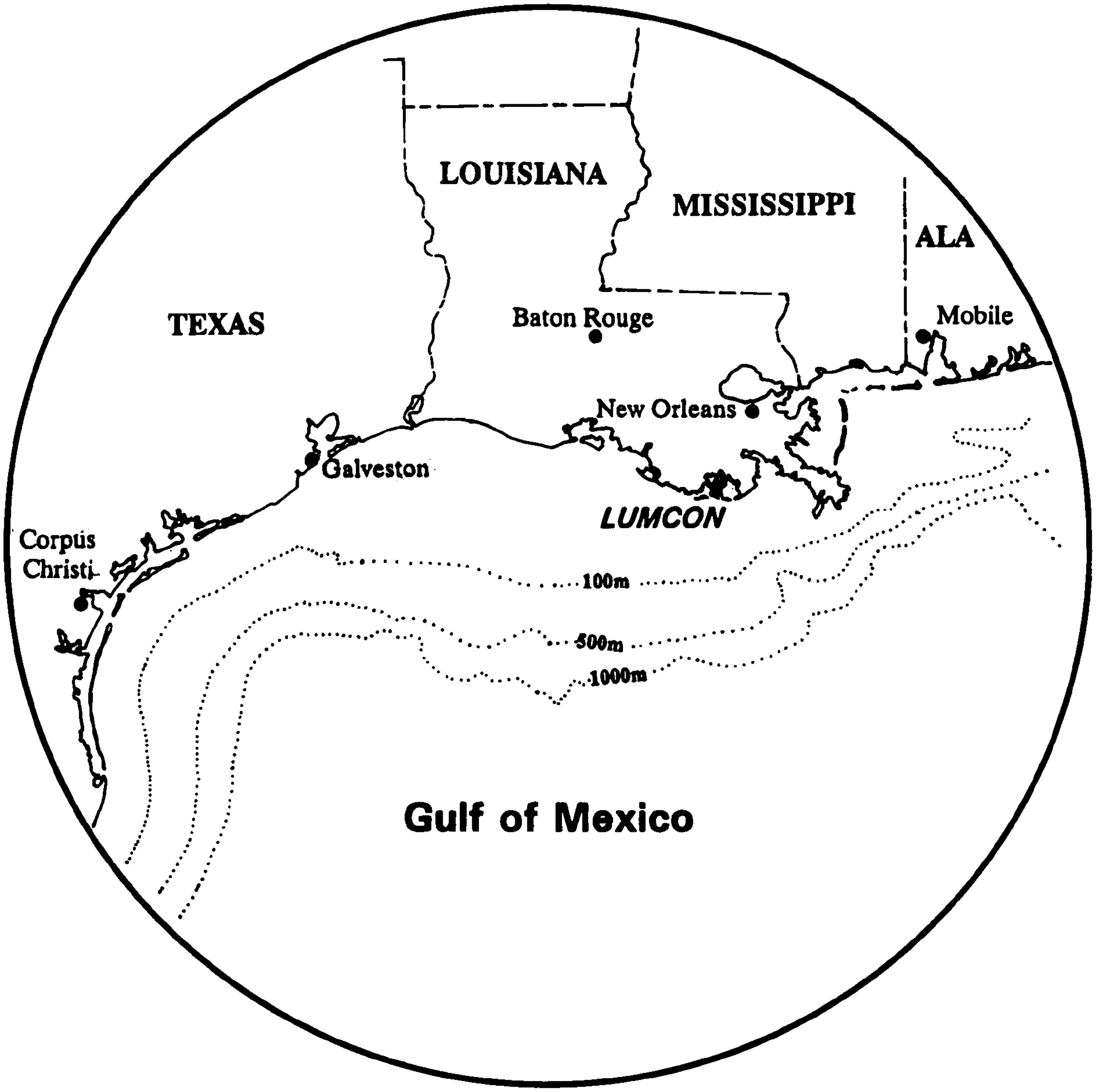
OCS Study
MMS 94-0007

University Research Initiative

Dominant Infaunal Communities at Risk in Shoreline Habitats: Burrowing Thalassinid Crustacea



U.S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region

Cooperative Agreement
University Research Initiative
Louisiana Universities Marine Consortium

OCS Study
MMS 94-0007

University Research Initiative

Dominant Infaunal Communities at Risk in Shoreline Habitats: Burrowing Thalassinid Crustacea

Authors

Darryl L. Felder
University of Southwestern Louisiana
Lafayette, Louisiana

and

Roger B. Griffis
University of Southwestern Louisiana
Lafayette, Louisiana

April 1994

Prepared under MMS Contract
14-35-0001-30470
by
Louisiana Universities Marine Consortium
8124 Highway 56
Chauvin, Louisiana 70344

Published by

U.S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region

Cooperative Agreement
University Research Initiative
Louisiana Universities Marine Consortium

DISCLAIMER

This report was prepared under contract between the Minerals Management Service (MMS), the Louisiana Universities Marine Consortium (LUMCON), and the University of Southwestern Louisiana. This report has been technically reviewed by the MMS and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of the Service, nor does mention of trade names or commercial products constitute endorsement or recommendation for use. It is, however, exempt from review and compliance with MMS editorial standards.

AVAILABILITY

Extra copies of this report may be obtained from the Public Information Unit (Mail Stop 5034) at the following address:

U. S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region
Attention: Public Information Unit (MS 5034)
1201 Elmwood Park Boulevard
New Orleans, Louisiana 70123-2394

Telephone Number: (504) 736-2519

CITATION

Suggested citation:

Felder, D. L., and R. B. Griffis. 1994. Dominant infaunal communities at risk in shoreline habitats: Burrowing thalassinid Crustacea. OCS Study MMS 94-0007. U. S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Regional Office, New Orleans, La. 87 pp.

ABSTRACT

This study documents the population biology and ecological role of ghost shrimp (*Lepidophthalmus* and *Callichirus*) in typical beachfront and bay habitats of the northern Gulf of Mexico. Seasonal variation in breeding, recruitment, growth, abundance, and biomass is documented in populations of these two common species. Size-class distributions are examined areally within intertidal and shallow subtidal habitats. Restoration of diminished populations occurs through a combination of planktonic recruitment and relocation of burrowed postlarvae. Both *Lepidophthalmus* and *Callichirus* influence the physical and chemical characteristics of intertidal habitats by increasing oxygenation and bioturbation of sediments during burrow construction and feeding. Populations of ghost shrimp increase the sediment-water interface by adding one to two m^2 of burrow wall surface area beneath each m^2 of sediment surface, and increase the flux of nutrients from sediments to the water column by pumping nutrient-rich water from burrows into the water column. Population estimates of bioturbation ranged from 1000 to 3500 g wet sediment m^{-2} day^{-1}. The relationships between these dominant burrowers and other macroinfauna, benthic microbiota, and benthic productivity are discussed. Previous studies suggest that ghost shrimp play important ecological roles in determining benthic habitat quality, and that reductions in their population densities may substantially alter physical, chemical, and biological characteristics of benthic habitats. In the northern Gulf of Mexico, ghost shrimp burrows on coastlines have been documented to form traps for entrainment of oil deep into sediments, and the shrimp themselves are subject to mass mortalities from beachfront oil accumulations. Oil contamination and physical perturbation of intertidal and shallow subtidal substrates threaten future mass mortalities of ghost shrimp that occur in extensive populations in many coastal habitats of the northern Gulf of Mexico.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Special thanks are due to a number of persons who helped in various phases of this project, especially those who volunteered their time without compensation. Visitors, family, and friends were often pressed into service, and this list includes Deborah Badgwell, John Christy, Peter Dworschak, Jennifer Felder, Robert Felder, Martha Griffis, Rafael Lemaitre, John Meriwether, Dennis Remmert, Sergio Rodrigues, and Ursula Schober. In addition, the contributions of a number of undercompensated student workers, technicians, and graduate students were essential to the success of this study, and this list includes Lisa Bennett, Ann Christian, Denise Guillot, John Matese, Tom Matthews, Ed Mouton, Sergio Nates, James Powers, Julie Roberts, Joseph Staton, Tami Tailliac, Philip Thevenet, and Todd Zimmerman. We also extend our gratitude to Mona Pomier whose secretarial skills were essential in report preparation and budget management throughout this project. Likewise, we were dependent upon Melanie Comeaux, our grants accountant, for keeping us on track in all matters of finance.

For their assistance in providing dependable access to small boats, we sincerely thank Steve Rabalais and his crew in the Vessel Operations office at the Louisiana Universities Marine Consortium (LUMCON) Marine Center in Cocodrie. Likewise, we acknowledge the contribution of supplementary funds to cover ancillary components of this project through the LUMCON Foundation Graduate Student Research Awards Program. These funds allowed RBG to expand certain facets of this project in ongoing research toward his doctoral degree. Similarly, we are grateful to Jose Vicente Mogollon, Gustavo Moreno and their associates at PROEXPO in Colombia who provided funding for several trips to estuaries on the Caribbean coast of Colombia which facilitated comparisons to thalassinid populations of that region and led to participation by DLF in a conference on thalassinid crustaceans held in Cartagena during October, 1992. The interest and support of Clara Maria Sanin Posada and her colleagues at the Asociacion Nacional de Acuicultores de Colombia is appreciated, and will lead to further study of these animals in coastal ecosystems of Mesoamerica in years to come.

We are grateful to Jennifer Lo, Harvey Landry, Paul Sammarco and others affiliated with the LUMCON Special Projects Office, Baton Rouge, for all of the bookkeeping, troubleshooting, reminding of deadlines, securing of budget adjustments, and granting of extensions that make a project of this scope work in spite of the difficulties. Finally, we offer our sincere thanks to the former Executive Director of LUMCON, Donald Boesch, who promoted the development of an MMS University Research Initiative for Louisiana, and encouraged our participation in this program.

CHAPTER 1. EXECUTIVE SUMMARY

This report details findings of a project which focused on the population dynamics and ecology of burrowing thalassinid mud shrimp, an assemblage which dominates infaunal communities of intertidal and shallow subtidal environments in the northern Gulf of Mexico. Given that loss of these dense assemblages had been previously reported to occur in the course of oil spills in this region, the intent of this project was to specifically document the potential scope and secondary ecological impacts of such losses. To document the scope for loss required detailed quantification of population densities, reproduction and growth potentials, recruitment potentials, biomass, bioturbation capacity and biogeochemical impacts. While it was primarily on these studies that the project focused, the process of investigation also led us into studies of genetics and diversification in these animal communities, particularly in those instances when such tangential studies were essential to scientific interpretations of our findings.

The approach for this study, which began in late summer of 1989, involved the selection of two typical sites, Bay St. Louis and Isles Dernieres, that were densely populated by the three most common intertidal species of northern Gulf thalassinid shrimp. At the time this study was initiated, these three species were considered by most workers to be members of the genus *Callianassa*, and it was thus thought that they were closely related, but with some obvious differences in physiological adaptations and habitat preference (Felder 1979). It was in the earliest phases of this study that we came to recognize that these three species were instead more correctly assignable to two separate genera (see Manning and Felder 1991), *Lepidophthalmus* and *Callichirus*. The subject species *Lepidophthalmus louisianensis* is typically concentrated along muddy shorelines of low salinity estuaries, while the species *Callichirus islagrande* and *C. major* densely populate sandy beaches facing higher salinity embayments and the Gulf of Mexico (Figure 1). Of the latter two species, *C. islagrande* was found to be by far the more common in the upper intertidal of sandy habitats, especially on high energy beaches facing the Gulf of Mexico, while *C. major* was typically restricted to the subtidal and extreme lower intertidal in much lower population densities than those for *C. islagrande*. Because of this inaccessibility and lower population density, few of our routine measures could be applied to the monitoring of *C. major* populations.

In order to define precisely the subject populations for this study, we found early into the project that we had to address a confusing history of taxonomy for these species. Ultimately we resolved the issue of identity by a combination of systematic methods including morphological studies and allozyme analyses, both of which were ancillary to the primary objective of the project but essential to definitively identify the subject populations (see Felder and Rodrigues 1993; Staton and Felder in press a, b). This resulted in our clearly documenting that *L. louisianensis* was a species of full rank, rather than a subspecies as implied in earlier treatments under *Callianassa jamaicense* var. *louisianenis*; this also showed that *L. louisianensis* was endemic to the northern and northwestern Gulf of Mexico and morphologically and genetically distinct from populations in the Caribbean, southwestern Gulf of Mexico, and Mesoamerica. *C. islagrande* was confirmed to be a northern and western Gulf of Mexico endemic with close relatives only in remote locations of west Africa and the eastern Pacific. Finally, *C. "major"* in the Gulf of Mexico, was found to be genetically distinct from other populations treated under that name along the southeastern U.S. Atlantic seaboard and the Atlantic coast of South America. However, as related systematic studies are still underway, the name *C. major* has been retained in usage for Gulf populations in the present report. Overall results of the background genetic and systematic studies did have bearing on the conclusions and recommendations stemming from this project, as are listed below. Of the two primary study sites selected, the estuarine western shoreline of Bay St. Louis, Mississippi, was

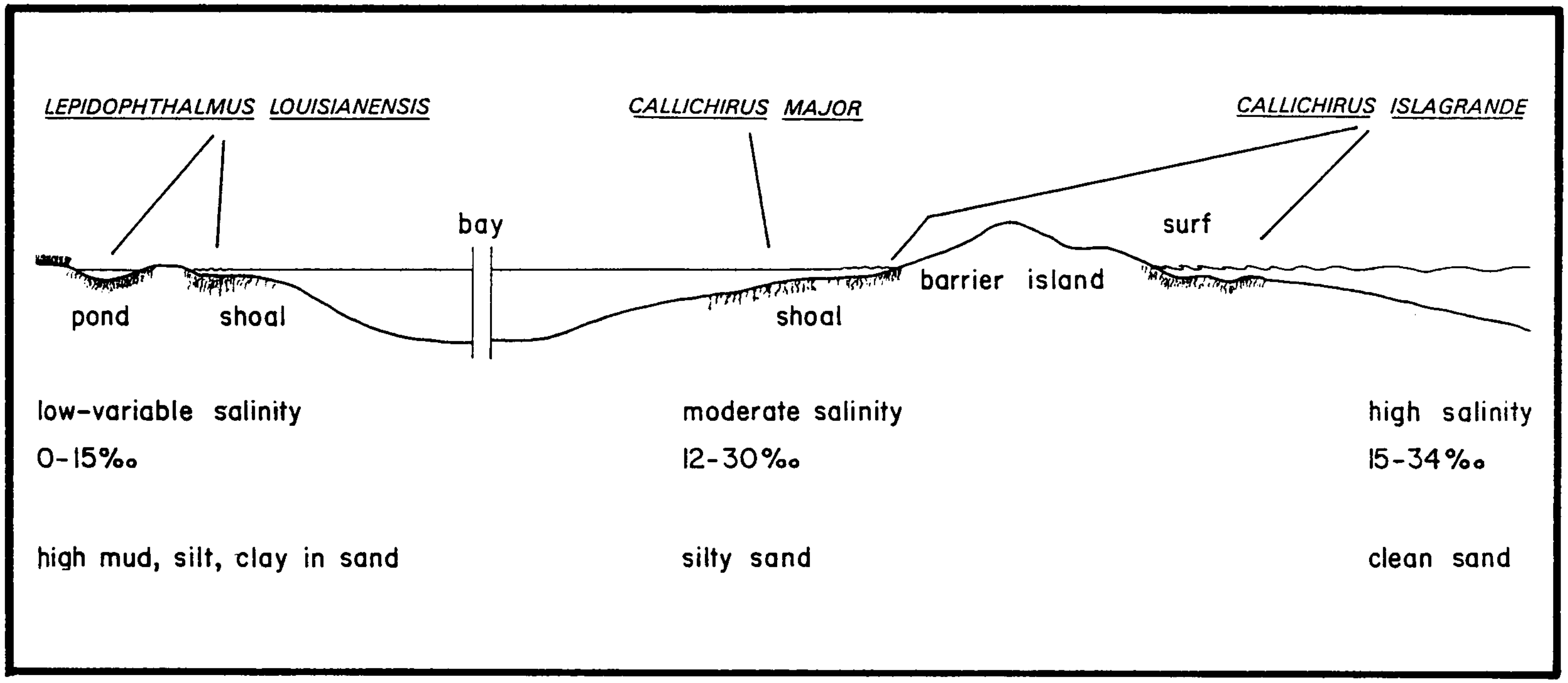


Figure 1. Typical habitats of the three most common thalassinid shrimp in the Gulf of Mexico.

chosen to be most appropriate for monitoring of *L. louisianensis*, and Isles Dernieres, a barrier island chain in Louisiana, was chosen to be most appropriate for monitoring of *C. islagrande* and *C. major* populations. Both selected sites are areas of potential impact by oil spills, one estuarine and the other open-beach marine. The site selected for study of *L. louisianensis* was different in this respect from a previously monitored population (Felder and Lovett 1989). Populations were monitored quarterly for a period of over two years, and measurements were made to determine densities, biomass, distributions, age and growth structure, and reproductive periodicity. Burrow depths, surface areas, and volumes were determined by resin casting in order to further characterize impacts of these populations. Grain sizes in burrow walls and the sedimentary matrix were measured and overall bioturbation rates were estimated. Other measures of biological activity in these populations included effects on oxidation-reduction conditions, pore and burrow water nutrient concentrations, subsurface oxygen concentrations, and relationships to benthic productivity. Determination of trophic relationships were based upon stomach content analyses and carbon ratio studies, as well as analyses of thalassinid fecal pellets and microbial flora of surrounding sediments.

