	0 157
AVERAGE	11.718	58.8	0.293	297.095	0.093	0.087	0.045	0.274	128	7 339	1.676
CLEAR LAKE TO MORGAN F	OINT										
Red Bluff Reef	11.839	85.0	0.323	75.765	0.029	0.096	0.272	8 4 2 6	142	14 916	2 763
San Leon Reef	18 977	37.5	0.141	66 637	0.021	0.018	0.008	0 424	112	3 095	0 412
Scott Reef	13.846	42.9	0.151	48.898	0.011	0.028	0.019	0 706	116	3 812	0.458
Yacht Club Reef	12.695	75.0	0.264	435.058	0.174	0.223	0.139	53.036	134	32 984	7 549
AVERAGE	14.339	60.1	0.220	156,590	0.059	0.091	0.110	15.648	126	13,702	2.796

Continued.

	Condition Index	P. marinus Prevalence	Infection Intensity	Egg Quantity	Gonadal- Somatic Index	Shell Volume	Crab Density	Musael Denaity	Clump Size	Oyster Biomase	Total Oyster Density
TRINITY BAY											
Big Beezley Reef	10.867	89.7	0.296	31.011	0.040	0.063	0.099	1 277	112	0 890	0 477
Dow Reef	9.769	80.0	0.264	0.000	0.000	0.003	0.010	0.804	100	0.030	0.477
Fisher Reef	-	40.0	0.132	0.000	0.000	0.006	0.031	0.693	110	0.121	0.055
Tem Reef	10.483	92.5	0.305	45.325	0.031	0.107	0.054	3 143	155	11 800	0.053
Trinity Reef	7.863	20.0	0.066	0.000	0.000	0.017	0.050	1 272	00	0.640	3.071
Vingt-et-un Reef	-	0.0	0.000	0.000	0.000	0.101	0.354	4 794	196	0.042	0.339
AVERAGE	9.746	53.7	0.177	12.723	0.012	0.049	0.100	1 997	117	0.043	0.025
WEST BAY							0.100			2.002	0.670
Confederate Reef	14.365	88.9	0.936	202.522	0.070	0.114	0.283	0.218	174	00 710	0.470
Green's Cut Shell	-	0.0	0.000	0.000	0.000	0.052	0 178	0 115	1/4	22.710	3.170
Carancahua Reef (north)		0.0	0.000	0.000	0.000	0.009	0.097	0.097	•	0.049	0.168
North Deer Island Reef	14.236	92.3	0.914	167.213	0.072	0.054	0 129	0.040	197	6.470	0.067
Carancahua Reef (south)		0.0	0.000	0.000	0.000	0.017	0.207	0.043	109	0.4/9	1.295
South Deer Island Reef	10.017	94.9	1.213	272.108	0 100	0 110	0.607	0.000	123	0.338	0.467
Pelican Island Reef		0.0	0.000	0.000	0.000	0.011	0.061	0.000	100	10.164	2.347
Shell Island Reef		0.0	0.000	0.000	0.000	0.033	0.001	0.000	100	0.294	0.587
AVERAGE	12,783	34.5	0.383	80.230	0.030	0.023	0.198	0.051		0.062	0.181
DICKINSON EMBAYMENT		••	01000	00.200	0.000	0.049	0.231	0.061	90	5.013	1.035
April Fools Reef	9.011	70.0	0.475	192,483	0.079	0.037	0.053	0 597	166	4 880	0 700
Dickinson Reef	14.339	65.0	0.240	51.023	0.024	0.060	0.261	1 940	120	9.302	0.723
Dollar Reef	19.795	31.3	0.258	410.627	0.160	0.013	0.005	0.005	89	1 780	1.482
Half Moon Reef	12.454	100.0	0.330	614.328	0.273	0.037	0 105	0.003	100	0.000	0.229
Levee Reef	20.349	90.0	0.297	222 481	0.081	0.016	0.056	0.021	120	2.290	0.503
Todd's Dump	15.304	25.7	0.085	250.211	0.116	0.014	0.050	0.004	107	3.592	0.504
AVERAGE	15.209	63.7	0.281	290.192	0.122	0.029	0.090	0.493	121	1.465	0.200

Continued.

	Condition index	P. marinus	Infection	Egg	Gonadal-	Shell	Crab	Mussel	Clump	Oyster	Total Oyster
		Prevalence	Intensity	Quantity	Somatic Index	Volume	Density	Density	Size	Biomass	Density
REDFISH BAR TO SMITH PO	INT										
Bart's Pass Reef	10.596	100.0	0.330	21.363	0.011	0.228	0.228	2.937	149	17.484	3.165
Bull Shoals	8.320	52.5	0.173	190.709	0.086	0.051	0.407	0.808	160	7.649	1.540
East Redfish Reef	10.205	50.0	0.165	193.955	0.082	0.223	0.446	2.813	168	45.557	6.852
South Redfish Reef (east)	8.922	25.0	0.083	310.459	0.178	0.187	0.068	1.633	162	20.719	4.082
Four Bit Reef	9.693	30.0	0.099	744.324	0.327	0.128	0.137	0.059	138	15.835	3.572
Gaspipe Reef	10.611	70.0	0.231	76.393	0.031	0.253	0.279	4.152	144	39.205	8.633
Lost Beezley Reef	10.934	85.0	0.281	334.301	0.129	0.139	0.456	0.837	148	22.341	6.033
North Redfish Reef	10.811	57.5	0.198	68.057	0.021	0.170	0.255	0.884	134	22.764	2.738
Possum Pass Reef	10.631	25.0	0.083	0.000	0.000	0.037	0.044	6.578	115	1.505	0.405
South Redfish Reef (west)	10.113	48.7	0.204	233.820	0.113	0.266	0.557	2.354	138	38.137	7.949
AVERAGE	10.084	54.4	0.185	217.338	0.098	0.168	0.288	2.306	146	23.120	4.497

TABLE 2. Continued.

	Juvenile Oyster	Submarket-sized	Market-sized		Sex	Coverage of	Coverage of	Coverage	Biomass of
	Density	Oyster Density	Oyster Density	Boxes	Ratio	Barnacles	Bryozoans	of Alga	Polychaets
EAST BAY									
Bull Hill	0.270	0.409	0.383	0.026	1.5	46	6	0	34.2
Frenchy's Reef	0.025	0.017	0.008	0.000	2.0	33	3	13	36.0
Gale's Reel	0.061	0.092	0.030	0.015	1.0	3.8	8	0	30.3
Lone Tree Reef	0.086	0.242	0.035	0.000	1.0	58	ő	ő	32.5
Mattie B. Reef	0.773	0.826	0.486	0.064	2.3	20	2	Å	32.5
Middle Reef	0.085	0.102	0.039	0.006	1.0	42	Â	,	7.6
Hanna Reef (north)	0.226	0.508	0.060	0.014	1.0	21	4	2	5.2
Pepper Grove Reef	0.000	0.090	0,166	0.035	1.0	28	18	2	36.4
Richard's Reef	0.534	1.068	0.153	0.109	1.5	40	0	ñ	5 3
Hanna Reef (south)	0.217	0.203	0.018	0.037	4.0	68	2	10	0.0
Stephenson Reef	0.020	0.107	0.010	0.000	2.3	32	0	0	3.5
Whitehead Reef	0.105	0.138	0.014	0.024	1.5	64	ő	ň	16.8
AVERAGE	0.200	0.317	0.117	0.027	1.7	41	Ā	å	15.2
HOUSTON SHIP CHANNEL							-	Ū	10.2
Buoy 53/55	0.346	0.608	0.186	0.101	2.3	16	10	0	
Buoy 59	0.728	0.299	0.135	0.068	2.3	14		č	0.8
Buoy 63	0.861	0.435	0.191	0.065	1.5	10	14	õ	9.5
Buoy 73/75	2.617	1.287	0.528	0 417	1.5	18	14 6	Š	11.3
Morgan Point Reef	0.061	0.083	0.013	0.030	0.4	24	0		20.4
AVERAGE	0.923	0.542	0.210	0.136	1.6	18	2	0	5.2
CLEAR LAKE TO MORGAN POINT				0.100		10	0	U	10.4
Red Bluff Reef	0.985	1,484	0.294	0.057	4.0	44		12	21.1
San Leon Reef	0.133	0.226	0.053	0.000	4.0	10	8	0	40.2
Scott Reel	0.105	0.219	0 134	0.000	1.0	12		~~	40.3
Yacht Club Reef	3.427	3.747	0.381	0.056	1.5	40		16	14.8
AVERAGE	1.163	1,419	0.215	0.028	2.6	27	5	14	44.4

Continued.