Most of the results of these monitoring efforts are detailed in the three chapters that follow. The data contained there serve to document such population parameters as (i) seasonality in density and biomass, relative to shoreline; (ii) size partitioning within these distributions; (iii) peak periods of ovarian development, egg laying, and larval recruitment; and (iv) typical rates of growth and mortality in healthy populations. Studies of burrow morphology have elucidated relationships between animal size and burrow characteristics which, together with data on burrow densities and population size structure, allow us to extrapolate burrow effects across large areas of habitat. Likewise, measurements of bioturbation rates by individual animals have facilitated estimates of sediment overturn by the overall populations, giving insight to overall impacts of their dominance in the infaunal assemblage and their conveyer-like effect on the vertical redistribution of sediments, nutrients, and microflora. Measurements of subsurface oxygen levels, redox conditions, and nutrient contents of burrow and pore waters have in turn further quantified direct impacts of these populations on cycling of nutrients between benthic sediments and the water column, and have suggested possible relationships to productivity of benthic microflora of shallow sediments and burrow walls. Measurements of carbon ratios, identification of stomach contents, and analyses of fecal pellets have helped to establish the food dependencies of these animals as well as nutrient contributions of fecal materials to the sediment surface.

Overall, our functional studies of these dense populations have shown them to convert intertidal and subtidal habitats to porous, hydrological processing grounds of intense biological activity. Somewhat analogous to the functioning of a "gill", greatly enhanced water exchange through these burrow-riddled shoreline sediments is facilitated by the very active ventilatory activity of subsurface thalassinids. In turn, subsurface burrow waters, pore waters, and sediments are oxygenated, high concentrations of reduced nutrients are moved to the sediment surface in expelled burrow water, food is brought in from surface waters and benthic sediments, and an abundance of nutrient-loaded fecal pellets is delivered to the sediment surface. While these animals consume oxygen when available, they are facultative anaerobes and can subsist for long periods of time under hypoxic or anoxic conditions (Felder 1979).

The findings of this study are relevant to management in terms of (i) providing an understanding of ecological value to be placed on these beach populations and their associated biota; (ii) documenting baseline measures of population and functional parameters in healthy stocks, against which impacted stocks might be later judged; (iii) providing insight into when (seasonally) and where (geographically) these thalassinid stocks are at greater or lesser risk from spill-related events; and (iv) suggesting ameliorative or mitigating measures that might be taken to reduce negative impacts of spills or clean-up efforts on these populations. Of the resources provided here for management, that concerning ecological value is deemed of particular importance. In simplest terms, the value of intertidal mudflat and beach habitats is easily underestimated, given their superficially barren and unvegetated appearance, especially in comparisons to such habitats as *Spartina* marshes, seagrass flats or oyster reefs. We provide measures for use in ecological valuation which, in addition to esthetic considerations, justify enhanced efforts to protect beach and tidal flat habitats in the Gulf of Mexico from spills and to properly ameliorate effects of such spills when and if they should occur. The high measures of standing biomass that we report, as well as the evidence that we present for positive impacts on nutrient cycling and system productivity, characterize extremely active biological assemblages that can now be quantitatively evaluated in comparison to other coastal biotopes at risk.

While not intended at the outset of this study, our ancillary genetic and morphological studies also proved to bear on management. For instance, we have found that all three of the species under study are genetic endemics to the northern and northwestern Gulf of Mexico; this infers that population dynamics or processes here reported and management strategies here inferred will not necessarily apply directly to other populations in other geographic areas. However, while unique populations, we have also found that they are widely distributed within the northern and northwestern Gulf, that local demes within the Gulf are not highly insular in terms of our allozymic genetic measures (= the populations are well mixed across the overall range, without evidence of locally divergent demes deserving individual conservation or management), and that there is thus not high risk of genetically significant extinctions from localized spill events.

The second area of contribution to management (items ii and iii above)--that of documenting density, distribution, biomass, growth and recruitment parameters in healthy populations of these dominant infaunal animals--provides baseline measures against which to judge future impacts of habitat oiling and success of recovery in these biotopes. For example, the population data demonstrate that there are inherent seasonal variations in numbers, biomass and areal distributions of both the *Lepidophthalmus* and *Callichirus* populations, and these should not be confused with locally induced mortalities attributable to spills. However, these data also portray such cycles as they have been documented to occur in healthy populations over several years of monitoring, and thereby establish benchmark population measures and measures of their secondary ecological effects for comparison to levels in potentially damaged or recovering populations. Documentation of seasonal periodicity of reproduction and recruitment, along with seasonal changes in just where such events are centered relative to the shoreline, serves to identify seasonal periods at which given population cohorts in given beach settings may be at greater risk of spill-induced mortalities.

Finally, the data presented in this report also bear on decisions by management regarding tools and techniques of cleanup or population restoration that may be undertaken following beaching of spilled oils in intertidal mudflat and beach environs. For example, we have documented burrow depths that commonly exceed 0.75 m and sometime exceed two meters in these populations; we have documented population survival after burrowed animals have been overlain by up to 1 m of new sand; we have evidence of beachward recruitment from subtidal components of the population following storm-induced mortalities on beachfronts. All of the foregoing bear upon sediment manipulations (scraping etc.) and subsequent population re-establishment as may follow an oil spill event. Likewise, we have documented nutrient quality of thalassinid fecal pellets and expelled burrow water that are comparable to microbe-stimulating fertilizers sometimes applied artificially to spilled oil in intertidal environs. Assuming that longshore transport of such nutrients serves to enhance microbial degradation of local shoreline oil accumulations, we have described a potentially important component of the degradation process in natural shoreline communities of the northern Gulf of Mexico. The management interest should then be vested in determining the levels and patterns of oiling that can be tolerated and accommodated by these populations and their associated microbes, without compromising their beneficial activities.

As a result of findings from the present study and in retrospect of our experience in this project, we suggest several topical areas for further investigation:

(i) Additional studies are needed to more clearly quantify the coupling of biogeochemical effects and fecal pellet production by thalassinid burrowing shrimp to primary production in the water column, benthic microbial productivity, and benthic microbial degradation processes. At present, we have only tangential evidence of these relationships. An ideal system for exploration of such relationships is afforded in closed systems which are richly populated by thalassinids, such as penaeid shrimp culture ponds in Colombia. As an ancillary component of this project, we have conducted some initial studies there of the species *L. sinuensis*, which reaches incredible densities and shows profound effects on pond production; our limited comparisons to that species are included occasionally in the following chapters. Much additional experimental work is needed, either with *L. sinuensis* where it has invaded artificial ponds of Colombia, or in similar artificial large-scale mesocosms established locally. We were not satisfied that our attempts to date to investigate nutrient cycling processes in smaller scale laboratory mesocosms produced results representative of those in natural settings, and we in general question the results reported from such systems where they have been reported in literature. We are currently working to measure flux in benthic plastic field enclosures, but even these appear to alter flow dynamics.

(ii) Additional work is needed to define the role of thalassinid fecal materials as natural fertilizers for oil-degrading microbes, as well as sublethal effects of oil spills on these thalassinid shrimp populations and their associated microflora. It is our intention to continue ongoing studies of fecal pellet nutrient concentrations and work toward overall estimate fecal pellet production rates. However, experimental studies of direct dependencies between these nutrients and populations of hydrocarbon-degrading microbes have yet to be undertaken.

(iii) Additional work is needed to define the relationship to associated meiofauna for each of the subject species. While we found that there was definite dominance of macro-infaunal populations by the subject species under study, we have only begun to study differential effects of each thalassinid species on associated meiofauna. Such studies will more completely defined the full scope of assemblage impacts that each of the subject species has in shoreline environments, and will thus more fully define the potential impact that may accompany loss or redistribution of thalassinid populations through oil spill or clean-up effects.

(iv) Additional work is needed to extend observations further into shallow subtidal shoreline environs. The present study was, by design, focused on intertidal and shallow subtidal shoreline environs accessible from selected beaches. However, we found evidence of differential population parameters at the seaward extremes of our study areas, at the limits of our wadable transects. Techniques must be developed for deep-core sampling from small, shallow-draft boats in order to extend observations seaward to the deepest extremes of the subject thalassinid populations. Only then can we fully estimate areal expanse and biomass of local populations, project loss from subtidal oiling, or appreciate recruitment or recovery potential of the populations when mortalities may be restricted to intertidal beaches.

(v) Detailed observations and recovery monitoring are needed following any future beaching of spilled oil in thalassinid-populated habitats. As almost all Gulf beaches are populated by these animals, the opportunities for such studies (provided funding is available) occur all too often. To date, the literature reports, while documenting mortalities in these thalassinid populations, are for the most part anecdotal and do not include detailed monitoring of population recovery. On the basis of our observations and a review of literature concerning unimpacted populations, we would predict mass mortalities would be accompanied by a major loss of shallow benthic and water column nutrient supply, major losses of primary and secondary production in these environments, compaction and reduction of overturn of beach sediments, highly altered subsurface redox conditions, and dramatic effects on the overall microbial, macroinfaunal and meiofaunal assemblages.

CHAPTER 2: POPULATION DYNAMICS OF THE ESTUARINE GHOST SHRIMP, *LEPIDOPHTHALMUS LOUISIANENSIS*

INTRODUCTION

The ghost shrimp *Lepidophthalmus louisianensis* (formerly treated as *Callianassa louisianensis*; see Felder and Rodrigues 1993) is a common member of the benthic macrofaunal community of estuaries in the northern Gulf of Mexico (Willis 1942, Hedgpeth 1950, Wass 1950, Phillips 1971, Felder 1973). Dense populations of these fossorial shrimp are found in intertidal and shallow subtidal benthic habitats where they construct burrows that permeate extensive areas of nearshore estuarine sediments (Felder and Lovett 1989, Lovett and Felder 1989). Previous studies suggest that the construction and maintenance of macrofaunal burrows by ghost shrimp and other burrowers may have significant effects on the flux of nutrients (Koike and Mukai 1983, Waslenchuk et al. 1983, Colin et al. 1986) and the turnover of sediments (Aller and Dodge 1974, Roberts et al. 1982, Suchanek 1983, Suchanek et al. 1986, Griffis and Suchanek 1991), which in turn may influence nutrient cycling and productivity in these habitats (Forbes 1976, Branch and Pringle 1987, Dobbs and Guckert 1988, Forster and Graf 1992, Murphy and Kremer 1992). The effects of ghost shrimp on these types of ecological parameters in habitats of the northern Gulf of Mexico were the subject of a separate study (see Chapter 4). Given the potential ecological importance of these species, this study was designed to determine the density, distribution, demographics, growth, and reproduction of a large population of the estuarine ghost shrimp *Lepidophthalmus louisianensis*. Little is known about the population dynamics and reproductive biology of most thalassinoid shrimp including *L. louisianensis*, making information on population dynamics critical to estimates of how populations may respond to physically or chemically induced habitat degradation.

METHODS

The distribution and population biology of *Lepidophthalmus louisianensis* was studied at the Washington Street Beach, a large public beach along the western shore of Bay St. Louis in Hancock County, Mississippi. This site has been occupied by an extensive population of ghost shrimp since before 1989 when it was first surveyed as part of this study. All distribution data and population samples were collected from this site on at least quarterly intervals from December 1989 through June 1993. The site consisted of an extensive intertidal flat composed of muddy quartz sands containing relatively little organic matter and exhibiting an alternating series of small bars and troughs typical of a low energy bay beach.

The density and distribution of the *Lepidophthalmus louisianensis* population were determined by counting burrow openings on the sediment surface. The number of burrows per 0.25 m^2 were counted during low tide at 2-5 m intervals along two permanent transects extending perpendicularly from the beach crest for approximately 90 meters. The circular, smooth-walled burrow openings of this species were distinguishable from the few other macrofaunal burrows (primarily of polychaetes) present at this site. Counts were also made of subsurface burrow openings after excavation of the surface sediment in order to correlate the actual numbers of burrows to burrow surface openings. The relationship between surface hole counts and subsurface burrow densities is shown in Figure 2. The relationship between surface and subsurface burrow counts did not appear to differ between seasons and had a slope close to 1 ($Y = 1.059(X) + 5.8459$; $r = 0.973$) indicating that over most of the observed range, surface hole counts were an accurate measure of actual burrow densities. Polyester resin casts of field burrows indicated that burrows typically have one opening to the surface, and that each burrow is usually occupied by a single individual (see Chapter 4). Thus population densities were estimated from surface hole counts assuming a 1:1 relationship between number of burrow openings and number of individuals per unit area.

Populations were collected during low tide using water pressure generated by a portable gas-powered pump to liquify the sediment and flush ghost shrimp from their burrows. This method allowed large numbers of individuals to be collected alive and undamaged. At each sampling period, collections were made from inner (25-35 m from beach crest) and outer (> 70 m from beach crest) sites in order to determine within population variation based on beach position. Ghost shrimp were immediately placed in individual plastic vials and then into large holding containers filled with local seawater for transport to the laboratory. In the laboratory, all individuals were sexed, weighed (WW; wet weight following blotting with tissue paper), and measured for carapace length (CPL) and total length (TL). Total length was measured as the distance from the tip of the rostrum to the posterior margin of the telson using a flat ruler to the nearest millimeter. All other morphometric measurements were made using dial calipers to the nearest 0.01 mm. Carapace length was measured as the distance between the tip of the rostrum and the posterior margin of the carapace. Chela measurements (made only on males) included chela height (ChH; maximum height of the propodus from ventral to dorsal margin), chela width (ChW; maximum width of the propodus from bulbous area on flexor to extensor surface) and chela length (ChL; maximum length of the propodus along ventral margin). Ovarian width (OW; width of right ovary visible dorsally within the third abdominal segment) was determined in females. After measurement, some population samples were lyophilized, weighed (DW; dry weight), and then ashed (480 °C for 6 hours) for calculation of ash-free dry weight (AFDW). Carapace length was used as the primary metric of body size because it was less variable with changes in reproductive state and less susceptible to measurement error than other body measures. Regression analyses were used to determine the relationships between CPL and ovary width to identify morphometric patterns of growth and reproduction in this population.

RESULTS

Distribution and Abundance

The distribution and abundance of *L. louisianensis* varied both spatially along the intertidal gradient and temporally by season and year at the Bay St. Louis study site. The density and distribution of *L. louisianensis* during the winter (December-February), spring (March-May), summer (June-August), and fall (September-November) quarters along the intertidal transect from beach crest to low water is shown in Figures 3-6 for each year sampled. Population density increased rapidly from the beach crest to 20 meters and then typically reached a plateau until after 50 meters when densities declined slightly and appeared to level off at lower levels. The highest population densities were recorded in the Fall 1990

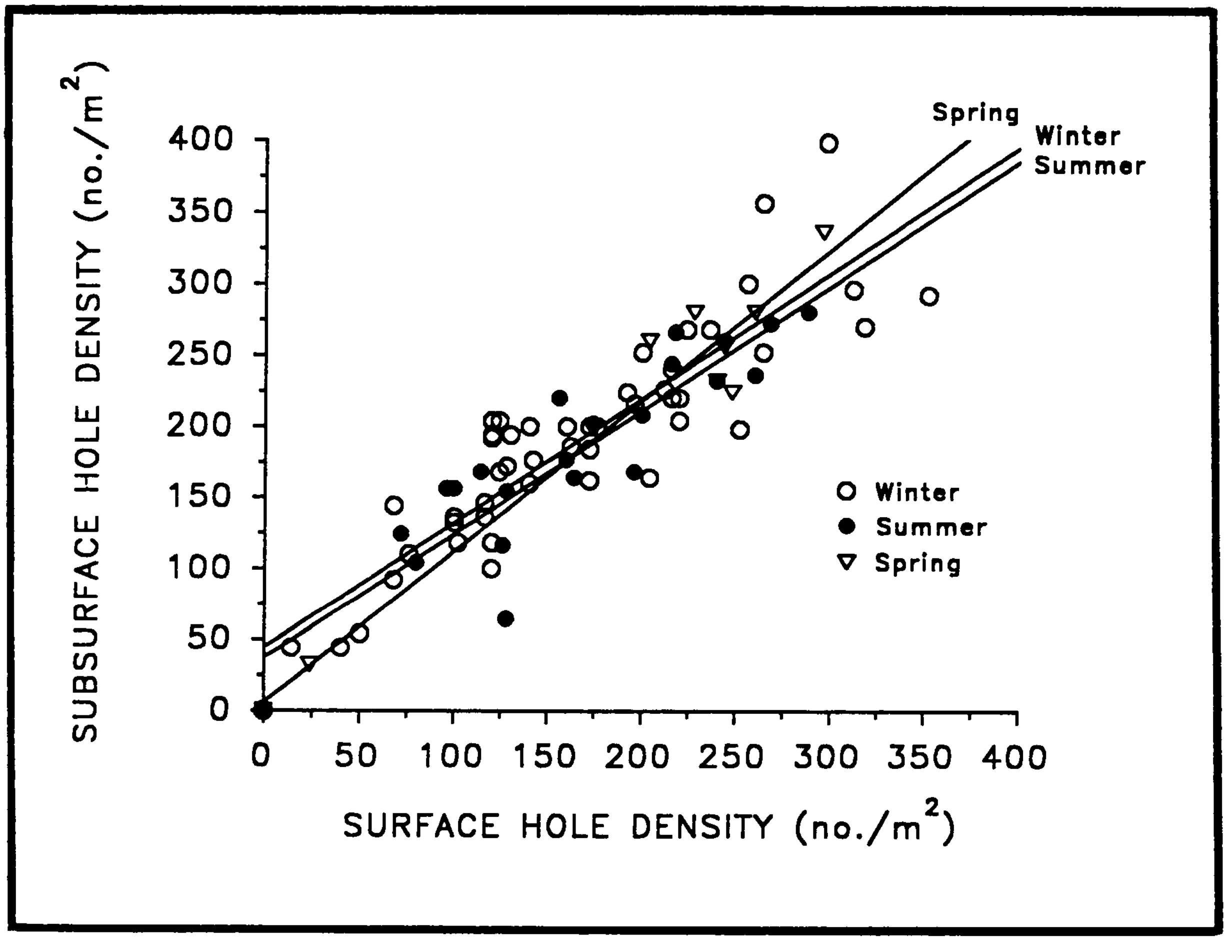


Figure 2. Relationship between surface and subsurface densities of *L. louisianensis* burrows in intertidal zone of study site in Bay St. Louis, Mississippi.