	Juvenile Oyster	Submarket-sized	Market-sized		Sex	Coverage of	Coverage of	Coverace	Biomass of
	Density	Oyster Density	Oyster Density	Boxes	Ratio	Barnacles	Bryozoans	of Alga	Polychaets
TRINITY BAY									
Big Beezley Reef	0.297	0.180	0.000	0.063	0.4	а	0	•	
Dow Reef	0.015	0.040	0.000	0.010	0.2	28	6	14	0.0
Fisher Reef	0.030	0.023	0.000	0.015		8	Ň	14	2.7
Tem Reef	0.851	1.765	0.455	0.732	1.5	14	ő		0.0
Trinity Reef	0.161	0.178	0.000	0.017	0.0	20	0	0	0.9
Vingt-et-un Reef	0.025	0.000	0.000	2.785		18	ŏ	0	0.0
AVERAGE	0.230	0.364	0.076	0.604	0.5	16		2	0.0
WEST BAY							,	2	1.0
Confederate Reef	1.275	1.111	0.784	0.065	4.0	6		•	
Green's Cut Shell	0.168	0.000	0.000	0.126		ő		0	14.1
Carancahua Reef (north)	0.067	0.000	0.000	0.043		ő	22		124.0
North Deer Island Reef	0.677	0.412	0.206	0.088	15	õ	~~~	~~~~	1204.5
Carancahua Reef (south)	0.467	0.000	0.000	0.058		ě	~		1.4
South Deer Island Reef	1,174	0.726	0.450	0.076	23	2	24	22	249.3
Pelican Island Reef	0.587	0.000	0.000	0 1 1 4	2.0	5		0	6.9
Shell Island Reef	0.181	0.000	0.000	0.056	-		00	0	47.3
AVERAGE	0.574	0.281	0.180	0.030		4	32	24	822.8
DICKINSON EMBAYMENT	0.074	0.201	0.100	0.078	2.0	2	19	9	308.8
April Fools Reef	0.239	0.279	0.206	0.027	4.0	10			
Dickinson Reef	0.490	0.762	0.229	0.027	4.0	14	12	0	4.5
Dollar Beef	0.030	0.163	0.026	0.000	4.0	14	12	0	2.4
Half Moon Reef	0.273	0.100	0.030	0.005	4.0	24	32	0	7.6
eves Beef	0.156	0.155	0.001	0.003	0.8	60	20	0	1.5
Todd's Dump	0.100	0.255	0.093	0.000	4.0	14	12	0	14.5
AVERAGE	0.030	0.140	0.018	0.032	4.0	24	10	6	3.3
	0.204	0.301	0.102	0.027	2.9	25	16	1	5.6

TABLE 2. Continued.

	Juvenile Oyster	Submarket-sized	Market-sized		Sex	Coverage of	Coverage of	Coverage	Biomass of
	Density	Oyster Density	Oyster Density	Boxes	Ratio	Barnacles	Bryozoans	of Alga	Polychaets
REDFISH BAR TO SMITH POINT									
Bart's Pass Reef	0.810	1.468	0.886	0.481	4.0	48	6	0	2.0
Bull Shoals	0.559	0.538	0.442	0.197	4.0	22	4	2	5.7
East Redfish Reef	2.015	2.980	1.857	0.279	1.5	26	6	ō	13.0
South Redfish Reef (east)	1.086	1.536	1.463	0.578	1.5	28	2	2	3.9
Four Bit Reef	1.336	1.354	0.892	0.275	2.3	6	26	ō	18.6
Gaspipe Reef	2.944	4.920	0.771	0.759	1.0	26	0	0	21.0
Lost Beezley Reef	2.901	2.164	0.968	0.038	9.0	18	12	0	11.8
North Redfish Reef	0.612	1.326	0.799	0.272	1.0	38	12	0	14.2
Possum Pass Reef	0.143	0.212	0.050	0.324	0.0	44	2	0	3.5
South Redfish Reef (west)	2.504	3.957	1.483	0.025	1.5	20	5	0	10.4
AVERAGE	1.491	2.046	0.961	0.323	2.6	28	8	0	10.4

volume of shells was collected at South Redfish Reef (west). In East Bay, highest shell volumes were recorded from Mattie B. Reef, Bull Hill, and Richard's Reef. Highest shell volumes in upper



Figure 1. Comparison of shell volume among bay sections.

Galveston Bay, above the Redfish Bar area, were collected from Buoy 73/75 along the Houston Ship Channel and Yacht Club Reef above Red Bluff. Although a large volume of shell was collected on Vingt-et-un Reef, only one live oyster was collected. Confederate and South Deer Island Reefs provided the highest shell volumes in West Bay. Generally, shell volume was correlated best with oyster biomass, the number of boxes, and juvenile abundance (Table 3).

Overall, the clumps were larger in the Redfish Bar area and the middle part of West Bay than elsewhere (Table 2, Fig. 2). Clump size was above the bay average (128 mm) at all sites except Possum Pass Reef (115 mm) in the Redfish Bar area.

TABLE 3.

P-values for partial regressions from the best 4-variable model.

Dependent Variable		Box Density	Salinity	Shell Volume		P-	values Mussel Density	Gonadal- Somatic Index	Maximal Clump Size		
	r-square				Condition Index	Crab Density				Mean Infection Intensity	Prevalence
Box Density	0.54			0.0001	0.0772	0.0057	0.0581				
Salinity	0.68			0.0011				0.0008		0.0001	
Shell Volume	0.90	0.0024			0.2142						
Condition Index	0.51		0.0013			0.0842		0.0200	0.0007		
Crab Density	0.55	0.0205			0.0192					0.0070	
Mussel Density	0.48										
Gonadal-Somatic Index	0.46		0.0001							0.0036	
Minimal Clump Size	0.34						0.0771			0.1482	
Maximal Clump Size	0.66				0.0116					0.0002	
Mean Infection Intensity	0.63		0.0005						0.0308		0.0006
Prevalence	0.51			0.0545						0.0001	
Oyster Biomass	0.97	0.0149								0.0726	
Juvenile Oyster Density	0.86			0.1890				0.0167		0.0098	
Submarket Oyster Density	0.93	0.1875									
Market Oyster Density	0.89				0.0192		0.0009				
Polychaete Biomass	0.59						0.0075	0.0223			
Coverage of Bryozoans	0.36		0.0001	0.0685						0.0069	
Coverage of Alga	0.64						0.0001	0.1084			
Coverage of Barnacies	0.25				0.2431				0.0560	0.0719	0.0737

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TABLE 3. Continued.

				P-values				
Dependent Variable		Submarket Ovster	Market Ovster	Polychaete	Coverage	Coverage	Coverage	Coverage
Dependent fundolo	r-square	Density	Density	Biomass	Bryozoans	of Alga	Barnacles	Barnacles
Por Depaitr	0.54							
Box Density	0.54							
Salinity	0.68				0.0102			
Shell Volume	0.90							
Condition Index	0.51							
Crab Density	0.55							
Mussel Density	0.48		0.0001	0.1875		0.0556		
Gonadal-Somatic Index	0.46			0.0567				
Minimal Clump Size	0.34	0.0033						
Maximal Clump Size	0.66		0.0002				0.2119	0.2119
Mean Infection Intensity	0.63				0.0668			
Prevalence	0.51		0.1548				0.1977	0.1977
Oyster Biomass	0.97	0.0001	0.0001					
Juvenile Oyster Density	0.86	0.0001						
Submarket Oyster Density	0.93		0.0004					
Market Oyster Density	0.89	0.0021						
Polychaete Biomass	0.59					0.0001		
Coverage of Bryozoans	0.36	0.1043						
Coverage of Alga	0.64			0.0001				
Coverage of Barnacles	0.25							

Largest clumps in the area were found at East Redfish Reef, South Redfish Reef (east), and Bull Shoals. The largest clumps in the entire Bay were collected from upper West Bay, the smallest at Dollar Reef. No clumps were collected on Green's Cut Shell, Carancahua Reef (north), and Shell Island Reef. Clump size was significantly correlated with the abundance of market-size oysters and mean *P. marinus* infection intensity (Table 3).



Figure 2. Comparison of clump size among bay sections.

Highest oyster abundances were found in the Redfish Bar area including Gaspipe Reef and Lost Beezley Reef (Table 2, Fig. 3). Locally high abundances elsewhere were at Yacht Club Reef, Buoy 73/75 along the Houston Ship Channel, Tern Reef in Trinity Bay, the Deer Island area of West Bay, Mattie B. Reef in East Bay, and Dickinson Reef. Regional oyster abundances averaged lowest in the Dickinson Embayment, East Bay, and Trinity Bay. Abundances in upper East Bay were lower than those in the lower bay. Only two sites (Yacht Club Reef and Dickinson Reef) had high abundances along the West side of the Houston Ship Channel from Morgan Point to Half Moon Reef. Yacht Club Reef, Red Bluff Reef, Buoy 73/75, and Tern Reef were major sites in terms of oyster density in upper Galveston Bay above the Redfish bar area. High abundance was observed only on Tern Reef in Trinity Bay.





In West Bay, most oysters were collected from Confederate Reef and the Deer Island area. Significant correlations existed between juvenile oyster and total oyster density, and between submarketsized and total oyster densities, suggesting that total oyster density is directly dependent on the frequency of juvenile and submarket-size oysters (Fig. 4). The correlation between total and market-size oyster density was obvious, but market-size oysters influenced the total density less than did the juvenile and submarket sizes. Also, juvenile oyster abundance was correlated


Figure 4. Total oyster abundance versus juvenile, submarket-size and market-size oyster abundances.

more strongly with submarket-size oyster density than with market size density (Fig. 5).

Juvenile oysters, i.e. smaller than 50 mm, were most abundant in the Redfish Bar area, on Yacht Club Reef, and at Buoy 73/75 (Table 2, Fig. 6). Lowest values were obtained in East Bay, the Dickinson Embayment, and Trinity Bay. Juvenile oyster abundances were lower in upper East Bay than in the lower bay. No juvenile oysters were collected at Pepper Grove Reef in East Bay. Tern Reef, B73/75, Red Bluff Reef, and Yacht Club Reef showed the highest juvenile oyster abundances among the upper Bay sites. The highest juvenile abundance in the entire bay was on Yacht Club Reef and the lowest value on Dow Reef in Trinity Bay. The abundance of juvenile oysters was significantly correlated with the abundance of submarket-size oysters, gonadal-somatic index, and mean infection intensity (Table 3).

Submarket-size oysters, i.e. between 50 and 76 mm, were most abundant around the Redfish Bar area and on Yacht Club Reef (Table 2, Fig. 7). Lowest values were from West Bay, the Dickinson Embayment, and East Bay. Except Possum Pass Reef and Bull Shoals, all reefs on the Redfish Bar area were high in submarket-size oyster abundance. The highest value in the entire bay was from Gaspipe Reef. Highest abundances in upper Galveston Bay were also obtained from Yacht Club to Tern Reef through Red Bluff Reef and Buoy 73/75. Submarket oysters in West Bay were collected only on Confederate Reef and in the Deer



Figure 5. Juvenile oyster abundance versus submarket-size and market-size oyster abundances.







Figure 7. Comparison of submarket-size oyster abundance among bay sections.

Island area. Submarket-size oysters were the most abundant size class at 32 of the 51 sites.

Market-size oysters, i.e. larger than 76 mm, were the most abundant size class on Pepper Grove Reef, the second most abundant size class at 6 sites, and the least abundant size class at the remaining 44 sites (Table 2). Market-size oysters were abundant in the Redfish Bar area, comprising 53% of the total market-size oysters collected in the entire bay (Fig. 8). Marketsize oysters in Trinity Bay and West Bay were collected only on Tern Reef and Confederate Reef, respectively. The abundances of market-size and submarket-size oysters, not surprisingly, were correlated with biomass.



Figure 8. Comparison of market-size oyster abundance among bay sections.

Most sites showed a typical bell-shaped size-frequency distribution with one or sometimes two modes between 36 and 76 mm (Fig. 9). Adult oysters larger than 110 mm were collected



Figure 9. Histograms for oyster size-frequency. The size class dimensions are: 1, 0-25 mm; 2, 25-35 mm; 3, 35-50 mm; 4, 50-63 mm; 5, 63-76 mm; 6, 76-89 mm; 7, 89-100 mm; 8, 100-110 mm; 9, 110-125 mm; 10, 125-160 mm.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.



Figure 9. Continued.

only from 15 sites, all of which were from the Redfish Bar area, along the Houston Ship Channel, in the Dickinson Embayment, and in West Bay. Sites dominated by juvenile oysters were largely confined to West Bay and the Pelican Island Embayment. With the exception of the Deer Island area, few adults were collected at sites in this region.

Oyster biomass was high in the Redfish Bar area, off Red Bluff, and in upper West Bay (Table 2, Fig. 10). The highest value in



Figure 10. Comparison of oyster biomass among bay sections.

Galveston Bay was obtained from East Redfish Reef. Lowest biomasses were generally found at sites noted for the salinity extremes; West Bay, upper East Bay, upper Trinity Bay, and Morgan Point. The line connecting Yacht Club to Tern Reef through Red Bluff and Buoy 73/75 circumscribed the highest biomasses in the upper Galveston Bay area. Figure 11 shows that substantial variation exists between sites in the length/mean weight



Figure 11. Biomass-length relationships for the 51 sampled sites.



Figure 11. Continued.



Figure 11. Continued.



Figure 11. Continued.



Figure 11. Continued.

relationship among sites. Over the range of sites sampled, marketsize oysters (>76 mm) could range from about 7.5 g wet weight (1.7 g dry wt.) to nearly 30 g wet wt (6 g dry wt).

Almost 50% of all boxes were collected from Trinity Bay, and the major portion of these were from Vingt-et-un Reef (Fig. 12). Boxes were rare elsewhere, especially in the Clear Lake area, East Bay, and the Dickinson Embayment. Only one live oyster was collected from Vingt-et-un Reef. Relatively high numbers of boxes were also collected at sites off Smith Point (Bart's Pass Reef, Possum Pass Reef, and Gaspipe Reef).



Figure 12. Comparison of box abundance among bay sections.

Average condition index ranged regionally from 9.75 g dry wt. per ml in Trinity Bay to 15.21 g dry wt. per ml in the Dickinson Embayment (Table 2). There were not enough large oysters for condition index to be calculated at some sites in Trinity Bay and West Bay. Highest regional condition indices were obtained from the Dickinson Embayment and the Clear Lake area (Fig. 13). Highest values were recorded from Levee, Dollar, and San Leon Reefs. Most sections of Galveston Bay showed similar average condition indices. In contrast, nearby reefs frequently differed considerably in condition index.



Figure 13. Comparison of condition index among bay sections.

The average weight of eggs in individual oysters ranged from 0 to 744 mg dry wt. The weight of eggs varied significantly within each region. Egg quantity was lowest at the extremes of the salinity range: West Bay, Trinity Bay, and the Morgan Point area (Fig. 14). In Trinity Bay, oysters with eggs were found only on Big Beezley Reef and Tern Reef. Female oysters with developed gonad were collected only in the Deer Island area of West Bay. Oysters at Mattie B. Reef and Hanna Reef in East Bay had high gonad contents. Except Morgan Point Reef, oysters from all Houston Ship Channel sites were high in egg quantity. Oysters from sites off Smith Point such as Possum Pass Reef, Gaspipe Reef, and Bart's Pass Reef, were low in egg quantity compared to the oysters from the Redfish Bar area. Regionally, oysters in the Houston Ship Channel sites and the Dickinson Embayment showed the highest quantity of eggs in the bay.



Figure 14. Comparison of egg quantity among bay sections.

Gonadal-somatic index is a quantitative measure of the development of gonadal material. Highest regional gonadalsomatic indices were obtained from oysters taken in the Dickinson Embayment, and the indices were similar for oysters taken on Redfish Bar, in East Bay, and along the Houston Ship Channel (Fig. 15). GSI and egg quantity showed similar trends: highest in the middle of the salinity range, and lowest at the extremes of the salinity range (West Bay, Trinity Bay, and the Morgan Point reach of the Houston Ship Channel). GSI was significantly correlated with salinity and the abundance of juveniles and inversely correlated with mean infection intensity of *P. marinus* (Table 3). Female/male sex ratio varied considerably, ranging from 0 (no females) to 9 (9 times more females than males). On average, females were proportionally more common in the higher salinity parts of the bay, but the variability between adjacent sites was generally high.