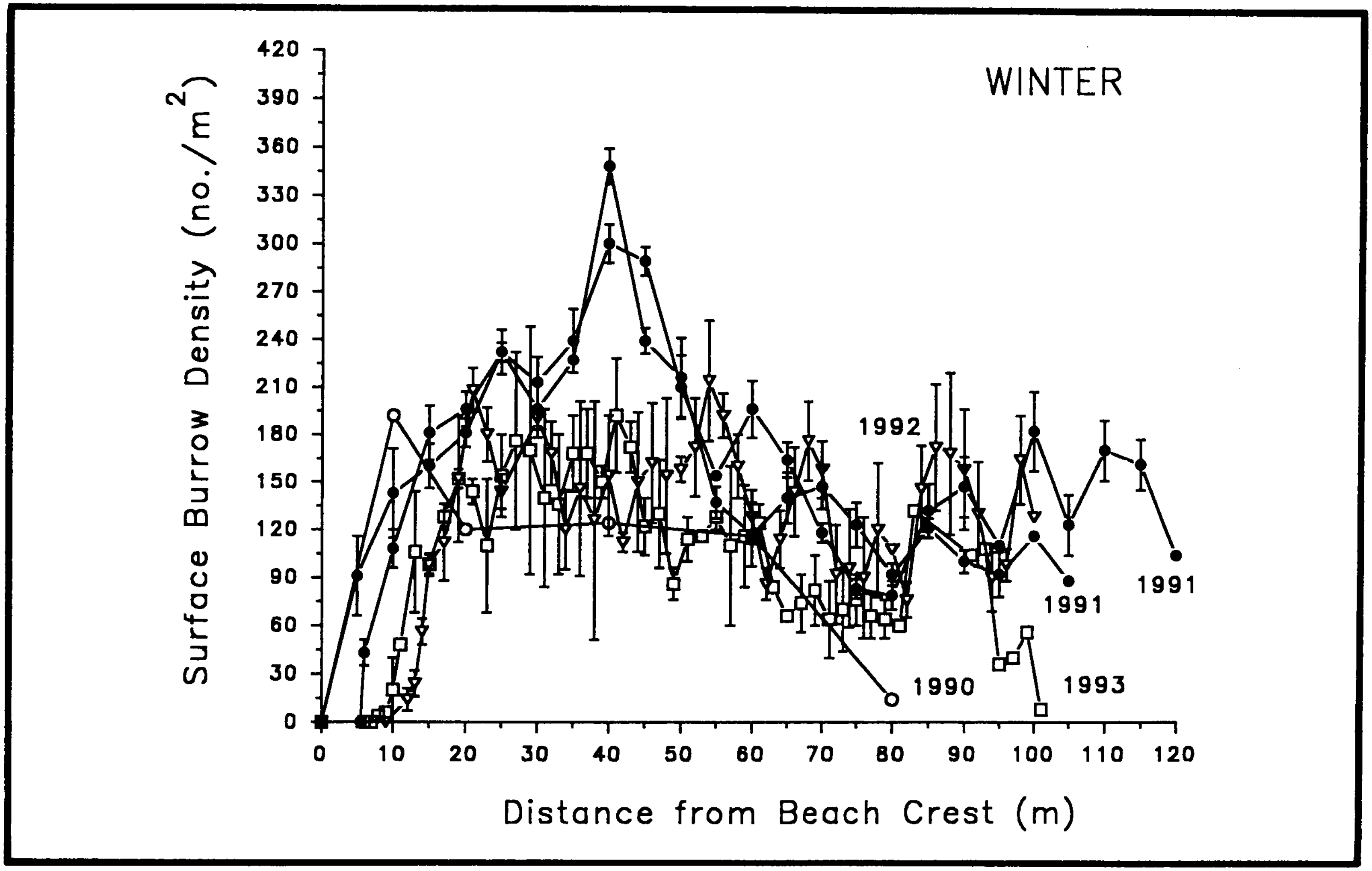


Figure 3. Changes in *L. louisianensis* burrow densities with distance from beach crest during winter surveys from 1990 to 1993.

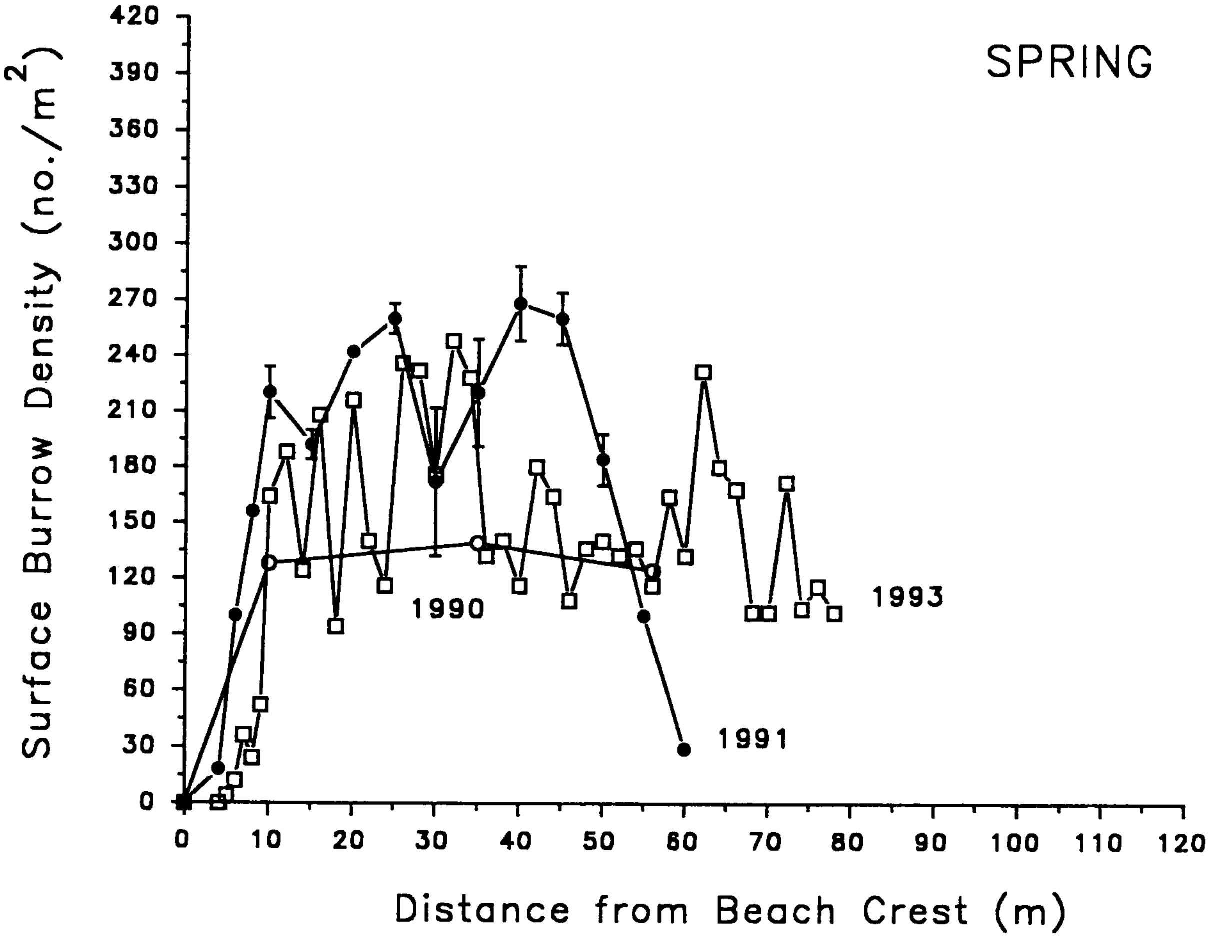


Figure 4. Changes in *L. louisianensis* burrow densities with distance from beach crest during spring surveys from 1990, 1991, and 1993.

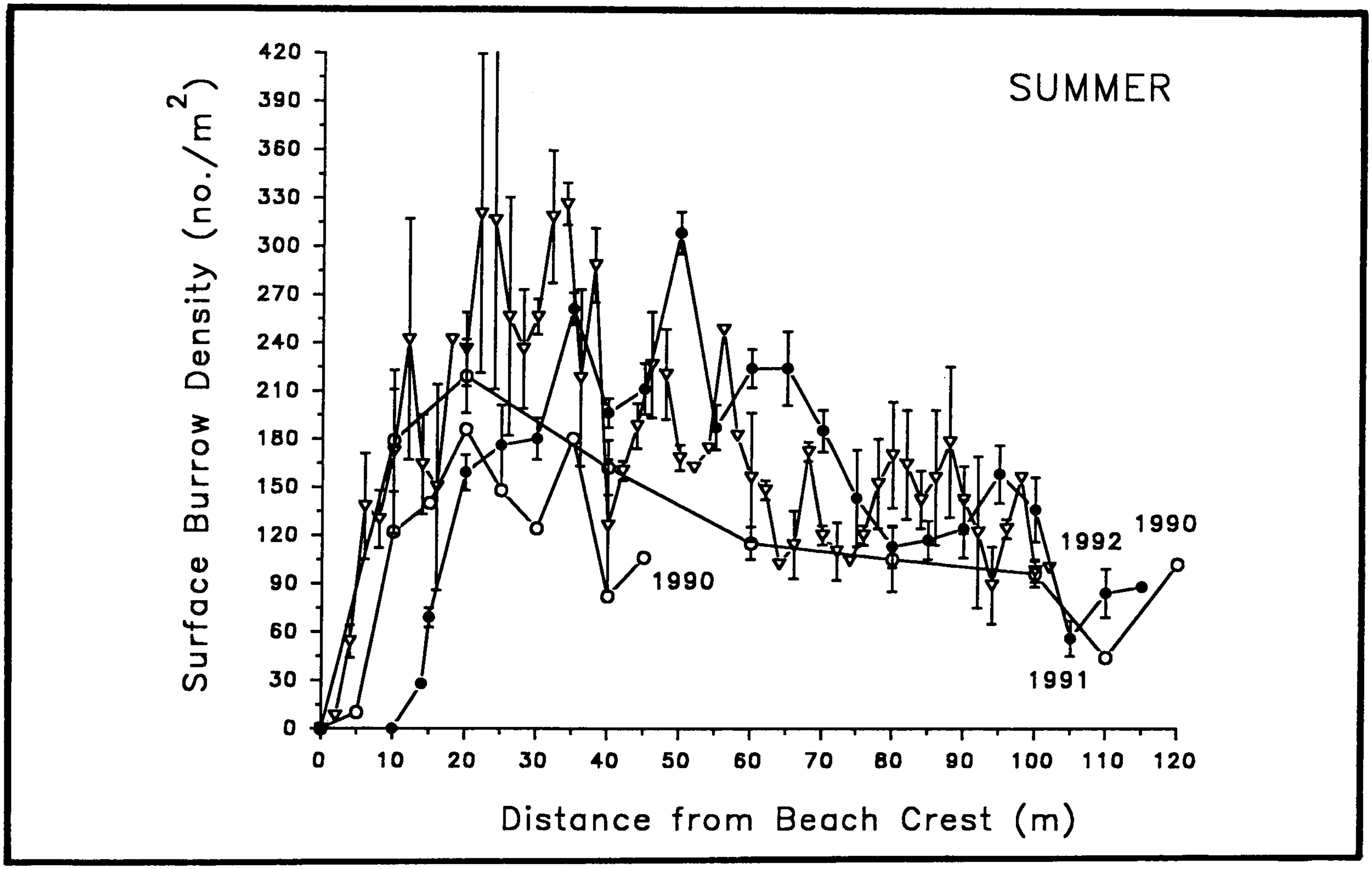


Figure 5. Changes in *L. louisianensis* burrow densities with distance from beach crest during summer surveys from 1990 to 1992.

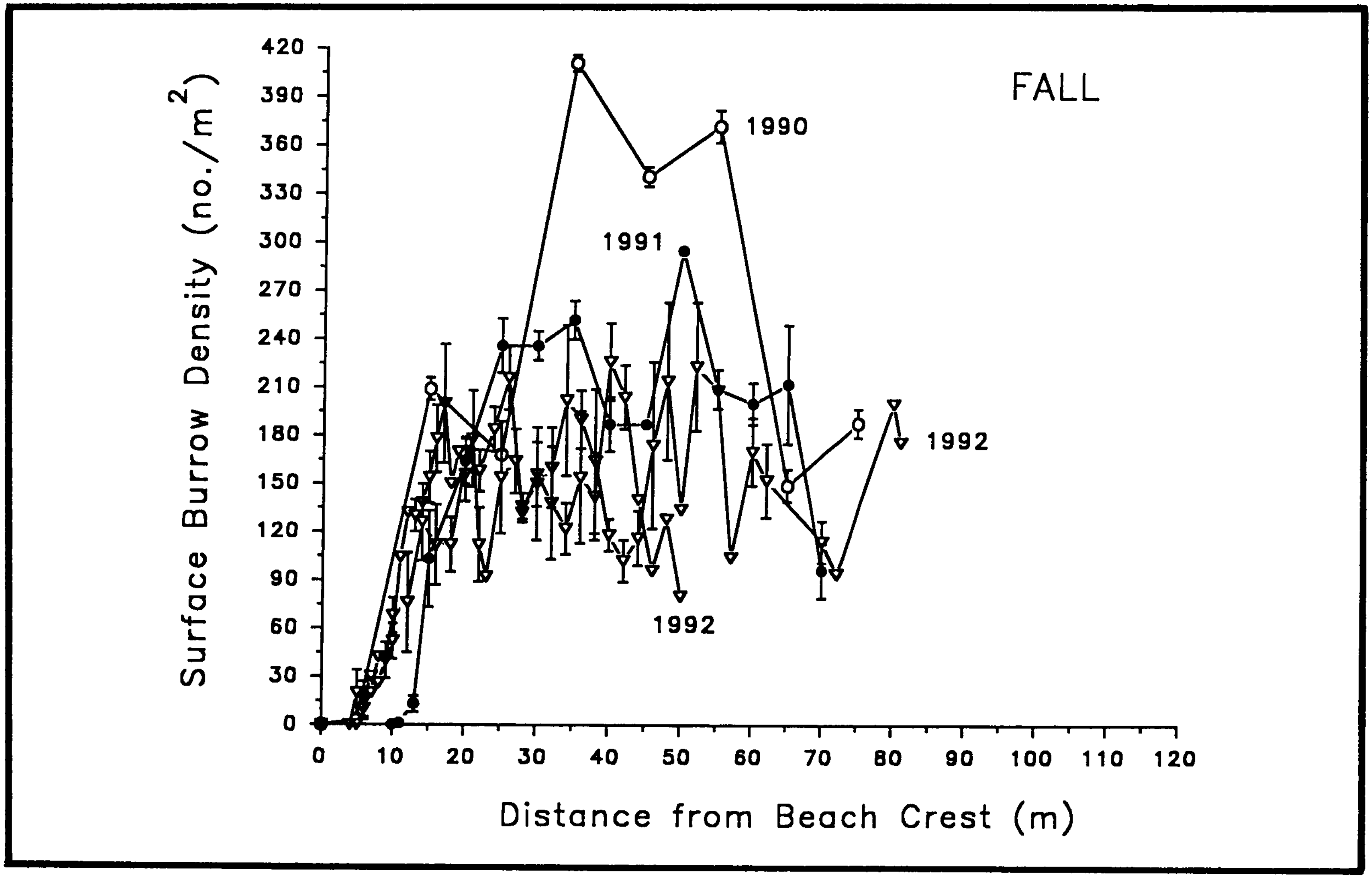


Figure 6. Changes in *L. louisianensis* burrow densities with distance from beach crest during fall surveys from 1990 to 1992.

and Summer 1992 when surface hole counts reached 420 m^{-2} in the mid-intertidal zone. Surface hole counts were generally higher in the summer and fall reflecting recruitment and perhaps increased burrowing activity. There was also significant within season, interannual variation in population densities. Burrow densities more than doubled from Summer 1990 to Fall 1990 and remained high through Winter 1991. Densities during the 1992 and 1993 Winter seasons were nearly half the densities observed during Winter 1991.

Demographics

The size-frequency distribution of males and females collected in population samples from the mid-intertidal (inner beach) and low-intertidal (outer beach) sites are shown in Figures 7 and 8, respectively. The dates, sample sizes, and sex ratios of the population samples are shown in Table 1. A total of 2122 individuals were collected from the inner ($n = 1102$) and outer ($n = 1020$) beach sites. Individuals ranged in size from 2 to 18 mm carapace length and 8 to 62 mm total length. Multiple cohorts were distinguishable from the size-frequency plots and growth rates were estimated by visual inspection of shifts in mean carapace length of cohorts through time. This preliminary review suggested that mean carapace length increases between 0.25 and 0.75 mm $month^{-1}$ or that individuals grow at a rate of 3 to 9 mm $year^{-1}$. Growth rates appeared to be similar for the inner and outer beach sites, higher for small individuals, and highest during the spring and summer months. Further analysis of the data is required for more quantitative estimates of growth rates for different sites, sizes and seasons.