Figure 15. Comparison of GSI among bay sections.

When *P. marinus* infection intensity is low, false negatives can be frequently recorded with the conventional thioglycollate method, lowering prevalence significantly (Choi *et al.* 1991). Figure 16 compares *P. marinus* prevalences using the semiquantitative method of Ray (1966) and the quantitative method of Wilson *et al.* (in press). Using the standard thioglycollate method, prevalence was over 60% at only 4 sites, and the average prevalence over the entire bay was only 12.9%. Further assessing negatives using the quantitative method increased prevalences up to 100% compared to the semiquantitative values, and raised the average prevalence of the bay to 53.3%.



Site

Figure 16. Comparison of *Perkinsus marinus* prevalence using the semiquantitative method and the quantitative method.

Prevalence was highest in the middle part of West Bay (90%). However, the regional average for prevalence was normally above 50%, indicating that *P. marinus* is more or less spread evenly throughout the bay including Trinity Bay where the prevalence was as high as 92.5%. The highest infection intensity of *P. marinus* was found in West Bay (0.38), followed by sites along the Houston Ship Channel area (0.29). The lowest intensity was in Trinity Bay (0.18). The Houston Ship Channel sites showed higher infection intensities than the nearby sites west of the channel. Infection intensity was highly variable in West Bay, ranging from 0 to 1.21. The values from Confederate Reef (0.914) and the Deer Island area (1.213) were much higher than the regional average (0.383).

Thais haemastoma was collected only in West Bay and on Half Moon Reef in Galveston Bay. Crabs were collected on all the reefs. Most crabs collected were mud crabs (*Petrolisthes armatus*, *Panopeus herbstii* and *Eurypanopeus depressus*). Highest crab densities were recorded in West Bay, the southwestern portion of Redfish Bar to Smith Point, and in the Red Bluff area. Lowest abundances occurred along most reaches of the Houston Ship Channel, Trinity Bay, East Bay and in the Dickinson and Clear Lake Embayments. The number of crabs was correlated with oyster biomass and *P. marinus* mean infection intensity, and inversely correlated with condition index. The carapace width sizefrequency distributions for the crabs collected are shown in Figure 17. Most crabs collected had carapace widths of 10 mm or less.



Figure 17. Crab size-frequency distribution.

S



Figure 17. Continued.



Figure 17. Continued.



Figure 17. Continued.

Larger crabs were collected at a few scattered sites such as South Deer Island Reef and Bull Shoals.

Highest mussel density was observed on Yacht Club reef. Lowest mussel densities were observed in West Bay and along the Houston Ship Channel. Highest densities were observed in northern East Bay, Trinity Bay, and the western part of Galveston Bay from the Clear Lake Embayment to Morgan Point. Mussels were significantly correlated with oyster biomass and inversely correlated with the abundance of market-size oysters. No significant correlation occurred with salinity in the regression analysis because the relationship with salinity was nonlinear. Most mussels were also small, less than 20 mm (Fig. 18). Some reefs, like Tern Reef, Todd's Dump, Buoy 63, and April Fools Reef, had a larger proportion of large mussels.

Barnacle encrustation was highest in the moderate-to-low salinity regions of the bay as may be typical for Texas Bays (e.g. Moore and Danglade, 1915). Coverage of barnacles was very rare in West Bay (Fig. 19). Bryozoan growth was highest in the high salinity regions of the bay, particularly West Bay and the Dickinson Embayment (Fig. 20). Bryozoans were uncommon in Trinity Bay. Polychaetes were common only in West Bay (Fig. 21). Algal coverage was high only in West Bay and from the Clear Lake Embayment to Morgan Point west of the Houston Ship Channel (Fig. 22). Only bryozoan coverage was significantly correlated with salinity. Polychaete, algae and mussel coverage were themselves significantly correlated, but none of them were significantly



Figure 18. Mussel length size-frequency distribution.



Figure 18. Continued.


Figure 18. Continued.



Figure 18. Continued.



Figure 18. Continued.











Figure 21. Comparison of polychaete biomass among bay sections.



Figure 22. Comparison of algal coverage among bay sections.

correlated with salinity. Barnacle coverage was not significantly correlated with any parameter.

Cluster Analysis and Autocorrelation

Stations were clustered into 12 groups primarily by salinity (Fig. 23). Secondary groupings occurred by region along the salinity gradient. For example, groups 1, 2, 3, 6, 7 and 8 were moderate salinity sites that generally were divided according to bay region. Groups 1, 2, and 3 fell on either side of the primary route of outflow of Trinity River water across the Hanna Reef Tract. Groups 6, 7, and 8 generally fell within the Trinity River plume across the same central section of the bay. These latter groups clustered in a more or less upstream-downstream orientation. Groups 4 and 5 were low salinity sites in East and Trinity Bays that clustered separately from the low salinity sites west of the Houston Ship Channel, group 10. High salinity sites were divided between the productive region in easternmost west Bay, group 9, and the depauperate areas of West Bay and the Pelican Island Embayment, group 12. Group 11 consisted of the two sites suffering flood-induced mortalities just prior to collection. Under normal conditions, these sites probably would have fallen into groups 7 or 8.

Correlograms were used to identify scales of similarity and dissimilarity in the measured variables. Stations farther and farther apart became increasingly less similar in salinity. The



Figure 23. Cluster diagram for community and health-related variables.



Figure 23. Continued.

scale of similarity in salinity was on the order of 30 km (Fig. 24). Variables associated with the oysters themselves, like clump size, shell volume, biomass, and abundance, showed scales of similarity (patch size) in the range of 10 to 15 km, a much smaller scale than observed with salinity (Fig. 25). A secondary, much weaker signal occurred in the 35 km range. Thus, similarity between sites in oyster variables only existed over short spatial scales, rarely more than 1 site removed from any given site. Measures of oyster condition, such as condition index, gonadal-somatic index and egg quantity, followed similar spatial trends (Fig. 26). P. marinus prevalence was patchy on scales less than 10 and about 50 km as was P. marinus infection intensity (Fig. 27). Values of Moran's I for mussel abundance were highly variable with distance; positive autocorrelation was detected at less than 10 km and at 35 km. Crab abundance was positively autocorrelated up to 10 km and between 30 and 40 km. Scales of similarity of P. marinus prevalence and infection intensity, crab abundance and mussel abundance were distinctly smaller, little less than 10 km. The four types of associated epibionts and endobionts, generally had longer scales of similarity, 15 to 20 km for bryozoans and barnacles and 10 to 15 km for algae and polychaetes (Fig. 28).

Results of directional autocorrelational analyses showed that the variables fell into three main groups in general. Directional trends for oyster density, crab density, juvenile and submarketsize density, and oyster biomass were similar to the distribution of shell volume which had a direction of similarity from 0.25

70



Figure 24. Correlogram of Moran's I versus distance for salinity.



Figure 25. Correlogram of Moran's I versus distance for oyster biomass and abundance, shell volume, and clump size.



Figure 26. Correlogram of Moran's I versus distance for variables associated with oyster condition.



Figure 27. Correlogram of Moran's I versus distance for mussel abundance, crab abundance, and variables associated with *Perkinsus marinus*.



Figure 28. Correlogram of Moran's I versus distance for variables associated with epibionts and endobiont.

radians (14°) to 2.5 radians (143°), with a peak between 86° and 143° (Fig. 29, Fig. 30). The predominantly east-west orientation of similarity in these variables approximates the directional trend of the barrier reefs. Salinity had a preferred orientation of 0.25 to 1.5 radians and 3.0 to 3.14 radians (14° to 86°, 171° to 180°), as did maximum clump size (Fig. 31). This directional trend was substantially different from that observed for oyster density and shell volume. The dominant north-south component follows the trend of the isohalines that parallel the Houston Ship Channel. Gonadal-somatic index, egg quantity, P. marinus prevalence, algal coverage, box frequency, and polychaete abundance follow this isohaline pattern with a preferred direction of similarity between 3.0 and 3.14 radians (171° to 180° from N) (Fig. 32, Fig. 33). Several other variables showed a trend diametric to salinity: condition index, bryozoan coverage, barnacle coverage, mussel density, and to some extent P. marinus infection intensity which also had attributes characteristic of the group defined by shell volume and oyster density (Fig. 34, Fig. 35). These variables had a predominant east-west direction of similarity, but the direction of similarity was much more focused than observed for oysters and shell volume.