Reproduction

Three components of the reproductive cycle of *L. louisianensis* were studied in detail. These were (1) ovary development, (2) timing of egg production, and (3) recruitment. Ovary width (mm) increased, peaked, and declined three times during the year in February, May, and July (Figure 9). Both sampling sites appeared to follow the same pattern of ovary development, and the size-specific ovary width data (ovary width/carapace ratio)(Figure 10) followed the same pattern of three peaks in ovary size. The decline in ovary width following the peak values in March and July reflected the transfer of eggs from ovaries to the pleopods and corresponded with the collection of gravid (egg-bearing) females in May, June, and July at both the inner (Figure 7) and outer (Figure 8) sites. The peak and decline in ovary width in February at both sites suggested that some females may develop mature ovaries during the winter months. However, it was not clear if this winter ovary development results in actual egg production as no gravid females were collected during this time of year. The winter ovary development cycle may reflect egg production and reabsorption in some individuals.

Recruitment of new individuals into the population usually occurred twice during each year based on the appearance of individuals with carapace lengths less than 4 mm (juveniles) in population samples. The size-frequency distribution plots for the inner site (Figure 7) show that juveniles appeared in January and June 1990, July and October 1992, and April and June 1993. No obvious recruitment cohorts were visible from the 1991 inner site samples. Juveniles were present in samples from January, May, and July 1990, January and March 1991, February and September 1992, and April 1993 for the outer site (Figure 8).

Table 1. Summary of *Lepidophthalmus louisianensis* population data collected from high (INNER) and low (OUTER) intertidal zones at study site in Bay St. Louis, Mississippi.

	INNER BEACH SITE				OUTER BEACH SITE			
Sampling Date	# Females	# Males	Total	Sex Ratio F:M	# Females	# Males	Sex # Total	Ratio F:M
10-12-89	32	76	108	0.42	20	22	44	0.91
1-26-90	57	63	120	0.9	29	46	75	0.63
5-16-90	12	14	28	0.86	52	43	95	1.21
6-20-90	42	45	87	0.93	41	13	54	3.15
7-18-90	43	43	86	1.00	28	42	70	0.67
10-2-90	29	4	33	7.25	66	13	79	5.08
1-27-91	24	25	49	0.96	32	17	49	1.88
3-9-91	26	17	43	1.53	24	24	48	1.00
6-24-91	34	28	62	1.21	28	33	61	0.85
8-2-91	25	28	53	0.89	46	29	75	1.59
2-27-92	29	30	59	0.97	24	27	51	0.89
7-9-92	32	26	58	1.23	29	33	62	0.88
9-18-92	34	30	64	1.13	34	41	75	0.83
10-17-92	37	28	65	1.32				
12-10-92	33	39	72	0.85	28	33	61	0.85
4-21-93	32	37	69	0.86	34	32	66	1.06
6-3-93	35	29	64	1.21	45	30	75	1.50
TOTAL	556	546	1102	1.02	542	478	1020	1.13

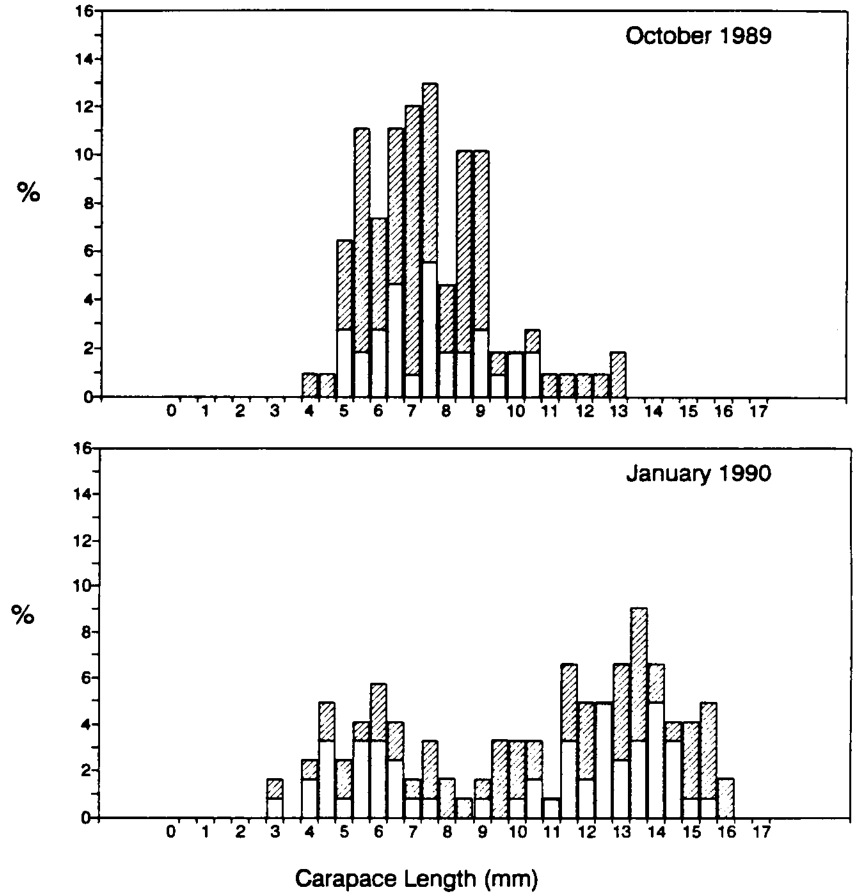


Figure 7. Size-frequency plots of monthly population samples of *L. louisianensis*. Samples were collected from mid-intertidal (inner beach) zone. Plots show the percent of sample in 0.5 mm carapace length size classes.

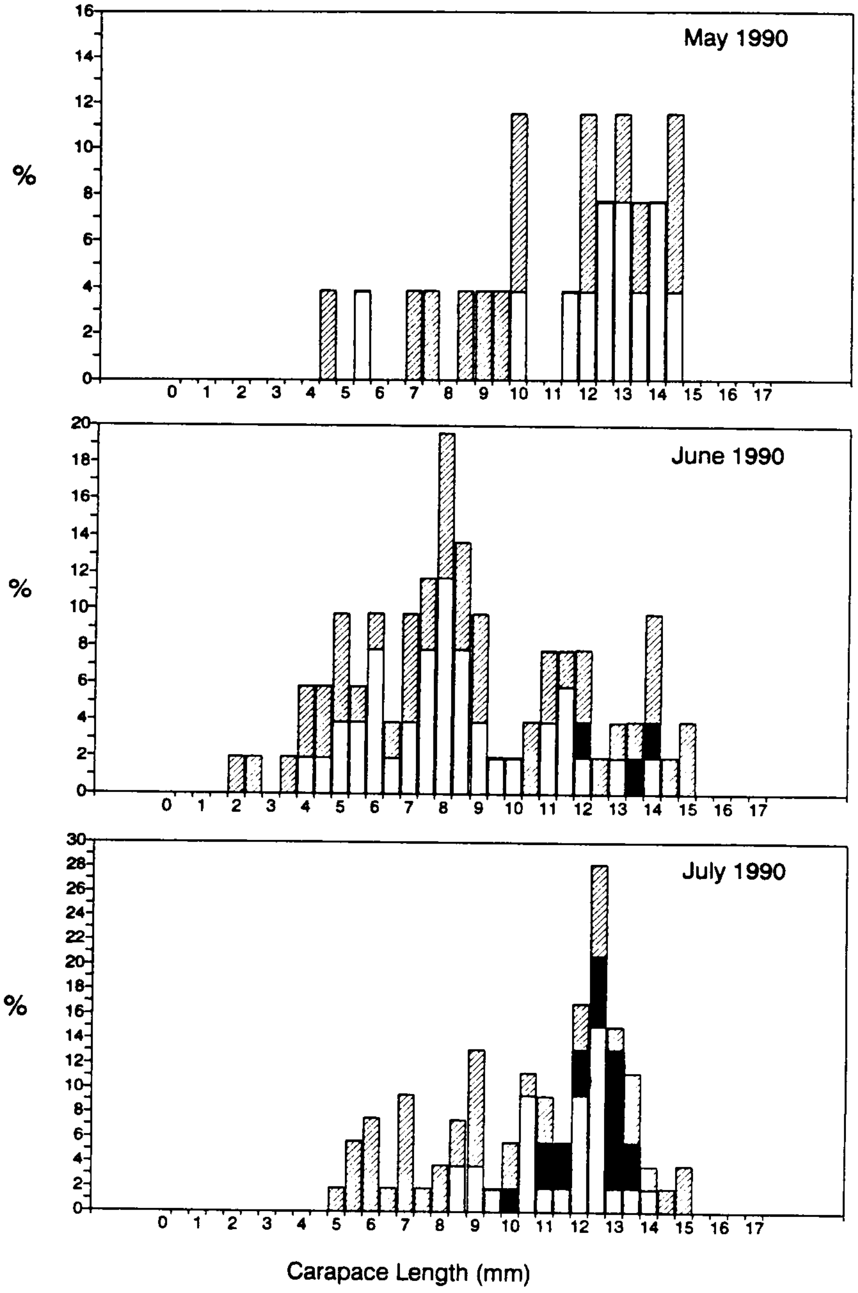


Figure 7. (continued).

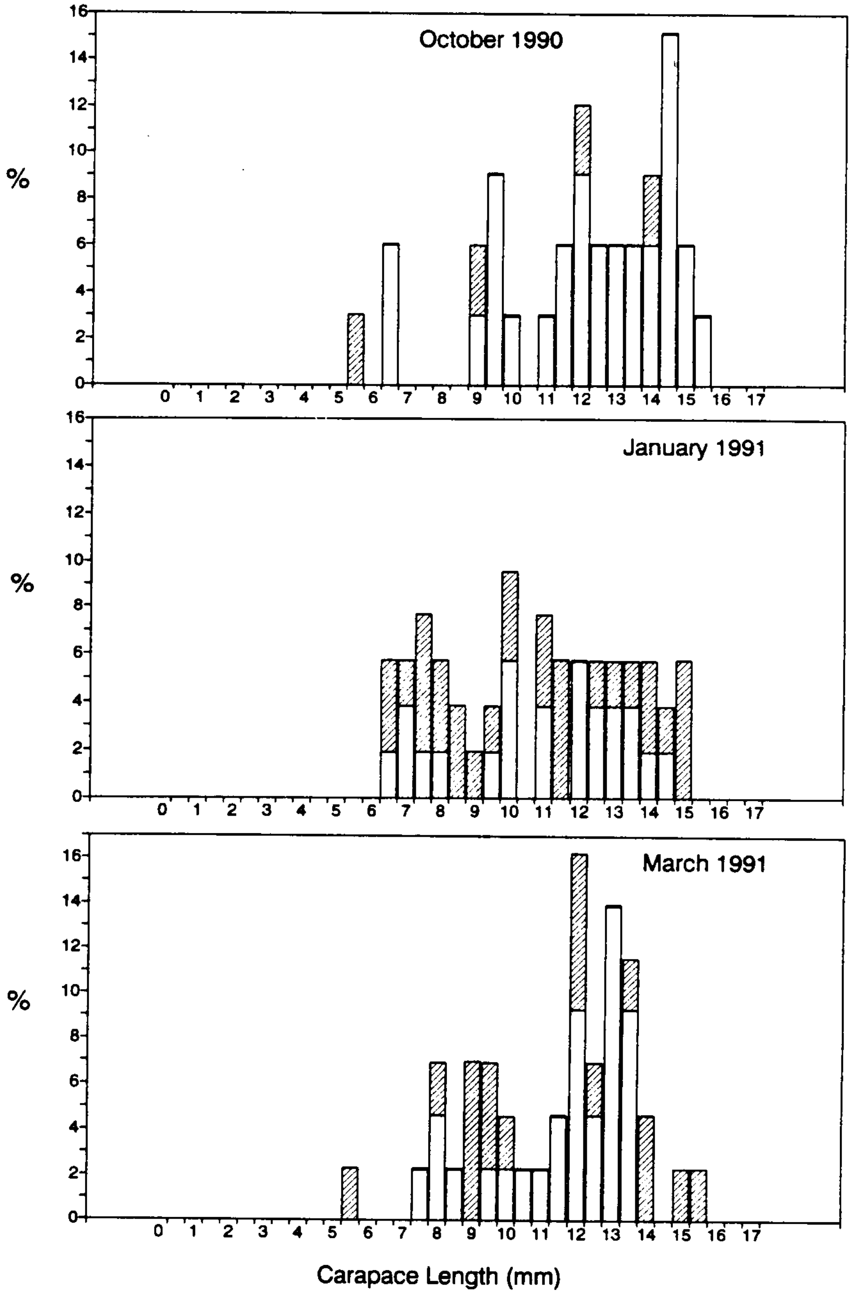


Figure 7. (continued).

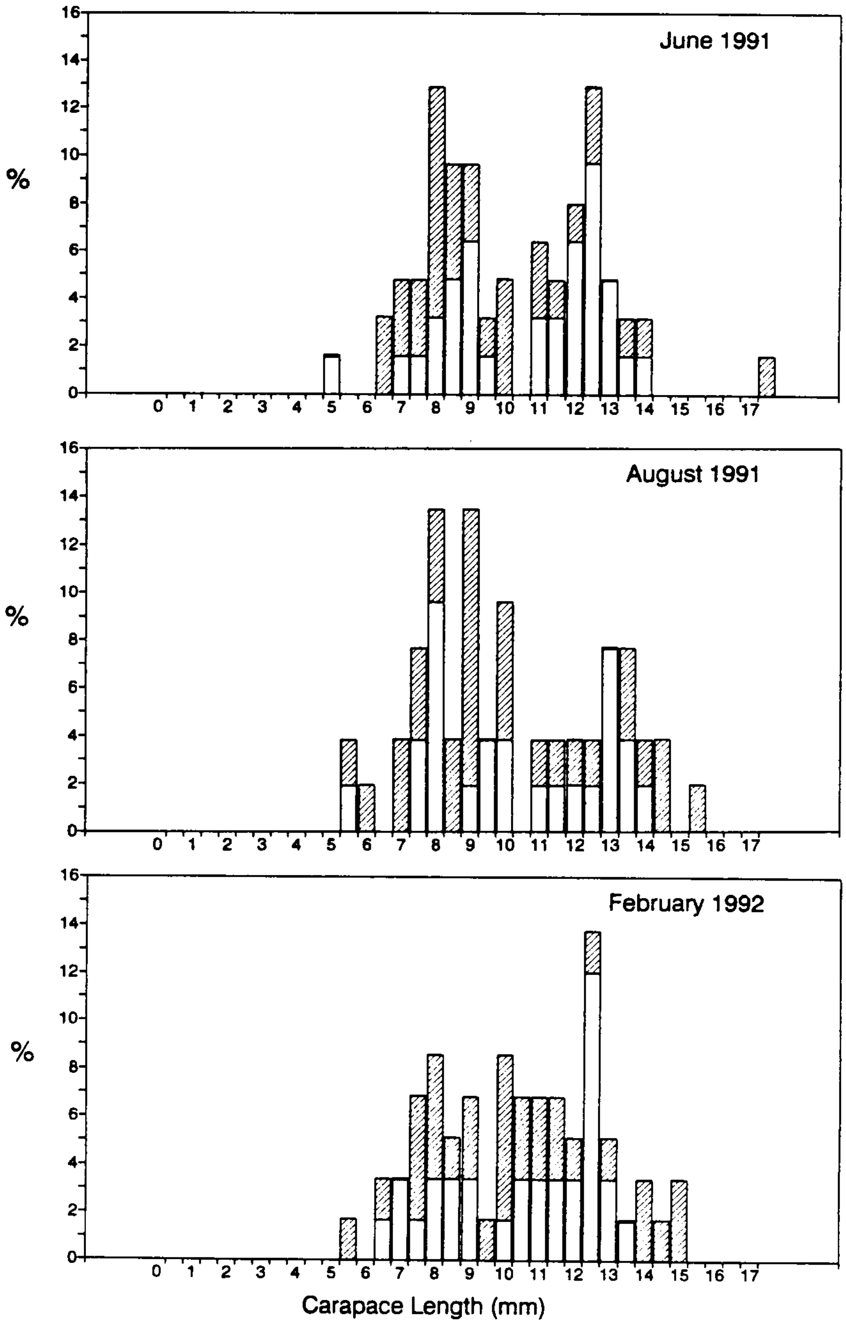


Figure 7. (continued).