Figure 29. Correlogram of Moran's I versus compass direction for oyster density, biomass, and shell volume.



Figure 30. Correlogram of Moran's I versus compass direction for crab and oyster densities.



Figure 31. Correlogram of Moran's I versus compass direction for salinity and clump size.



Figure 32. Correlogram of Moran's I versus compass direction for GSI, egg quantity, and *Perkinsus marinus* prevalence.



Figure 33. Correlogram of Moran's I versus compass direction for algal coverage, box frequency, and polychaete biomass.



Figure 34. Correlogram of Moran's I versus compass direction for condition index and mussel density.



Figure 35. Correlogram of Moran's I versus compass direction for *Perkinsus marinus* infection intensity and epibionts.

DISCUSSION

Both spatial scale and directional trends in spatial structure of community and health-related attributes of Galveston Bay ovster populations differed significantly among the variables assayed. Four spatial scales of similarity (akin to patch sizes) could be differentiated. Salinity had the longest spatial scale of similarity, about 30 km, followed by a variety of endobionts and epibionts at a slightly smaller scale of similarity, then oysters and associated measures defining condition, and finally predators, P. marinus and the mussel competitor. The smaller scale of patchiness suggests a significant influence of some factors besides the salinity gradient. Three types of directional similarity were present; predominant trends parallel to the salinity isohalines, predominant trends perpendicular to the isohalines, and predominant trends determined, possibly, by the geological orientation of the reefs that presumably follow the pre-1900 isohaline structure of the bav.

According to the cluster and autocorrelation analyses, salinity was the primary structuring force in the bay. Cluster analyses, taking into account all measured variables, produced groupings primarily defined by salinity. Many of the directional trends were related to salinity and many of the variables had significant partial correlations with salinity or with other variables, themselves significantly correlated with salinity. However, a considerable portion of the spatial structure did not follow salinity gradients. Two or more distinct groups were defined by cluster analysis within broad salinity categories. Furthermore, most variables had a spatial scale of patchiness much smaller than would have been expected from salinity. In effect, patch sizes extended over a significantly smaller area than explained by the local variation in salinity. Many variables had directional trends different from salinity and some even had trends diametric to salinity, implying that, besides salinity, other factors influence the spatial structure of oyster reefs in Galveston Bav.

Possible local factors changing the spatial distribution of oyster populations within the salinity gradient are the commercial fishery, food supply, and current flow. Even though separating the effect of fishery activity from others using current data was difficult, there were some variables indicating possible linkage between the fishery and trends in community attributes such as shell volume. The largest clumps, for example, were obtained from West Bay, the Redfish Bar area, Red Bluff area, and upper East Bay. These areas include those closed to the fishery and open to the fishery during the winter fishing season. They also include closed areas typically fished during the summer relay program and areas rarely fished at all. Therefore, The possibility that continued dredging and culling result in a less consolidated reef surface is not supported by the present data.

Some variables such as oyster density and egg quantity were higher along the Houston Ship Channel than in adjacent areas. This trend may indicate that faster current flow increases food concentration permitting oysters to be in better condition compared to the surrounding area. Sites west of the Houston Ship Channel were also low in turbidity (unpublished data). Oysters can obtain more food under condition of lower turbidity because filtration rate increases (Powell *et al.*, 1992).

Dredging efficiency was estimated to be around 12% for this study by comparing the present data to data obtained by Soniat and Brody (1988) and Soniat (1982). However, since short-term changes in weather and site-related factors affected the efficiency of dredging from site to site, the values for this study (Table 2) were not corrected for dredging efficiency, but were corrected for the area sampled by the dredge. Assuming a dredging efficiency of 12%, highest true densities averaged between 50 and 100 oysters per m². Soniat et al. (1989) reported densities from 16 reefs in Galveston Bay. Values from the present study show lower densities than those observed by Soniat et al. (1989) (Table 4). To some extent, however, this could be a misleading statistic because many of the reefs sampled by Soniat et al. (1989) were in low salinity areas of the bay where, during the current study period, salinities had been below 5 ppt for nearly 6 months. The distribution of boxes recorded by Soniat et al. (1989) differed substantially from the present study. Boxes were much more common in the current study on low salinity reefs than observed by Soniat et al. (1989). Weighted incidences for P. marinus were also significantly lower in the current study. In general, the values obtained for condition index in this study were about double the

TABLE 4.

Comparison between sites sampled by Soniat et al. 1989 and this study.

Site	Oyster Density ('85)	Oyster Density ('92)	Percentage of Boxes ('85)	Percentage of Boxes ('92)	Condition Index ('85)	Condition Index ('92)	Weighted Incidence ('85)	Weighted incidence ('92)
April Fools Reef	25.87	6.02	8.9	3.5	6.3	9.0	3.00	0.44
Big Beezley Reef	34.93	3.97	0.0	11.7	6.8	10.9	0.00	0.01
Confederate Reel	52.00	26.42	10.5	2.0	11.5	14.4	3.40	0.94
Dow Reef	25.20	0.46	0.5	15.4	6.6	9.8	0.00	0.07
Fisher Reef	2.27	0.44	5.9	22.2			0.08	0.00
Frenchy's Reef	11.07	0.42	1.2	0.0	6.0	15.4	0.17	0.06
Hanna Reef (north)	3.87	6.62	0.0	1.7	7.3	13.1	0.83	0.02
Red Bluff Reef	44.40	23.03	4.0	2.0	5.8	11.8	1.75	0.11
San Leon Reef	13.37	3.43	4.8	0.0	6.0	19.0	2.08	0.06
Todd's Dump Reef	4.67	1.67	2.8	13.7	6.2	15.3	2.80	0.02
Vingt-et-un Reef	23.33	0.21	0.5	99.1	7.5		0.08	-
Yacht Club Reef	45.47	62.96	2.9	0.7	6.5	12.7	2.17	0.05

values obtained by Soniat *et al.* probably because of sampling earlier in the reproductive season.

Large oysters (110 mm) were rarely obtained. This rarity included fished and unfished reefs, reefs in all salinity regimes, and all areas of the bay. Powell *et al.* (submitted a) suggested that Galveston Bay, as a whole, has a food supply barely sufficient to support large oysters. The field data support the contention of Powell *et al.* (submitted a) that food supply in Galveston Bay is just barely adequate to support a market-size population.

Shell length-biomass relationships did not vary predictably with salinity, fishing status (use by the oyster fishery), or bay region. Reef-to-reef variation predominated. These data emphasize the danger of basing management decisions on a linear determination for the size-frequency distribution. Most biological variables vary with weight rather than length, and so could vary by a factor of 5 for a given shell length in the market-size classes. Furthermore, the failure of some reefs to support the larger biomass size classes might not be obvious based on length.

No previous studies quantifying reproductive effort are available for comparison besides a few data in Choi *et al.* (1993). Furthermore, since the data from Choi *et al.* (1993) were collected from only one site (Confederate Reef), reproductive values from only that site could be compared (Table 5). Even though oysters in the current study were about three times as large as ones in 1989, mean GSI for 1992 was less than 50% of the value in 1989. While no eggs were detected in some oysters in 1989, GSI values

TABLE 5.

Comparison of GSI between Choi *et al.* 1993 and this study. Oysters were collected on Confederate Reef in April 1989 for Choi *et al.* 1993, and in April 1992 for the present study.

	Mean Size Dry wt (mg) ± SD	Mean GSI GSI ± SD	Median	Lowest	N	
Choi <i>et al.</i> 1993	1051.6 ± 689.5	0.157 ± 0.188	0	0.422	0	9
This Study	3066.25 ± 744.5	0.070 ± 0.052	0.052	0.144	0.013	8

averaged higher (up to 0.422). In 1992, the highest value was only 0.144.