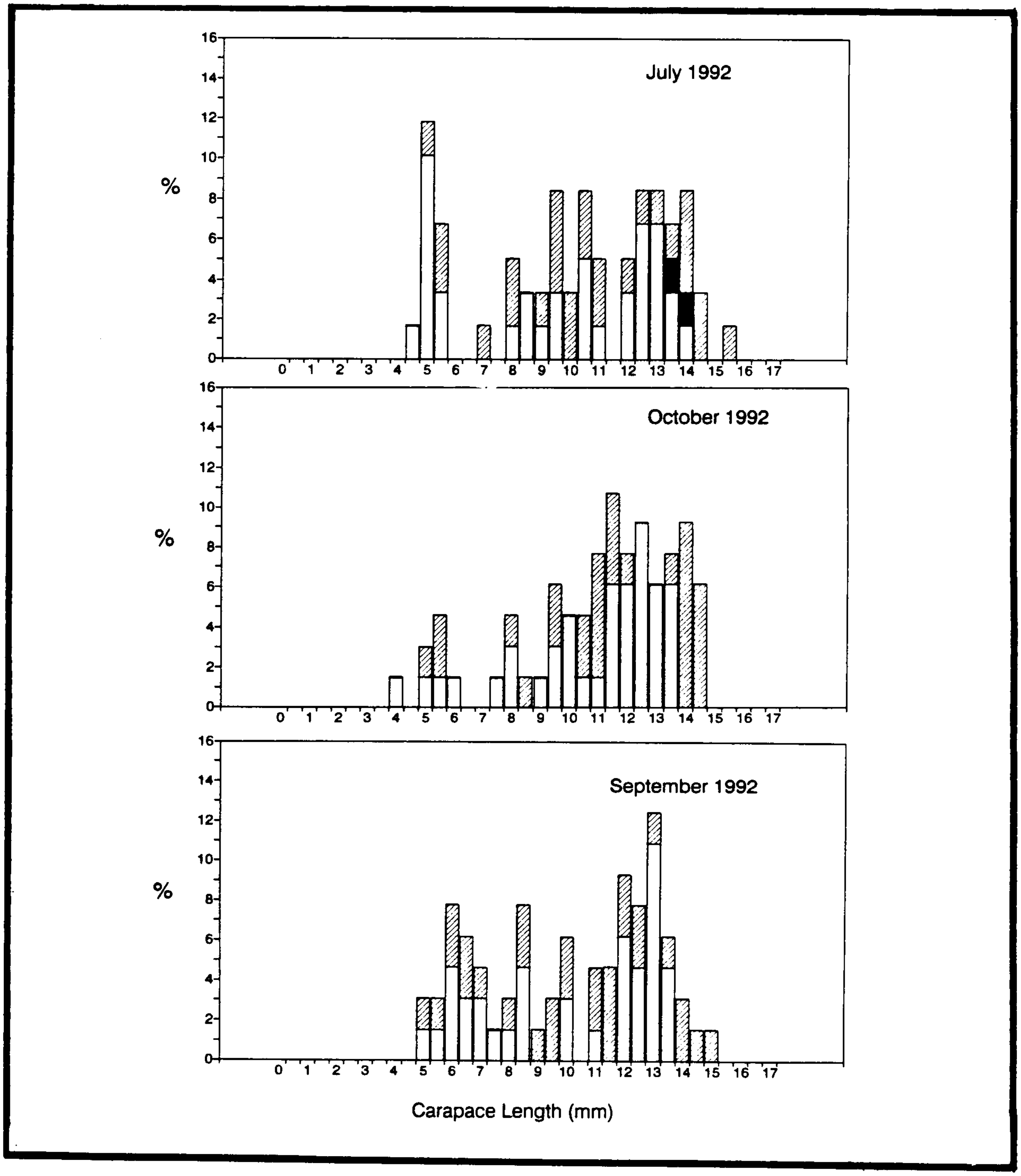


Figure 7. (continued).

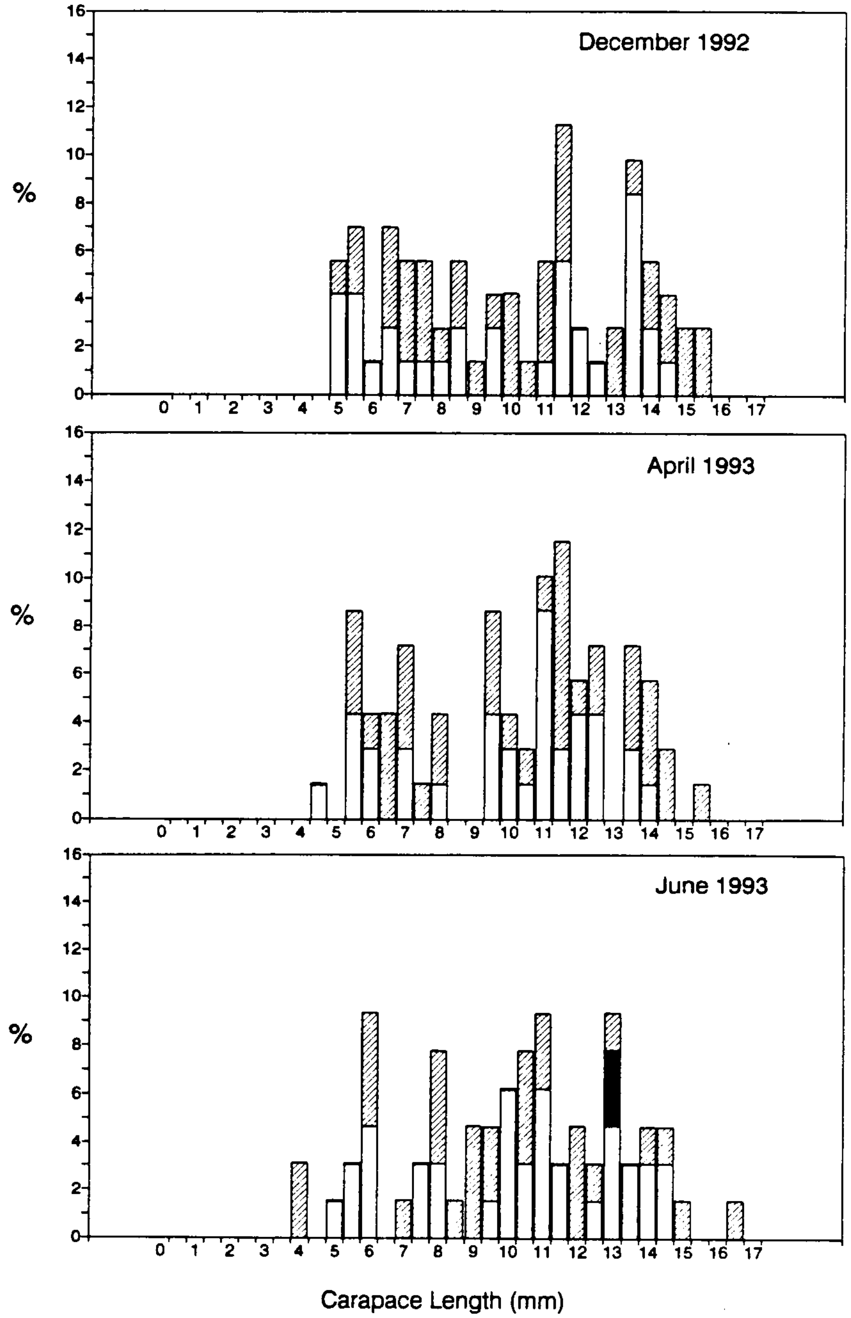


Figure 7. (continued).

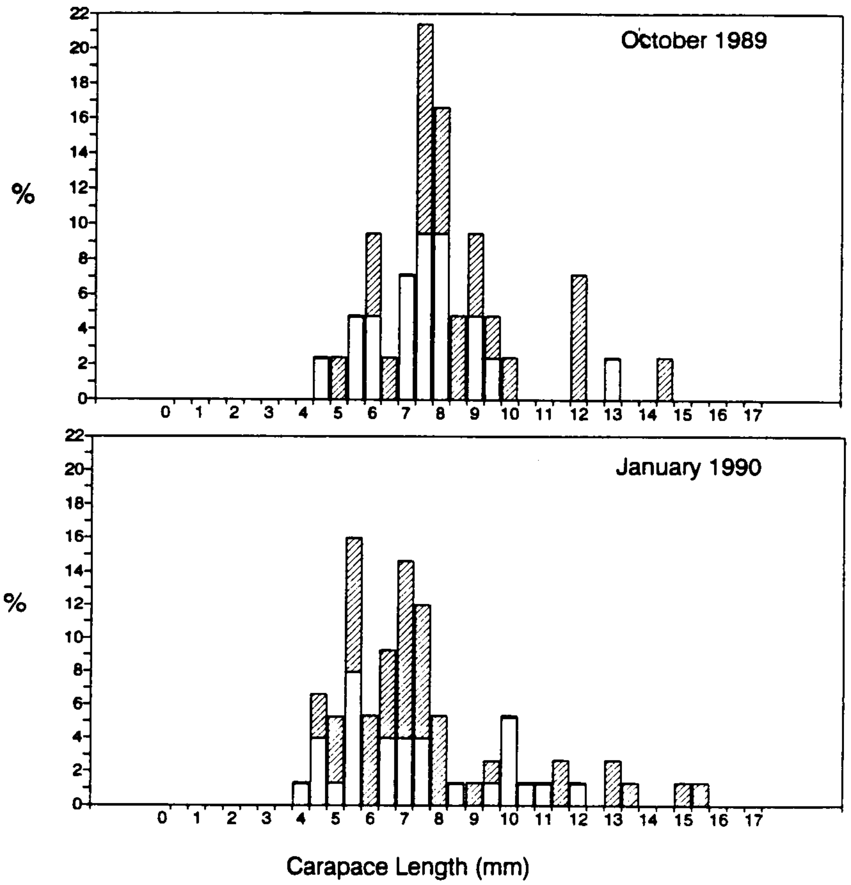


Figure 8. Size-frequency plots of monthly population samples of *L. louisianensis*. Samples were collected from low intertidal (outer beach) zone. Plots show the percent of sample in 0.5 mm carapace length size classes.

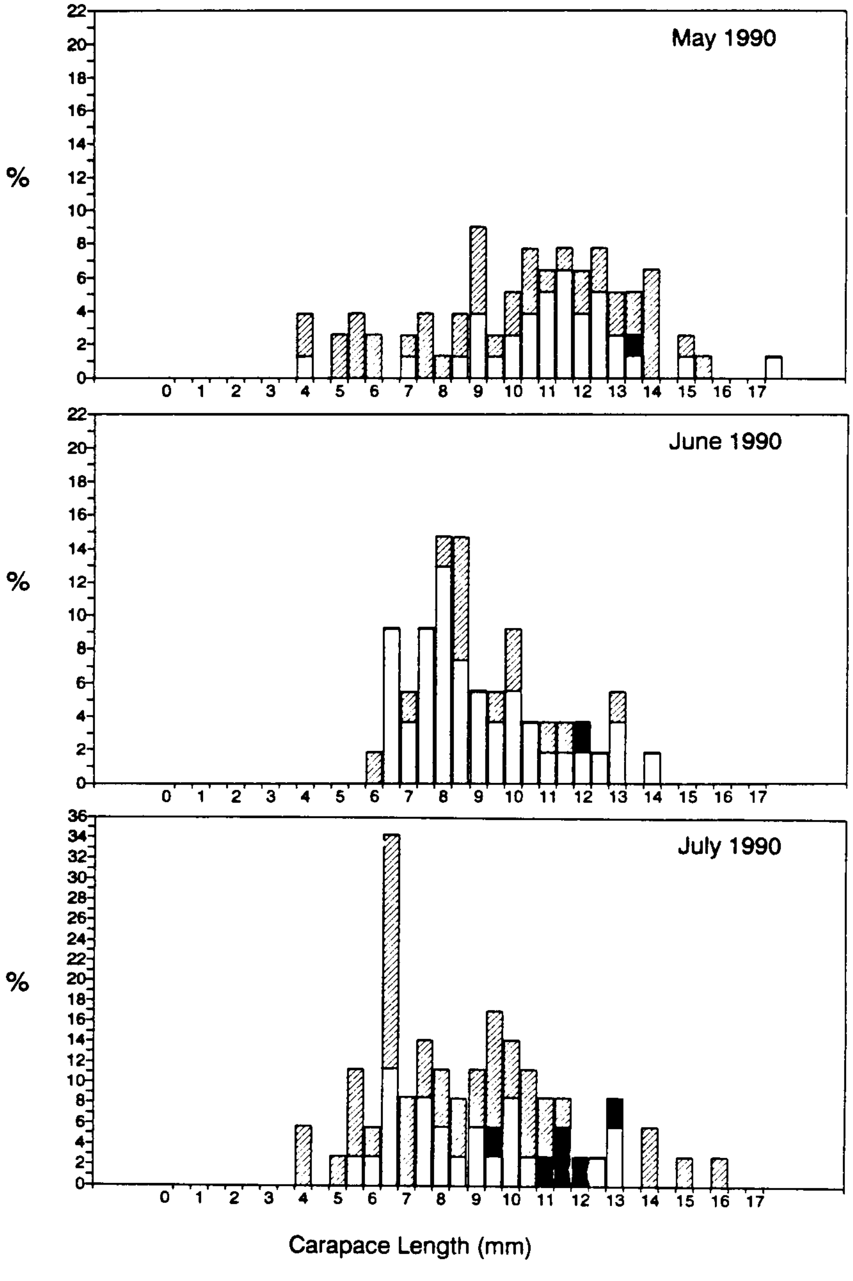


Figure 8. (continued).

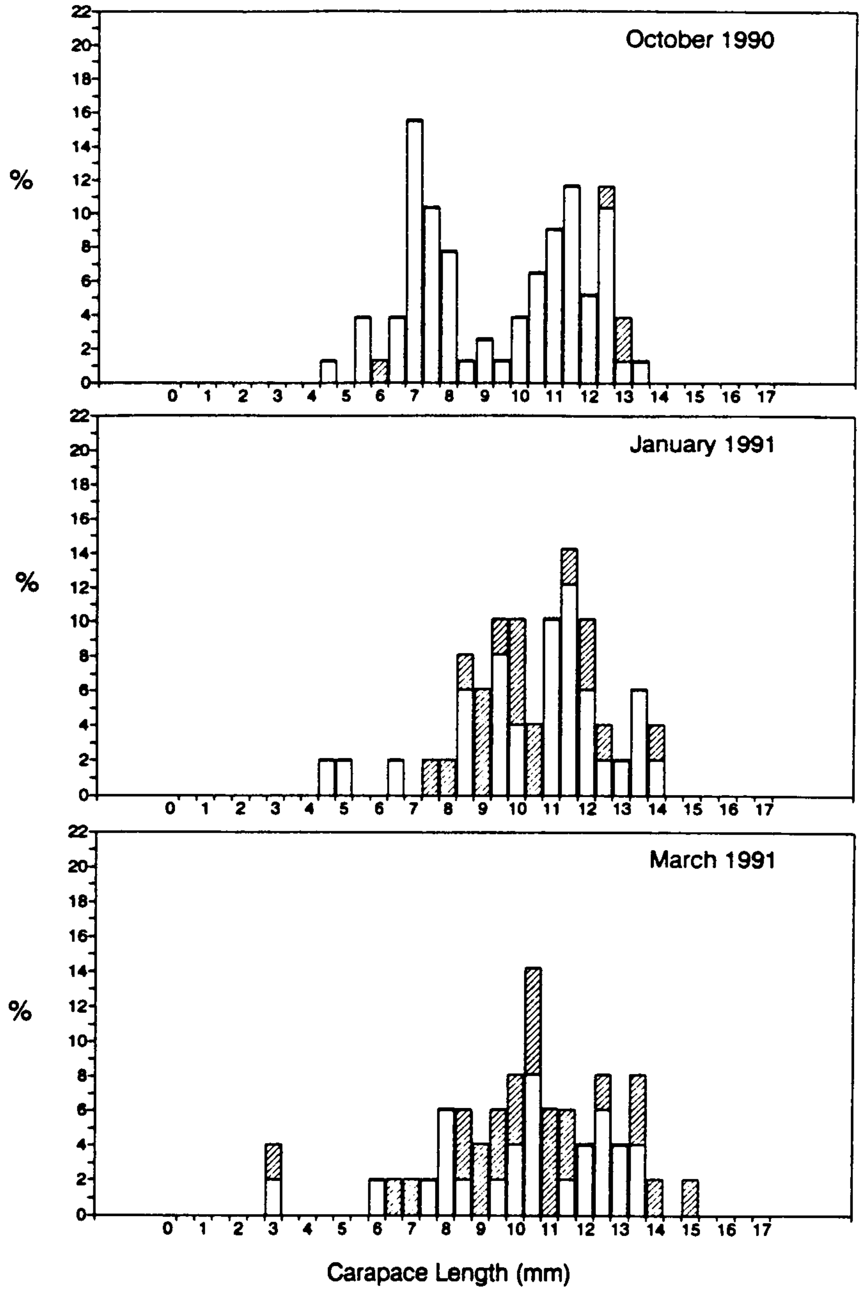


Figure 8. (continued).

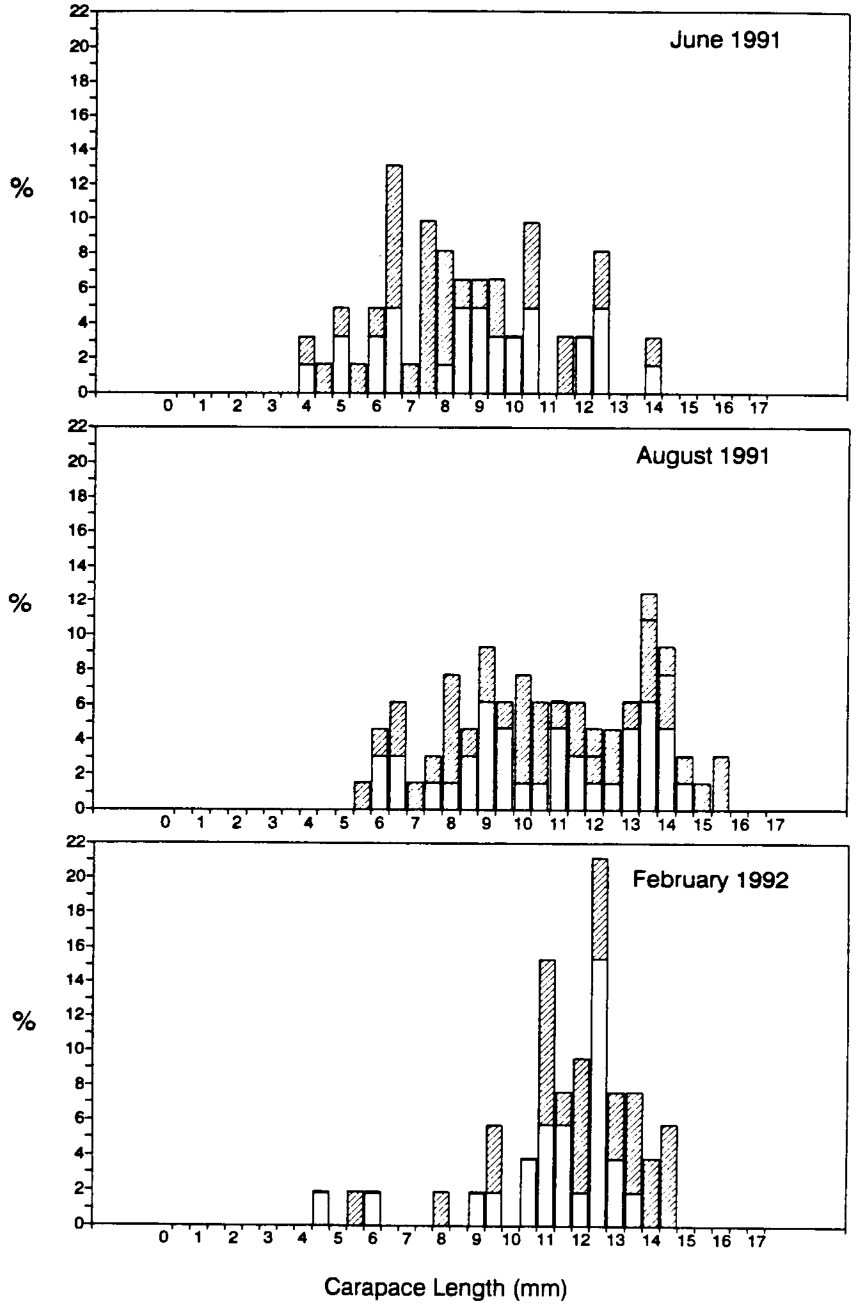


Figure 8. (continued).

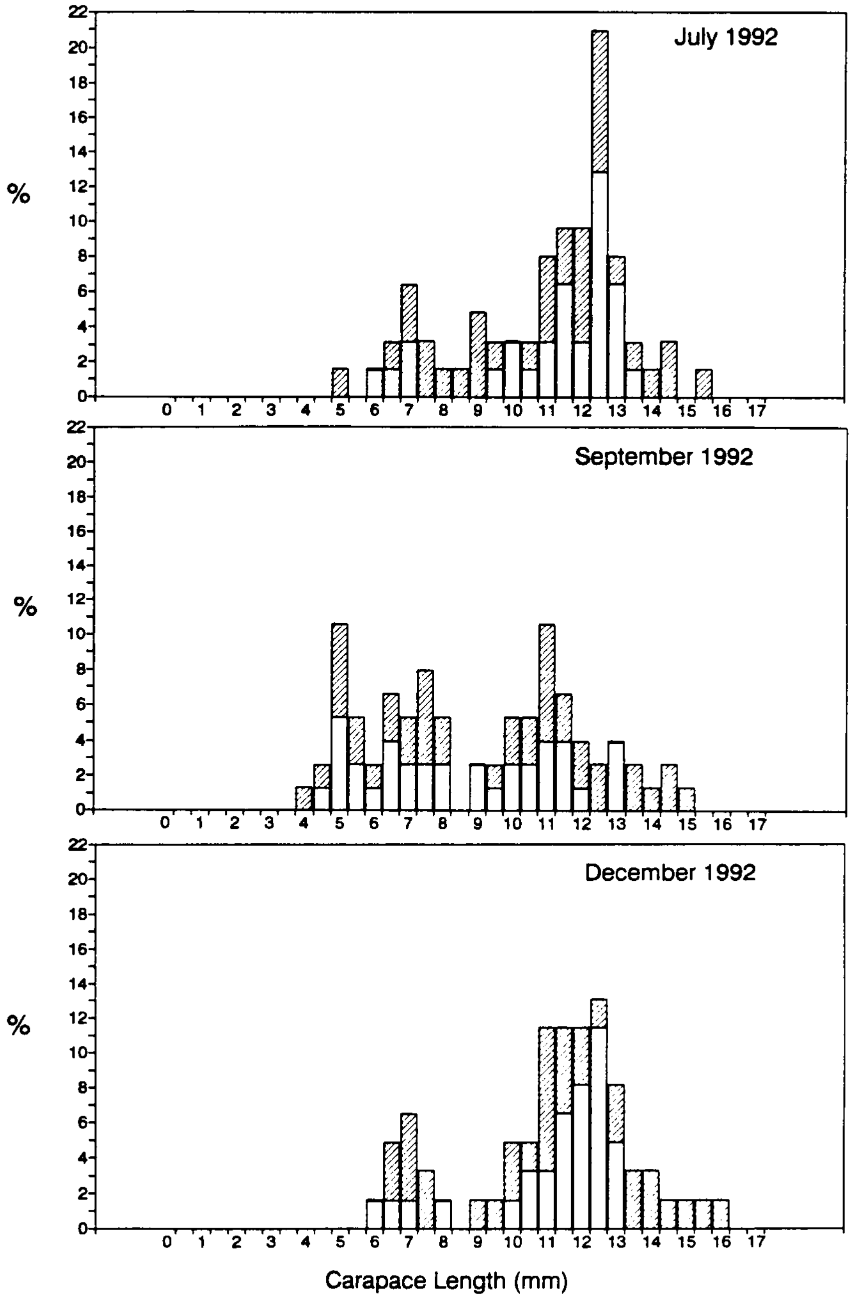


Figure 8. (continued).

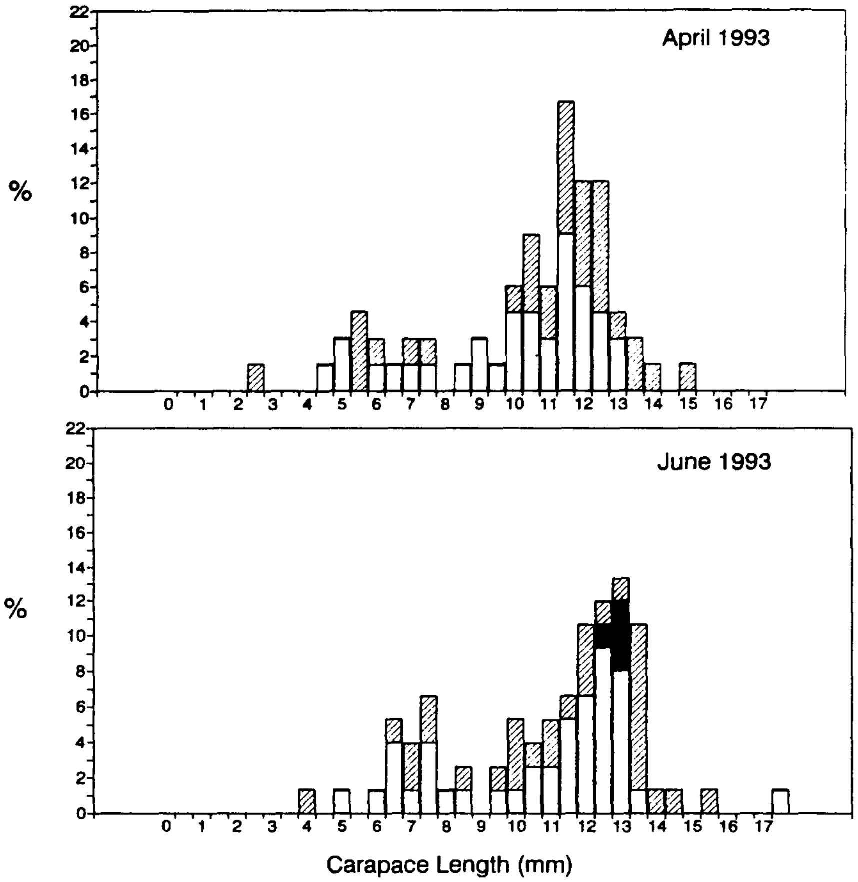


Figure 8. (continued).

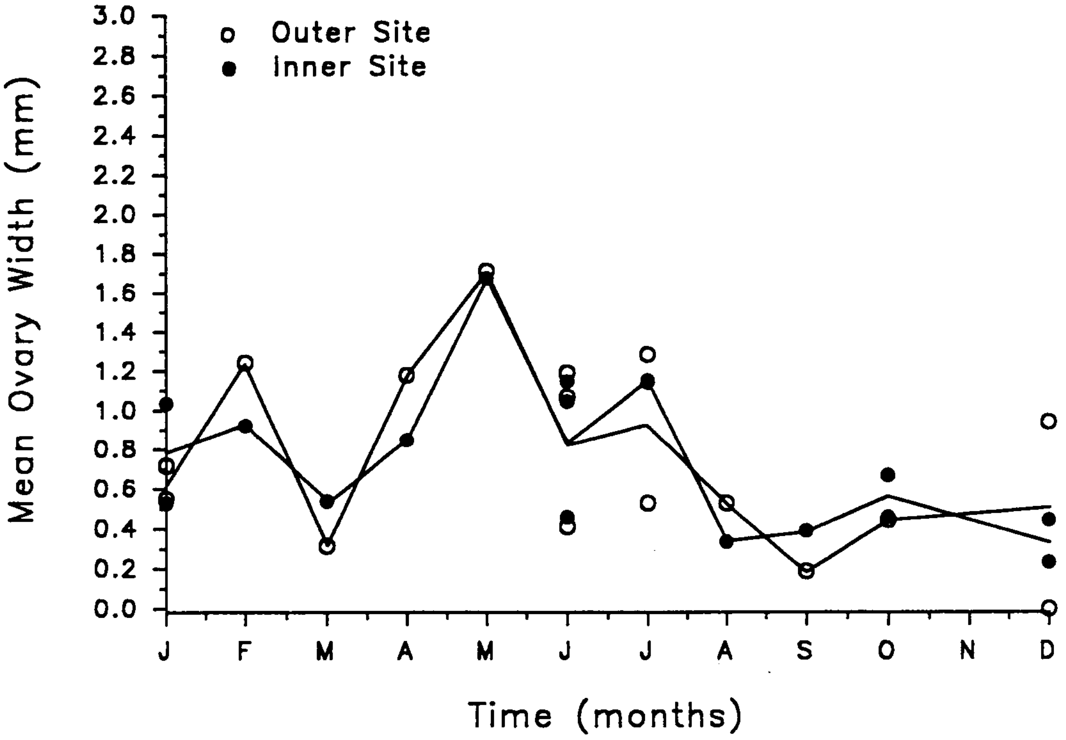


Figure 9. Changes in mean ovary width (mm) with time (months) for *L. louisianensis* females with carapace lengths > 7.0 mm. Individuals were collected in population samples from 1989 to 1993. Values from multiple years are plotted along a single year period for both inner and outer beach sampling sites. Lines connect average monthly values for each sampling site.

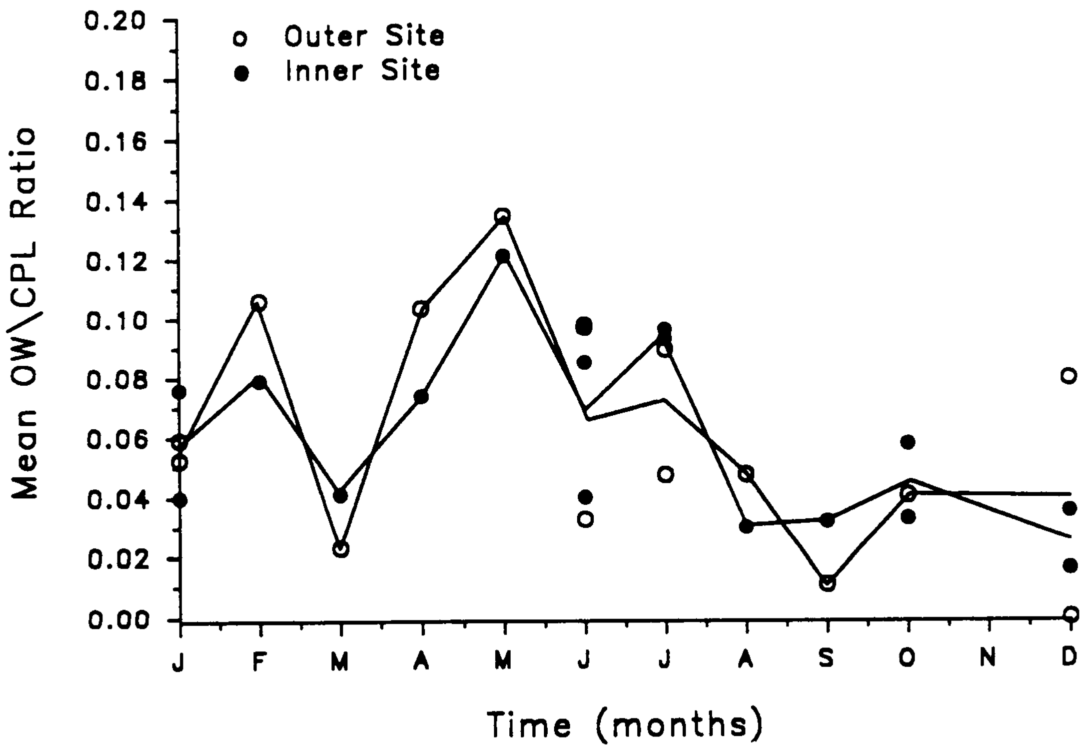


Figure 10. Changes in mean ratio of ovary width (OW): carapace length (CPL) ratio with time (months) for *L. louisianensis* females with carapace lengths > 7.0 mm. Individuals were collected in population samples from 1989 to 1993. Values from multiple years are plotted along a single year period for both inner and outer beach sampling sites. Lines connect average monthly values for each sampling site.

Biomass

Population biomass for both inner and outer sampling sites was estimated from the relationship between wet weight (g) or ash-free dry weight (AFDW)(g) and carapace length for a total of 424 individuals from the 1990 sampling year. All regression equations and statistics are listed in Table 2. The relationship between carapace length and wet weight was exponential and highly significant ($R=0.91$, $p<0.05$) for both males and females at the inner (Figure 12) and outer (Figure 13) sampling sites. The relationship between carapace length and wet weight did not differ between the sexes, so males and females were pooled for comparisons between sampling sites. The pooled sex data for the inner and outer sampling sites is shown in Figure 14. The carapace length-wet weight relationship between the inner and outer sampling sites was similar for individuals of carapace lengths less than approximately 13 mm. Individuals with carapace lengths greater than 13 mm from the outer site had higher wet weights than individuals of equal carapace length from the inner site. The relationship between carapace length and AFDW was also exponential and highly significant (see Table 2) for both males and females collected from the inner (Figure 15) and outer (Figure 16) sites. This relationship did not appear to differ between the sexes so pooled data were used for the comparison between sampling sites shown in Figure 17. The relationship between carapace length and AFDW of individuals collected from the inner and outer sites was again nearly identical for carapace lengths less than approximately 13 mm. Individuals with carapace lengths greater than 13 mm from the inner site were consistently lower in AFDW biomass than individuals of equal carapace length from the outer site.

Population biomass estimates were made by calculating the wet weight (or AFDW) for an average individual using the relationship between mean carapace length and wet weight (or AFDW) for each population sample (Table 2). This produced an estimate of the mean wet weight (or AFDW) per individual for each sampling period, which was then multiplied by the mean number of individuals m^{-2} at inner (30 m from beach crest) and outer (80 m from beach crest) sites at each census period. This produced estimates of wet weight biomass m^{-2} (Figure 18) and AFDW m^{-2} (Figure 19) for each sampling interval over the entire study period. These estimates indicate that population biomass (wet weight and AFDW) was greater at the inner beach sites than outer beach sites. Mean wet weight estimate was 248 g m^{-2} (range 111-705) for the inner site and 95 g m^{-2} (range 5-219) for the outer site. Mean AFDW estimate was 39 g m^{-2} (range 18-111) for the inner site and 14 g m^{-2} (range 1-34) for the outer site.

DISCUSSION

Lepidophthalmus louisianensis is an abundant macrofaunal burrower in the intertidal zone of Bay St. Louis, Mississippi. The species is distributed from the high to low intertidal and extends into subtidal areas for unknown distances. Counts of surface burrow openings m^{-2} indicate that the species is very abundant in the intertidal zone, reaching maximum densities of approximately 400 individuals m^{-2} in the mid-intertidal zone and declining to moderate levels of 100 - 200 m^{-2} in lower intertidal regions. Seasonal and annual variation in densities was observed over the three year study period suggesting that the population readily responds to changes in the environment, although the specific physical and biological factors that regulate population density are not known. Estimates of population biomass using wet

Table 2. Summary of results from regression analyses between carapace length (mm) and wet weight (g) or ash-free dry weight (g) for males and females from inner and outer beach collection sites. Asterisks denote significance at $p < 0.05$.