Prevalence was not significantly correlated with any variable. The failure of prevalence to correlate with other variables is not uncommon along the Gulf of Mexico coast (Powell *et al.*, 1992). Prevalences of *P. marinus* could be compared at some sites with previous studies (Table 6). Prevalences were relatively low in comparison to previous studies (Wilson *et al.*, 1990; Powell *et al.*, 1992; Soniat *et al.*, 1989) because of the unusually low salinity conditions present for the 5 months prior to sampling. Sites with low true prevalence, assessed quantitatively, and sites with high true prevalence, were just about as likely to show low prevalence by the semi-quantitative technique, because low infection intensities were found during the sampling period at sites with high prevalence.

According to Hofmann *et al.* (submitted) and Powell *et al.* (submitted a), an increase in infection intensity is not just a function of size or biomass in infected oyster populations. The larger size classes may not always be the most heavily-infected individuals nor may they always be representative of the entire population, even though they are the normally-sampled size class for the thioglycollate assay. Figure 36 represents four examples of the relationship between infection intensity and length or biomass, chosen from three different regions of the bay. There were no significant correlations. Powell *et al.* (submitted a) argued for the necessity of measuring *P. marinus* prevalence and

Table 6.

Comparison of *Perkinsus marinus* prevalence between previous and present studies. 1986 data were from Craig *et al.* 1989; 1987 from Wilson *et al.* 1990; 1988 and 1989 from Powell *et al.* 1992 a; 1992 from the present study.

	1986	1987	1988	1989	This study
Confederate Reef	98	95	100	97	89
Hanna Reef	98	82	100	63	82.5
Todd's Dump Reef	100	93	82	85	26
Yacht Club Reef	100	86	92	93	75
Average	99	89	94	85	68



Figure 36. Example plots of *Perkinsus marinus* infection intensity versus biomass or length chosen as typical for broad areas of Galveston Bay.



Figure 36. Continued.



Figure 36. Continued.



Figure 36. Continued.

infection intensity throughout the size classes of oyster populations to adequately evaluate the disease process. Table 7 shows substantial variation in prevalence and infection intensity between size classes, confirming that prevalence or infection intensity of market-size oysters alone can not be used as a reliable representation for an entire oyster population. Thus, absolute dependence on the market-size classes for analysis may misrepresent infection intensity and prevalence in the entire population.

Environmental factors such as food supply (Powell et al., submitted) and climatic cycles such as El Niño (Powell et al., 1992) can contribute to a change in population variables such as density, disease intensity, fecundity, and condition. The substantial variations in population variables between the current study and Soniat et al. (1989) might be attributed to climatic cycles which affect rainfall and consequently salinity. Since *P. marinus* infection intensity may vary significantly according to the size and age structure of the sampled population, and since both variables vary from year to year, long-term data sets are necessary to separate climatic changes from other factors. Unfortunately, the few previous studies are not adequate to unequivocally determine the importance of the climatic cycles in determining infection intensity in Galveston Bay.

To determine the most favorable growing region for oysters in Galveston Bay, five variables, related directly to the condition and production of oyster populations, were chosen: oyster

TABLE 7.

Distribution of *Perkinsus marinus* prevalence and infection intensity among three size classes of oysters.

	Prevalence			Mean Infection Intensity			Median Infection Intensity		
Site	Juvenile	Submarket	Market	Juvenile	Submarket	Market	Juvenilė	Submarket	Market
April Fools Reef	25	61.5	73.7	0.083	0.385	0.632	0	0.33	0.67
Buoy 53/55	10	6.7	0	0.067	0.022	0	0	0	0
Buoy 73/75	33.3	75	84.2	0.37	0.667	0.719	0	0.67	0.67
Bart's Pass Reef	0	0	0	0	0	0	0	0	0
Big Beezley Reet	0	5.9		0	0.019		0	0	-
Bull Hill	22.2	0	21.1	0.073	0	0.069	0	0	0
Bull Shoals	0	0	5.6	0	0	0.018	0	0	0
Buoy 59	0	0	5.3	0	0	0.017	0	0	0
Buoy 63	10	9.1	15.8	0.033	0.03	0.175	0	0	0
Confederate Reef	75	85.7	100	0.499	0.929	1.191	0.33	1.00	1.33
Dickinson Reef	0	15	7.1	0	0.1	0.024	0	0	0
Dollar Reef	0	4.76	0	0	0.016	0	0	0	0
Dow Reef	33.3	14.3		0.11	0.047		0	0	
East Redfish Reef	10	0	0	0.033	0	0	0	0	0
South Redfish Reef (east)	12.5	0	5.3	0.041	0	0.017	0	0	0
Fisher Reef	0	0		0	0		0	0	
Four Bit Reef	0	0	0	0	0	0	0	0	0
Frenchy's Reef	0	0	-	0	0		0	0	
Gale's Reef	0	0	0	0	0	0	0	0	0
Gaspipe Ree!	0	5.6	0	0	0.018	0	0	0	0
Half Moon Reef	0	0	0	0	0	0	0	0	0
Lost Beezley Reef	0	15.4	10.5	0	0.051	0.035	0	0	0
Levee Reef	14.3	0	0	0.047	0	0	0	0	0
Lone Tree Reef	0	8.3	0	0	0.028	0	0	0	0
TABLE 7.

Continued.

	Prevalence			Mean Infection Intensity			Median Infection Intensity		
Site	Juvenile	Submarket	Market	Juvenile	Submarket	Market	Juvenile	Submarket	Market
Mattie B. Reef	0	0	0	0	0	0	0	0	0
Middle Reef	8.3	0	16.7	0.028	0	0.222	0	ò	ō
Morgan Point Reef	0	50	0	0	0.229	0	0	0.17	ō
Green's Cut Shell	0		-	0			ō	-	
Carancahua Reef (north)	0		-	0			ò		
North Deer Island Reef	55.6	81.3	100	0.741	0.896	0.951	0.67	0.67	0.84
Hanna Reef (north)	0	4.8	11.1	0	0.016	0.037	0	0	0
North Redfish Reef	0	0	22.2	0	0	0.111	ō	ō	ō
Pelican Island Reef	0			0	-		0		
Pepper Grove Reef		0	21.1		0	0,105	-	0	0
Possum Pass Reef	0	4.5	12.5	0	0.015	0.041	0	ō	ő
Red Bluff Reef	0	13.63	45.5	0	0.045	0.303	ō	ō	0
Richard's Reef	0	3.85	0	0	0.013	0	ō	ŏ	ő
San Leon Reef	14.3	10	15.4	0.047	0.033	0.102	ò	0	ò
Carancahua Reef (south)	0	-		0	-	•	0		
Scott Reef	0	11.1	0	0	0.056	0	ō	0	0
South Deer Island Reef	70	70	100	1.067	1.134	1.26	1.33	1.67	1 99
Hanna Reef (south)	10	15.4	0	0.167	0.115	0	0	0	0
Shell Island Reef	0			0			ō		
Stephenson Reef	0	0	0	0	0	0	ō	0	٥
Tern Reef	0	0	0	0	ō	ō	ō	ő	ŏ
Todd's Dump	20	0	25	0.066	Ó	0.083	ò	ő	ő
Trinity Reel	0	0		0	ō		õ	ŏ	
Vingt-et-un Reef									
Whitehead Reef	0	9.5	0	0	0.031	0	0	n n	0
South Redfish Reef (west)	10	0	29.4	0.033	0	0 196	ő	ŏ	ň
Yacht Club Reel	20	9.5	22.2	0.066	0.031	0.073	ő	ő	ő

abundance, oyster biomass, gonadal-somatic index, *P. marinus* infection intensity, and condition index. All sites and regions were ranked in each parameter and weighted. Each site and region was given a weight from 1 (for lowest ranking) to 51 (for highest ranking) for site comparisons and from 1 to 7 for regional comparisons. With infection intensity, lowest weights were given to the most highly infected locations. Highest ranked sites were Yacht Club Reef in the Clear Lake area and the Redfish area (Table 8). Of the top 11 sites, 6 sites belonged to the Redfish Bar complex, two came from lower East Bay, and 3 sites came from the Clear Lake area, along the Houston Ship Channel, and upper West Bay. Most sites of West Bay, Trinity Bay, and upper East Bay were ranked among the lowest in the entire bay.