Independent Variable	Dependent Variable	Site	Sex	Regression Equation	N	R
Carapace Length	Wet Weight	Inner	Female	$Y = 0.047 * e^{0.298X}$	125	0.91*
			Male	$Y = 0.041 * e^{0.311X}$	75	0.95*
			All	$Y = 0.044 * e^{0.305X}$	200	0.93*
	Ash Free Dry Weight		Female	$Y = 0.008 * e^{0.288X}$	125	0.73*
			Male	$Y = 0.006 * e^{0.308X}$	75	0.90*
			All	$Y = 0.007 * e^{0.298X}$	200	0.83*
	Wet Weight	Outer	Female	$Y = 0.028 * e^{0.354X}$	170	0.91*
			Male	$Y = 0.024 * e^{0.361X}$	72	0.96*
			All	$Y = 0.027 * e^{0.354X}$	242	0.94*
	Ash Free Dry Weight		Female	$Y = 0.003 * e^{0.387X}$	170	0.81*
			Male	$Y = 0.005 * e^{0.341X}$	72	0.77*
			All	$Y = 0.003 * e^{0.379X}$	242	0.80*

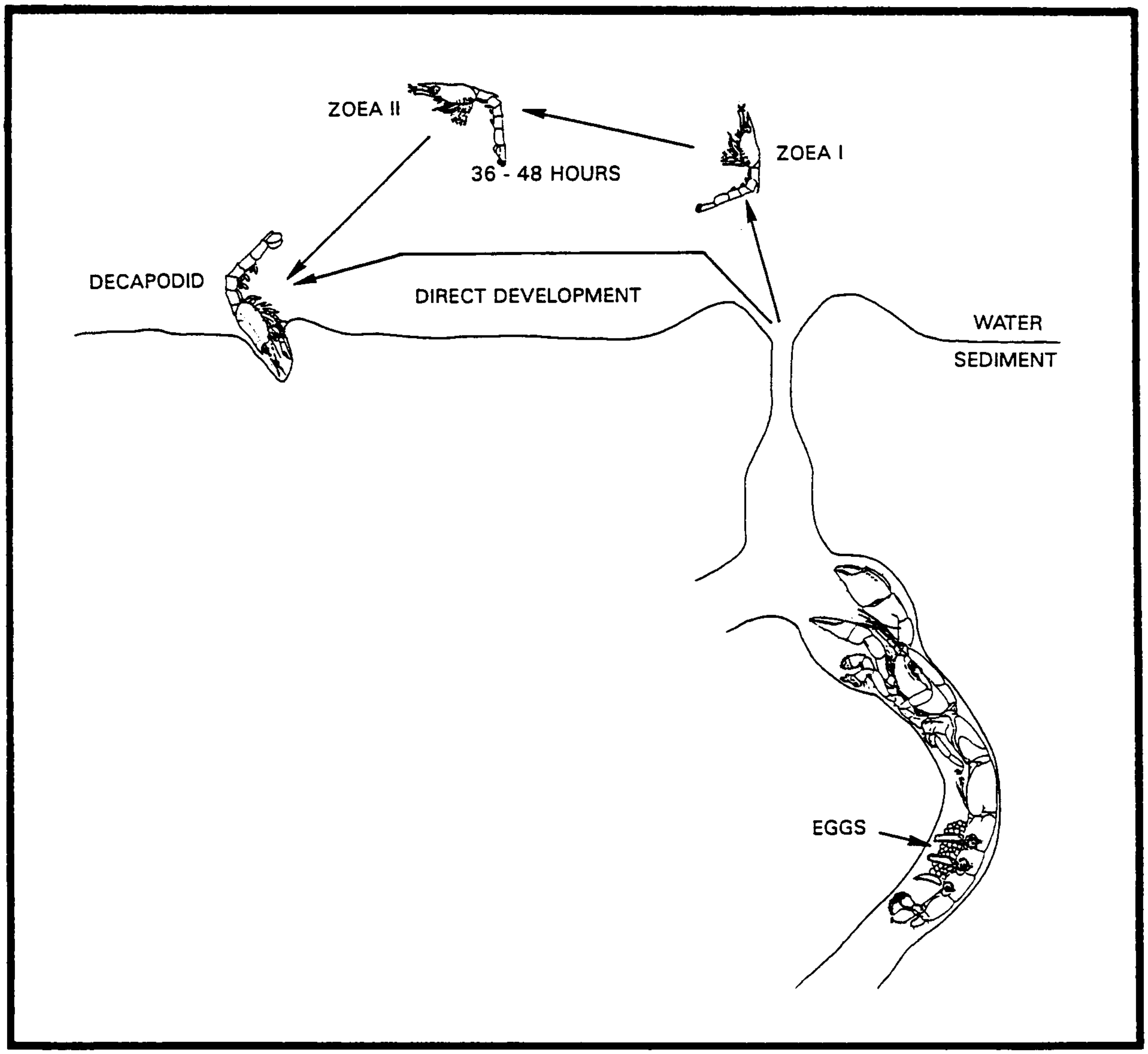


Figure 11. Illustration of abbreviated larval life history of *L. louisianensis*.

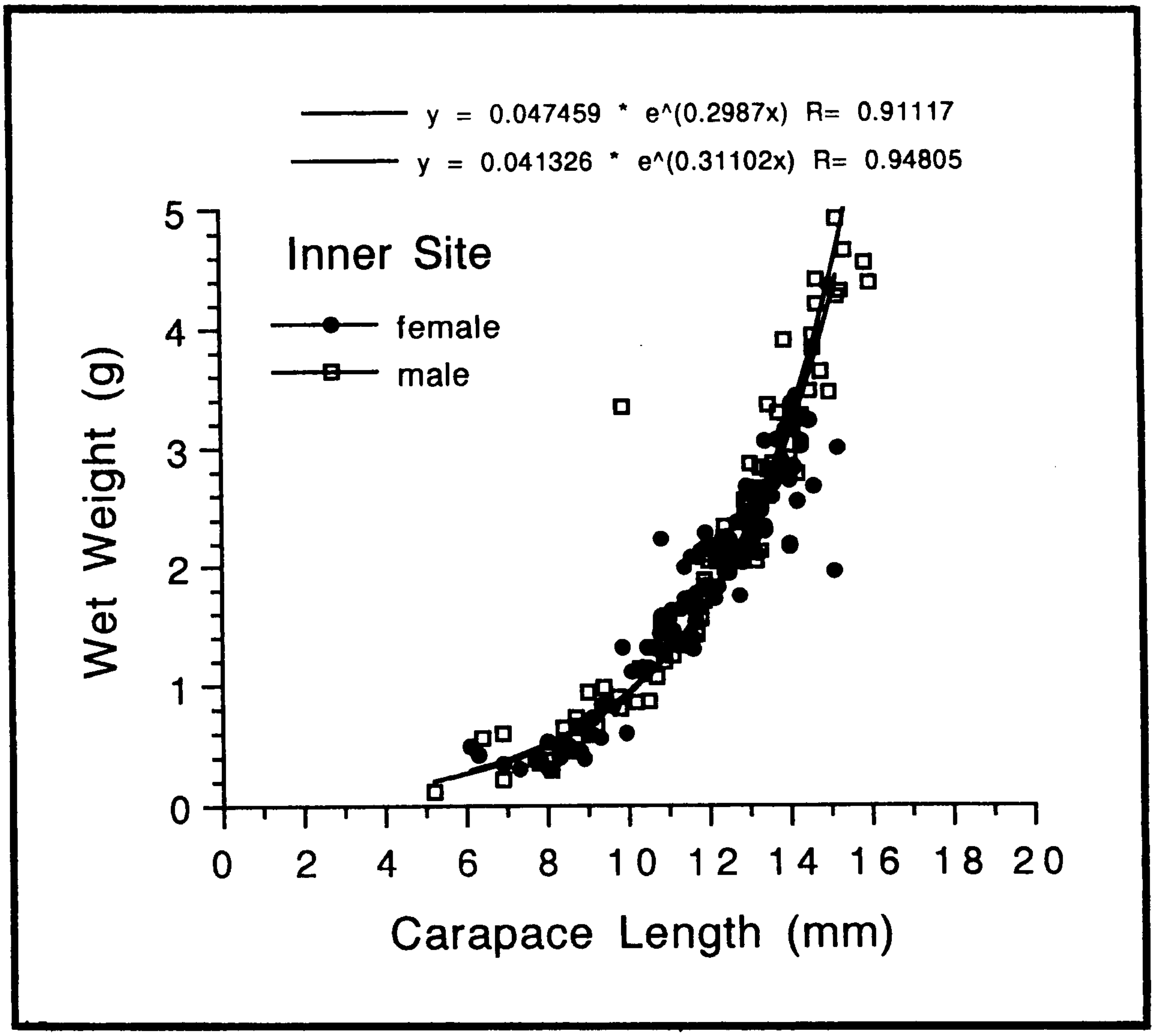


Figure 12. Relationship between carapace length (mm) and wet weight (g) for female and male *L. louisianensis* from the inner beach site.

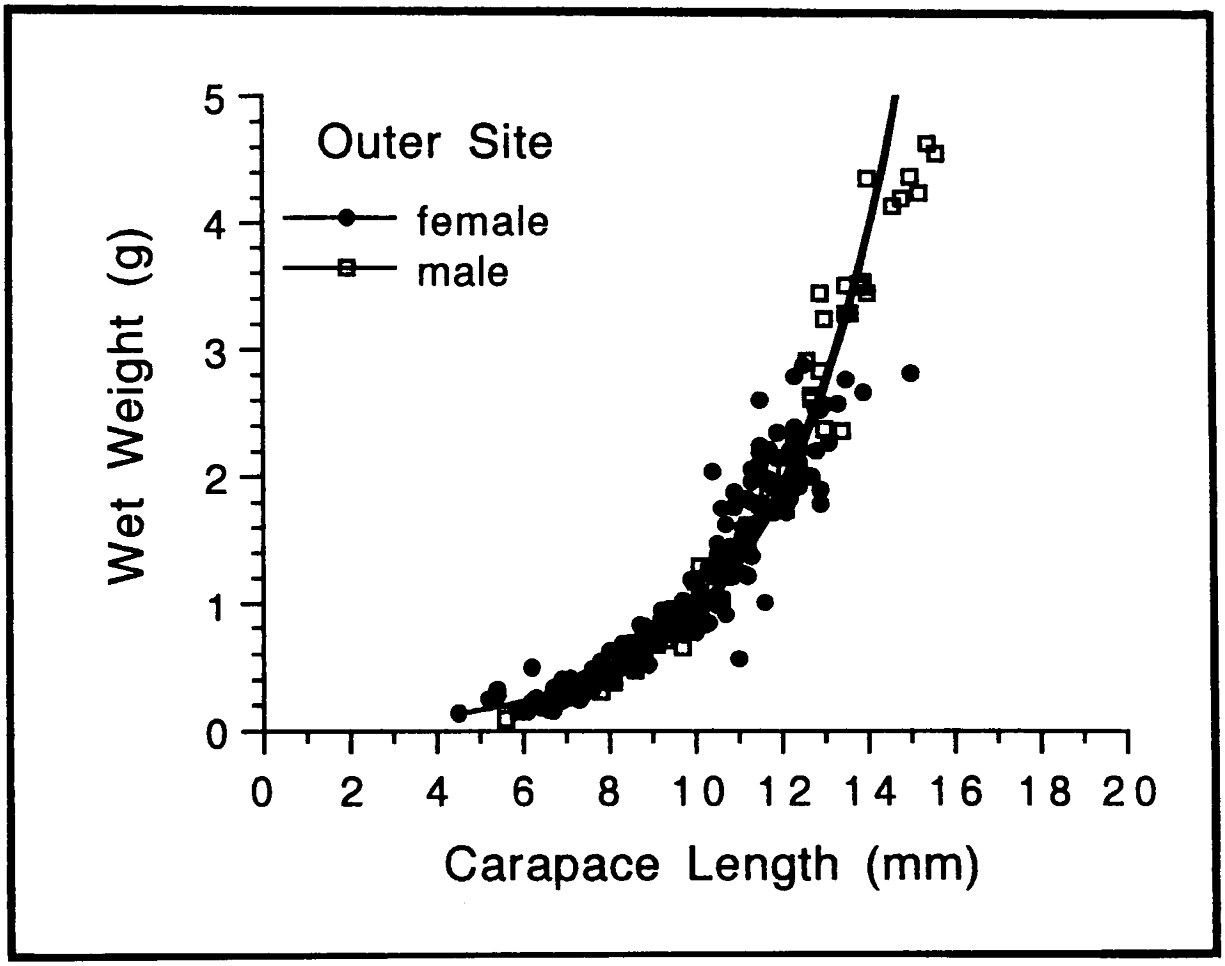


Figure 13. Relationship between carapace length (mm) and wet weight (g) for female and male *L. louisianensis* from the outer beach site.

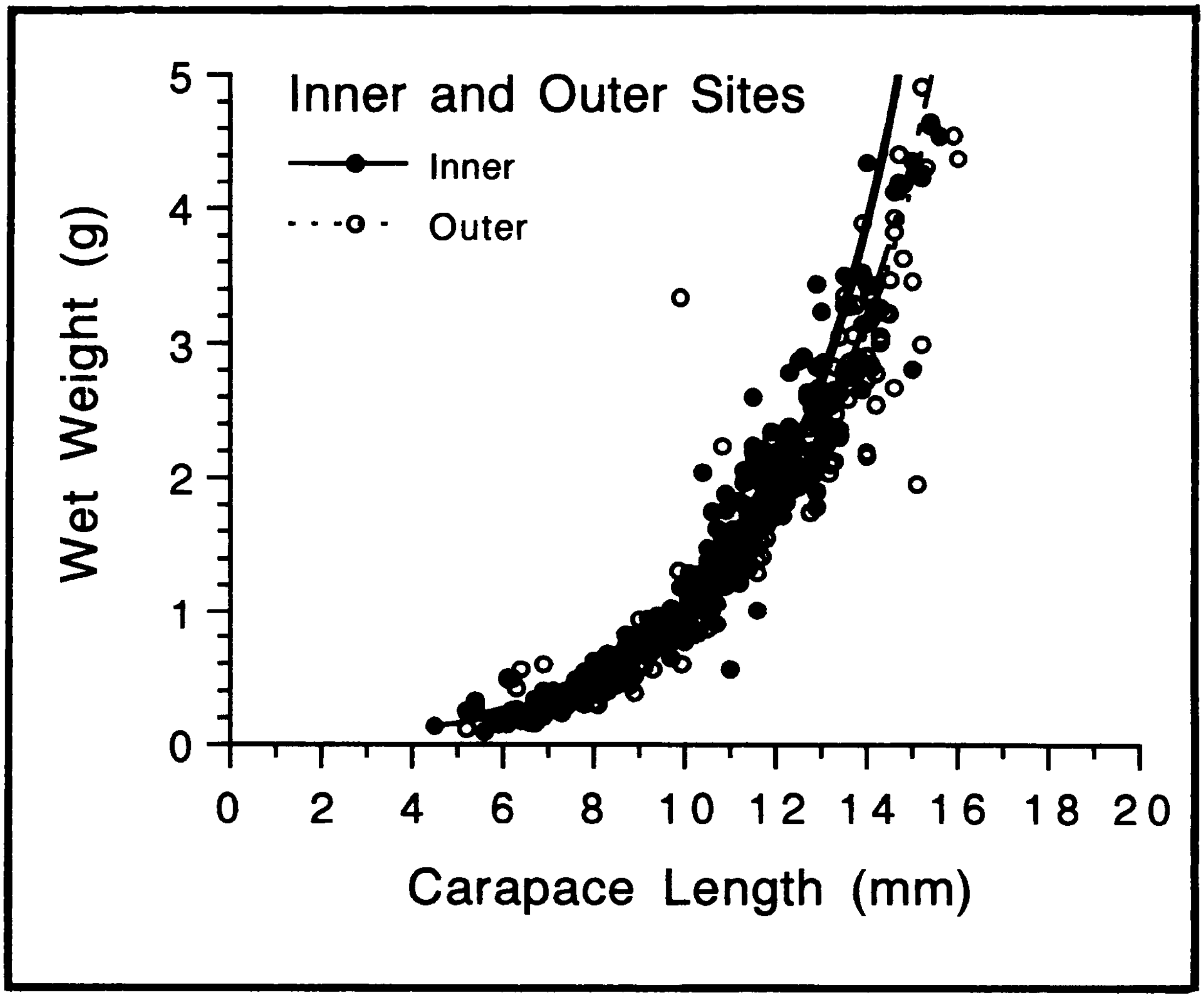


Figure 14. Relationship between carapace length (mm) and wet weight (g) for *L. louisianensis* from the inner beach site.

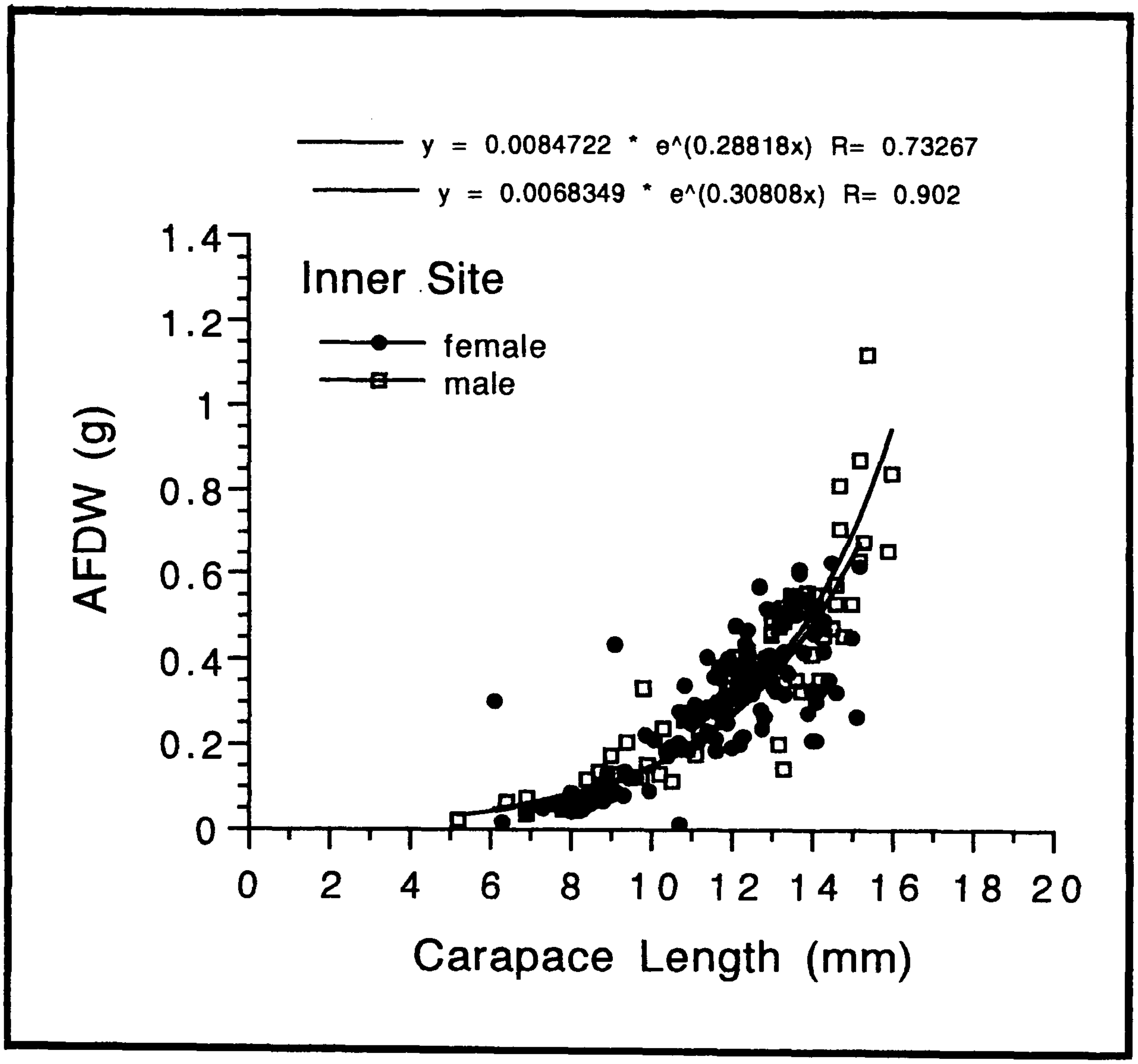


Figure 15. Relationship between carapace length (mm) and ash-free dry weight (AFDW)(g) for female and male *L. louisianensis* from the inner beach site.