In regional comparisons, the Redfish Bar complex ranked highest, and the Clear Lake to Morgan Point area ranked second mainly because of highly ranked Yacht Club Reef (Table 9). Based on the weighting comparison, the Redfish Bar complex and the Clear Lake area near Red Bluff are most favorable for oyster growth, and Trinity Bay and West Bay areas are least favorable (Table 10). Those most favorable areas are also the locations most heavily fished by the commercial fishery. Although a high possibility exists that the results of the comparisons may vary according to the variables or/and weighting system used, the trend is expected that the Redfish Bar complex is regarded as most suitable, and Trinity Bay least suitable for oyster populations.

TABLE 8.

Site comparison by weighting. Weight is given to each site up to

51. For infection intensity, weight 1 is given to the highest ranked site. For other variables, weight 1 is given to the lowest ranked site. Weight 0 is to sites without variable values.

			Condition	Infection	Gonadai-	Oyster	Oyster
Rank	Site	Total Weight	Index	Intensity	Somatic Index	Biomass	Abundance
1	Yacht Club Reef	185	27	16	45	48	49
2	Four Bit Reef	183	6	40	51	42	44
з	South Redfish Reef (east)	182	3	44	46	44	45
4	East Redfish Reef	174.5	12	31	32.5	51	48
5	South Redfish Reef (west)	171	10	25	37	49	50
6	Hanna Reel (north)	169	32	33	47	29	28
7	Lost Beezley Reef	165	19	13	41	45	47
8	Buoy 59	164	29	36	40	28	31
9	Gaspipe Reet	158.5	15	21	21.5	50	51
10	Confederate Reef	158	39	2	28	46	43
11	Mattie B. Reef	157	11	22	49	38	37
12	Todd's Dump	147	40	41	39	16	11
13	North Redfish Reef	145.5	17	26	16.5	47	39
14	Dickinson Reef	145	38	20	18	36	33
15	Buoy 53/55	145	31	23	27	34	30
16	Buoy 63	142	20	15	42	31	34
17	Bull Hill	142	33	19	26	35	29
18	Buoy 73/75	139	5	4	43	41	46
19	Richard's Reef	137	8	37	24	32	36
20	Dollar Reef	137	43	18	44	19	13
21	Gale's Reef	136	35	39	38	14	10
22	San Leon Reef	135.5	42	35	16.5	23	19
23	Levee Reef	135	44	11	31	24	25

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TABLE 8. Continued.

	Site	Total Weight	Condition Index	Infection Intensity	Gonadal- Somatic Index	Oyster Biomass	Oyster Abundance
24	Bull Shoais	133	2	29	34	33	35
25	Hanna Reef (south)	131	37	6	48	20	20
26	Red Bluff Reef	130	21	9	20	40	40
27	North Deer Island Reef	130	36	з	29	30	32
28	Half Moon Reef	128	26	7	50	21	24
29	Scott Reef	125.5	34	34	11.5	25	21
30	Tern Reef	124.5	13	10	21.5	39	41
31	Whitehead Reef	121	30	42	19	15	15
32	South Deer Island Reef	120	9	1	35	37	38
33	Bart's Pass Reef	118.5	14	8	11.5	43	42
34	Frenchy's Reef	114.5	41	30	32.5	9	2
35	Stephenson Reef	108	22	32	36	12	6
36	Lone Tree Reef	107	25	28	15	22	17
37	Pepper Grove Reef	101	24	24	13	26	14
38	Possum Pass Reef	99.5	16	43	5.5	17	18
39	Middle Reef	95	28	14	23	18	12
40	April Fools Reef	93	4	5	30	27	27
41	Big Beezley Reef	91	18	12	25	13	23
42	Morgan Point Reef	82	23	27	14	11	7
43	Fisher Reef	51.5	0	38	5.5	5	3
44	Dow Reef	39.5	7	17	5.5	6	4
45	Pelican Island Reef	38.5	0	0	5.5	7	26
46	Carancahua Reef (south)	35.5	0	0	5.5	8	22
47	Trinity Reef	32.5	1	0	5.5	10	16
48	Shell Island Reef	18.5	0	0	5.5	4	9
49	Green's Cut Shell	16.5	0	0	5.5	3	8
50	Carancahua Reef (north)	11.5	0	0	5.5	1	5
51	Vingt-et-un Reef	8.5	0	0	5.5	2	1

TABLE 9.

Regional comparison by ranking.

Region	Condition Index	Infection Intensity	Gonadal- Somatic Index	Oystər Biomass	Oyster Abundance
Redfish Bar to Smith Point	6	6	2	1	1
Clear Lake to Morgan Point	2	4	5	2	2
Dickinson Embayment	1	3	1	5	7
Houston Ship Channel	5	2	4	3	3
East Bay	4	5	3	6	6
West Bay	3	1	6	4	4
Trinity Bay	7	7	7	7	5

TABLE 10.

Regional comparison by weighting. Weight is given to each region up to 7. For infection intensity, weight 1 is given to the highest ranked region. For other variables, weight 1 is given to the lowest ranked region.

Region	Total Weight	Condition Index	Infection Intensity	Gonadal- Somatic Index	Oyster Biomass	Oyster Abundance
Redfish Bar to Smith Point	28	2	6	6	7	7
Clear Lake to Morgan Point	25	6	4	3	6	6
Dickinson Embayment	21	7	3	7	3	1
Houston Ship Channel	19	3	2	4	5	5
East Bay	18	4	5	5	2	2
West Bay	16	5	1	2	4	4
Trinity Bay	13	1	7	1	1	3

CONCLUSIONS

The spatial structure of oyster community attributes and health-related variables of Galveston Bay oyster populations showed that there are some other factors affecting oyster populations besides salinity, which was a major structuring force in the bay. These factors produced patch scale, or scale of similarity between sites, of 10 to 15 km and directional trends that often did not run parallel to salinity isohalines.

Three types of directional trends were observed: east-west orientation similar to the direction of the barrier reefs; northsouth orientation following the isohalines parallel to the Houston Ship Channel; and a trend diametric to the salinity isohaline sturcture.

Based on this study, the more productive areas are in the moderate-to-high salinity regions of the bay. The most productive areas in the bay are the Redfish Bar complex, Yacht Club Reef, the Dickinson Embayment, and sites along the Houston Ship Channel from Buoy 53 to Buoy 73/75. These areas produced the healthiest oyster populations in terms of density, biomass, and gonadal state.

Besides the broad regional patterns of conditions in the bay, one or two sites were locally more productive than the others in each region in terms of oyster density, biomass, egg quantity, and condition index. Sites at the extreme range of salinity such as in Trinity Bay, upper East Bay, and West Bay were characterized by oyster populations in poor condition based on health-related characteristics.

Comparison of the two sets of *P. marinus* analyses showed that false negatives were obtained at most sites due to the prolonged low-salinity episode that kept infection intensities low. Although the false negatives were corrected for, average prevalence for the entire bay was still unusually low compared to other historic data due to the long-lasting low salinity episode. To get the best estimate of *P. marinus* infection intensity and prevalence, examination of different oyster size classes is essential. Market-size and submarket-size oysters often varied in prevalence and infection intensity.

REFERENCES

- Andrews, J. D. 1965. Infection experiments in nature with Dermocystidium marinum in Chesapeake Bay. Chesapeake Sci. 6:60-67.
- Andrews, J. D. 1967. Interaction of two diseases of oysters in natural waters. Proc. Natl. Shellfish. Assoc. 57:38-49.
- Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U. S. Environmental Protection Agency, EPA-600/3-77-033, PB-269 604. 114 pp.
- Butler, P. A. 1954. Summary of our knowledge of the oyster in the gulf of Mexico. U.S. Fish Wildl. Serv. Fish. Bull. 55: 479-489.
- Choi, K-S., D. H. Lewis, E. N. Powell, P. F. Frelier & S. M. Ray. 1991. A polyclonal antibody developed from *Perkinsus marinus* hypnospores fails to cross react with other stages of P. marinus in oyster (*Crassostrea virginica*) tissue. J. Shellfish Res. 10:411-415.
- Choi, K-S., D. H. Lewis, E. N. Powell & S. M. Ray. 1993. Quantitative measurement of reproductive output in the American oyster, *Crassostrea virginica*, using an enzyme-linked immunosorbent assay (ELISA). Aquaculture Fish. Manag. 24:299-322.
- Choi, K-S & E. N. Powell. in press. Development of an immunological probe for quantification of oyster gonad. In: Sampling and analytical methods of the National Status and Trends Program National Benthic Surveillance and Mussel Watch Projects 1984-1992 Vol. II Comprehensive descriptions

of complementary measurements. NOAA Tech. Mem., Natl. Oceanic & Atmospheric Admin., Dept. Commerce.

- Choi, K-S., E. A. Wilson, D. H. Lewis, E. N. Powell & S. M. Ray. 1989. The energetic cost of *Perkinsus marinus* parasitism in oysters: quantification of the thioglycollate method. J. Shellfish Res. 8: 125-131.
- Cliff, A. D. & J. K. Ord. 1973. Spatial autocorrelation. Pion Limited. London, 178 pp.
- Craig, A., E. N. Powell, R. R. Fay & J. M. Brooks. 1989. Distribution of Perkinsus marinus in Gulf Coast oyster populations. Estuaries 12:82-91.
- Fisher, W. S., J. D. Gauthier & J. T. Winstead. 1992. Infection intensity of *Perkinsus marinus* disease in *Crassostrea virginica* (Gmelin, 1791) from the Gulf of Mexico maintained under different laboratory conditions. J. Shellfish Res. 11:363-369.
- Gabriel, K. R. & R. R. Sokal. 1969. A new statistical approach to geographic variation analysis. Syst. Zool. 18:259-278.
- Gauthier, J. D. & W. S. Fisher. 1990. Hemolymph assay for diagnosis of *Perkinsus marinus* in oysters *Crassostrea virginica* (Gmelin, 1791). J. Shellfish Res. 9:367-371.
- Gittings, S. R., T. J. Bright & E. N. Powell. 1984. Hard-bottom macrofauna of the East Flower Garden brine seep: impact of a long-term, sulfurous brine discharge. *Contrib. Mar. Sci.* 27:105-125.

- Hofmann, E. E., E. N. Powell, J. M. Klinck & G. Saunders. submitted. Modeling diseased oyster populations. 1. Modeling *Perkinsus marinus* infections in oysters.
- Hofmann, E. E., E. N. Powell, J. M. Klinck & E. A. Wilson. in press. Modeling oyster populations. III. Critical feeding periods, growth and reporduction . J. Shellfish Res.
- Hofstetter, R P. 1977. Trends in population levels of the American oyster, Crassostrea virginica Gmelin on public reefs in Galveston Bay, Texas. Texas Parks and Wildl. Dept. Tech. Series. No. 24. 90 pp.
- Hofstetter, R P. 1983. Oyster population trends in Galveston Bay 1973 - 1978. Texas Parks and Wildl. Management Data Series. No. 51. 33 pp.
- Jumars, P. A., D. Thistle & M. L. Jones. 1977. Detecting twodimensional spatial structure in biological data. *Oecologia* (Berl.) 28:109-123.
- Kennedy V. S. & L. B. Krantz. 1982. Comparative gametogenic and spawning patterns of the oyster *Crassostrea virginica* (Gmelin) in central Chesapeake Bay. J. Shellfish Res. 2:133-140.
- Mackin, J. G. 1955. Dermocystidium marinum and salinity. Proc. Natl. Shellfish Assoc. 46:116-128.
- Mackin, J. G. 1962. Oyster disease caused by Dermocystidium marinum and other microorganisms in Louisiana. Publ. Inst. Mar. Sci. Univ. Texas. 7:132-229.
- Mackin, J. G., H. M. Owen & A. Collier. 1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium*

marinum, n. sp. in Crassostrea virginica (Gmelin). Science (Wash. D. C.) 111:328-329.

- Marble, D. F. 1967. Some computer programs for geographic research. Special Publ. no. 1, Dept. Geography, Northwestern Univ., Evanston, Illinois.
- Moore, H. F. & E. Danglade. 1915. Condition and extent of the natural oyster beds and barren bottoms of Lavaca Bay Texas.
 Appendix II, Report United States Commissioner fisheries, Bureau of Fisheries Doc. no. 809, App. 2, 45 pp.
- Morales-Alamo, R. & R. Mann. 1989. Anatomical features in histological sections of *Crassostrea virginica* (Gmelin, 1791) as an aid in measurements of gonad area for reproductive assessment. J. Shellfish Res. 8:71-82.
- Powell, E. N., E. E. Hofmann, J. M. Klinck, E. & S. M. Ray. 1992. Modeling oyster populations I. A commentary on filtration rate. Is faster always better? J. Shellfish Res. 11:387-398.
- Powell, E. N., E. E. Hofmann, J. M. Klinck, E. Wilson-Ormond & M. S. Ellis. submitted a. Modeling oyster populations V. Declining phytoplankton stocks and the population dynamics of American Oyster (*Crassostrea virginica*) populations.
- Powell, E. N., J. Song & M. S. Ellis. submitted b. The status and longterm trends of oyster reefs in Galveston Bay, Texas.
- Ray, S. M. 1954. Experimental studies on the transmission and pathogenicity of *Dermosystidium marinum*, a fungus parasite of oysters. J. Parasitol. 40:235.

- Ray, S. M. 1966. A review of the culture method for detecting Dermocystidium marinum, with suggested modifications and precautions. Proc. Natl. Shellfish. Assoc. 54:55-69.
- Ray, S. M. 1987. Salinity requirements of the American oyster, Crassostrea virginica. In: Freshwater Inflow Needs of the Matagorda Bay System with Focus on Penaeid Shrimp. pp E.1-E.28. Eds. A. J. Mueller and G. A. Matthews. U. S. Dept. Commerce, NOAA Tech. Mem. NMFS-SEFC-189.
- Sokal, R. R. & N. L. Oden. 1978. Spatial autocorrelation in biology.

 Methodology. Biol. J. Linn. Soc. 10: 199-228.
- Sokal, R. R., N. L. Oden & J. S. F. Barker. 1987. Spatial structure in Drosophila buzzatii populations: simple and directional spatial autocorrelation. Am. Nat. 129:122-142
- Soniat, T. M. 1982. Studies on the nutritional ecology and ecological energetics of oysters from Galveston Bay, Ph.D. dissertation, Texas A&M University. 162 pp.
- Soniat, T. M. & M. S. Brody. 1988. field validation of a habitat suitability index model for the American oyster. *Estuaries* 11:87-95.
- Soniat, T. M. & M. L. Koenig. 1982. The effects of parasitism by Perkinsus marinus on the free amino acid composition of Crassostrea virginica mantl tissue. J. Shellfish Res. 2:25-28.
- Soniat, T. M. & S. M. Ray. 1985. Relationships between possible available food and the composition, condition and reproductive state of oysters from Galveston Bay, Texas. *Contrib. Mar. Sci.* 28:109-121.

- Soniat, T. M., L. E. Smith & M. S. Brody. 1989. Mortality and condition of the American oyster in Galveston Bay, Texas. *Contrib. Mar. Sci.* 27:127-141.
- Ward, G. H. & N. E. Armstrong. 1992. Ambient water and sediment quality of Galveston Bay: present status and historical trends, v. 1. Galveston Bay National Estuary Program Publ. 22, 181 pp.
- White, M. E., E. N. Powell, S. M. Ray & E. A. Wilson. 1987. Host-tohost transmissions of *Perkinsus marinus* in oysters (*Crassostrea virginica*) populations by the ectoparasite snail *Boonea impressa* (Pyramellidae). J. Shellfish Res. 6:1-5.
- Wilson, E. A., E. N. Powell, M. A. Craig, T. L. Wade & J. M. Brooks. 1990. The distribution of *Perkinsus marinus* in Gulf coast oysters: its relationship with temperature, reproduction, and pollutant body burden. *Int. Rev. gesamten Hydrobiol.* 75:533-550.
- Wilson, E. A., E. N. Powell, T. L. Wade, R. J. Taylor, B. J. Presley & J. M. Brooks. 1992. Spatial and temporal distributions of contaminant body burden and disease in Gulf of Mexico oyster populations: the role of local and large-scale climatic controls. *Helgo. Meeresunters.* 46:201-235.
- Wilson-Ormond, E. A., E. N. Powell, K-S. Choi & J. Song. in press. *Perkinsus marinus* assay. In: Sampling and analytical methods of the National Status and Trends Program National Benthic Surveillance and Mussel watch Projects 1984-1992 Vol. II Comprehensive descriptions of complementary measurements.

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