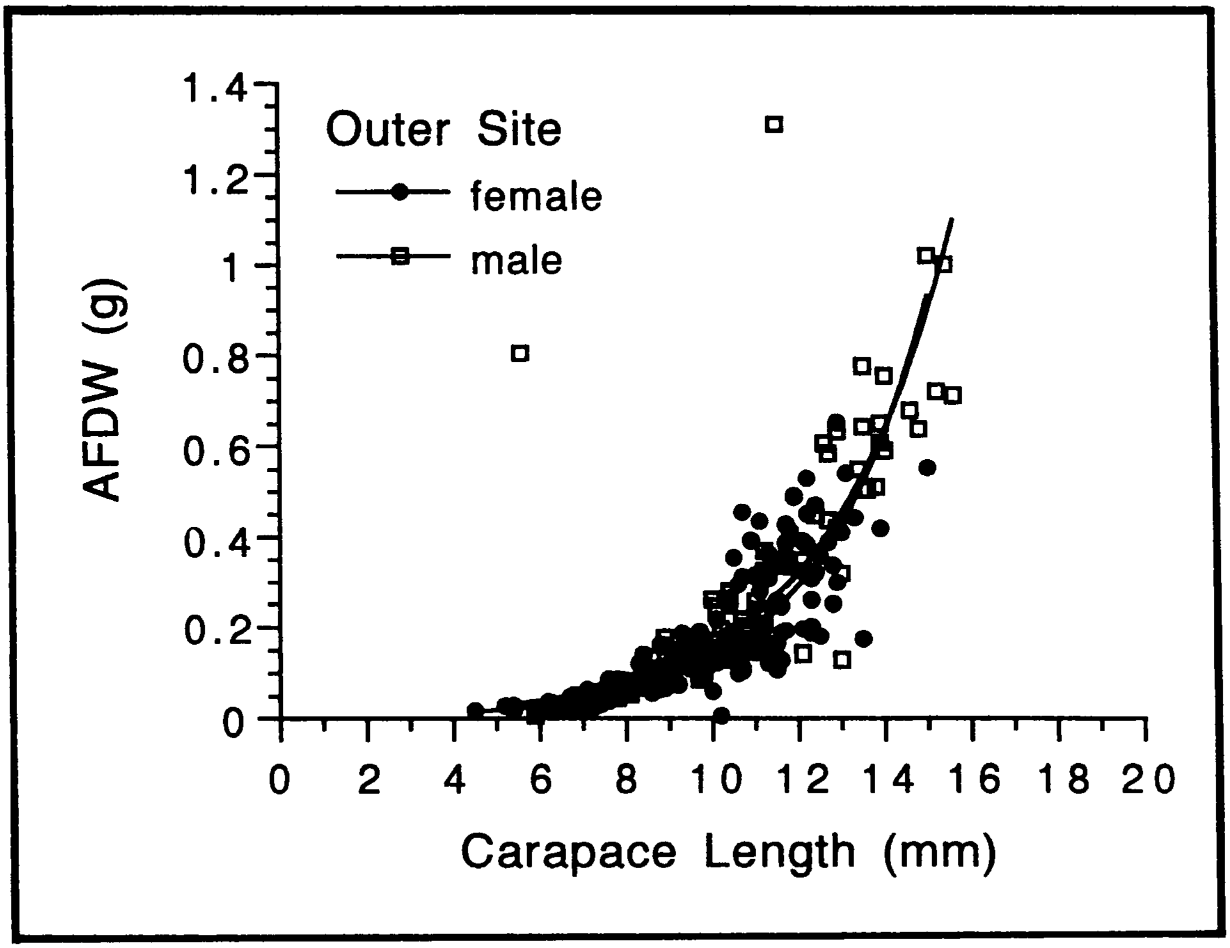


Figure 16. Relationship between carapace length (mm) and ash-free dry weight (AFDW)(g) for *L. louisianensis* from the outer beach site.

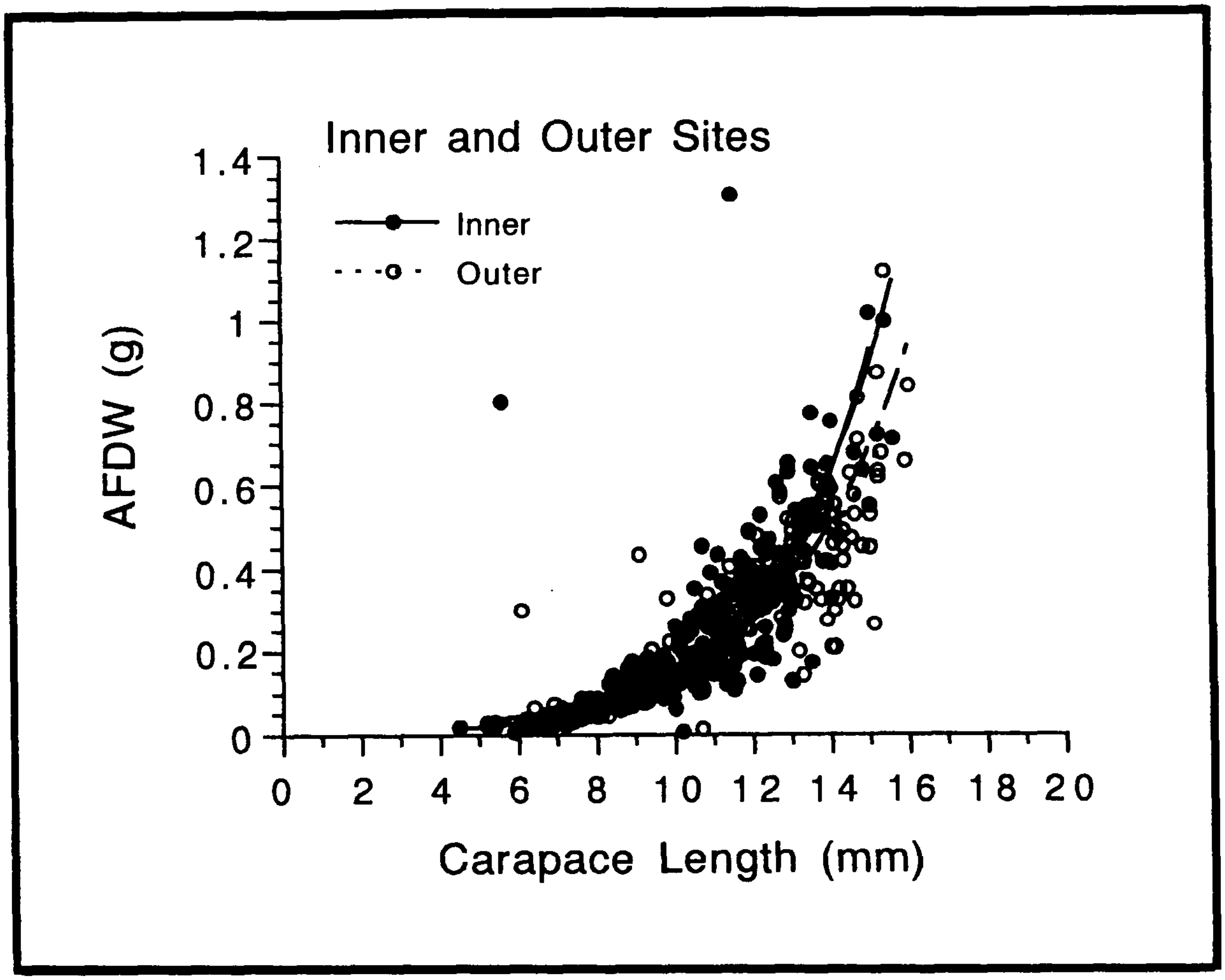


Figure 17. Relationship between carapace length (mm) and ash-free dry weight (AFDW)(g) for *L. louisianensis* from inner and outer beach sites.

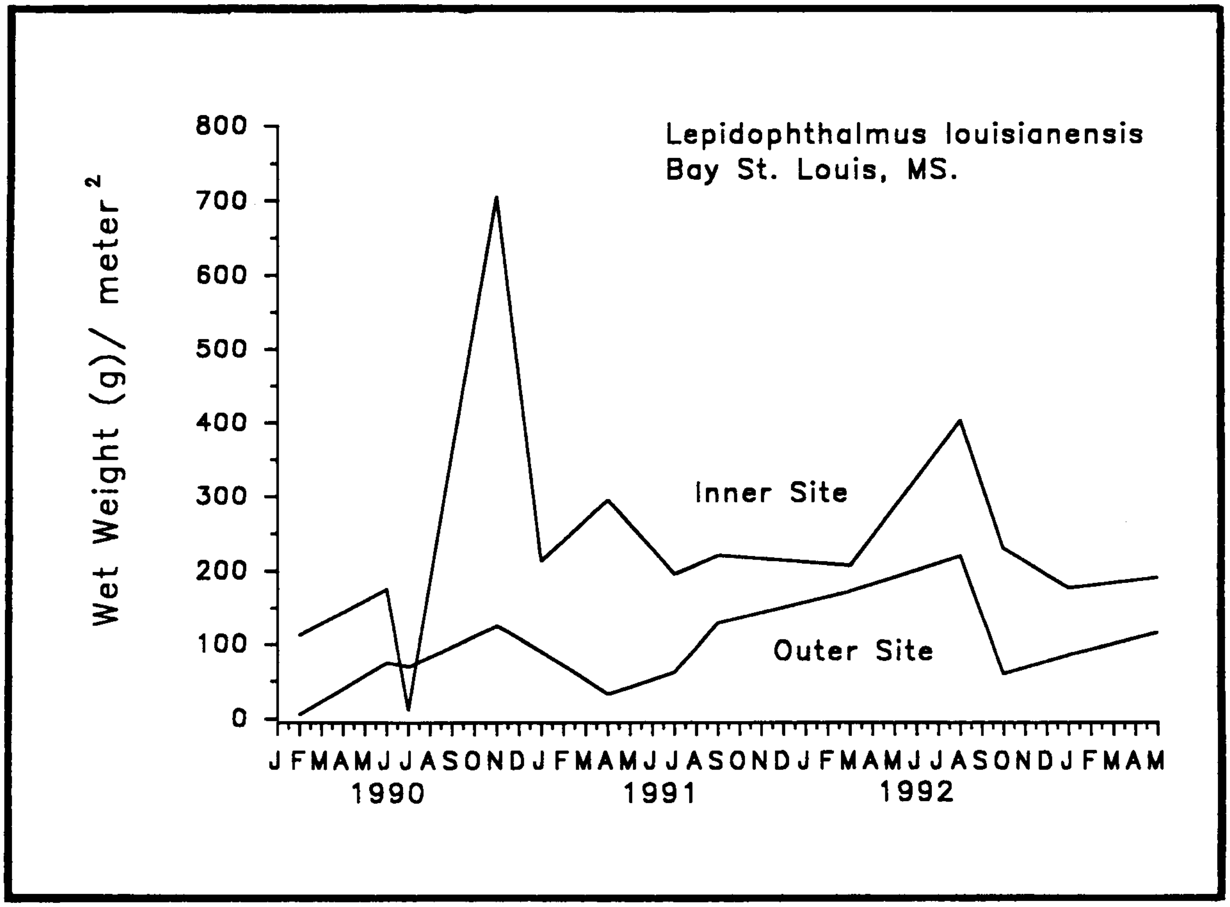


Figure 18. Changes in *L. louisianensis* population biomass (wet weight (g) m^{-2}) with time at inner and outer beach sampling sites.

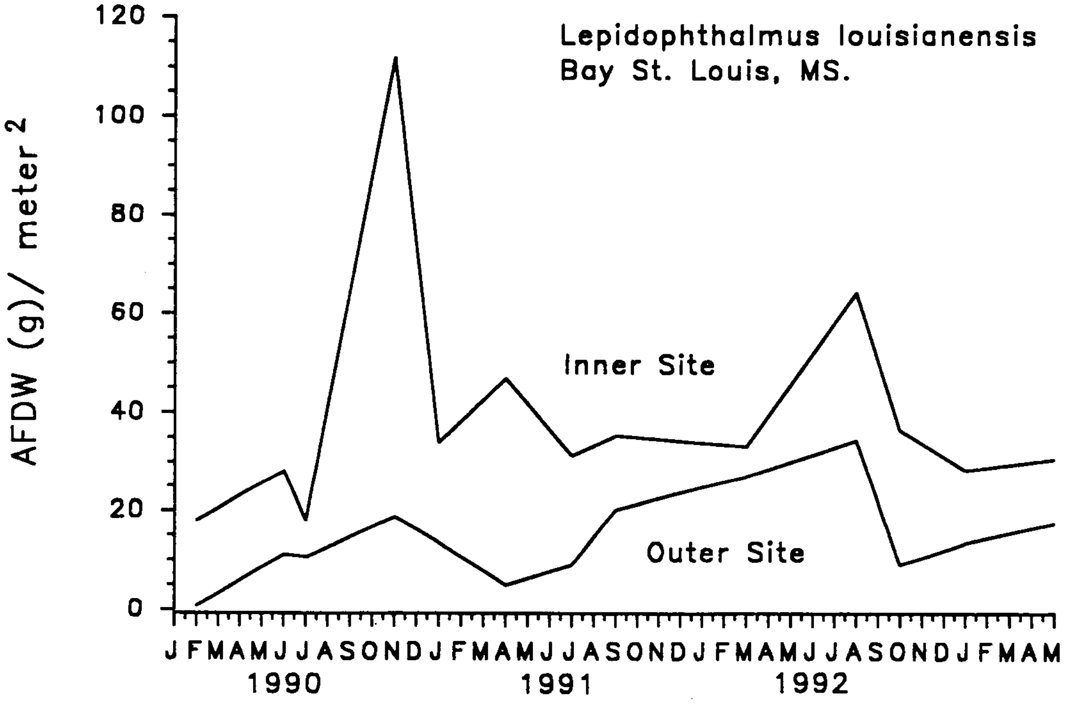


Figure 19. Changes in *L. louisianensis* population biomass (ash-free dry weight (g) m^{-2}) with time at inner and outer beach sampling sites.

weight (g m^{-2}) and ash-free dry weight (g m^{-2}) indicate that biomass is greatest in the high and mid-intertidal zone where population densities are greatest. However, the relationships between individual wet weight (g) or ash-free dry weight (g) and carapace length (mm) differ between inner beach and outer beach sites for individuals with carapace lengths greater than 13 mm. Individuals with large carapace lengths from outer beach (lower intertidal) sites have greater biomass than individuals from inner beach sites (higher intertidal) suggesting that food levels or energy requirements may differ along the intertidal gradient. The mean estimate of wet weight biomass was 248 g m^{-2} (range 111-705) for the inner beach sites and 95 g m^{-2} (range 5-219) for the outer site over the study period. The mean estimate of ash-free dry weight was 39 g m^{-2} (range 18-111) for the inner sites and 14 g m^{-2} (range 1-34) for the outer site. The trophic base supporting these large populations and the high standing biomass is not yet known, although much of the primary production in this habitat is produced by benthic microalgae which have also been observed in the gut contents of the burrowing shrimp (Figure 20).

The sex ratios in population samples were close to one for both the inner and outer collection sites, although sex ratio was highly variable between sampling periods. Multiple cohorts were visible in most population samples, and visual inspection of changes in mean cohort carapace length over time suggested that carapace length increased at rates of 0.25-0.75 mm $month^{-1}$ or 3-9 mm $year^{-1}$.

The reproductive cycle of the estuarine ghost shrimp appears to include two or three annual peaks in ovarian development in February, May, and July. Gravid females then appear in the population in May, June, and July. Larvae and postlarvae of varying sizes were present in plankton samples taken in July 1990 indicating that eggs had already hatched by this time (Figures 21 and 22). Recruits less than 4 mm carapace length appeared in the population samples two or three times a year suggesting that in general there is a winter (January and February) and summer (April through July) recruitment each year, and occasional recruitment during the fall. However, because the sampling technique did not facilitate collection of very small (> 0.1) individuals and the growth rates of small individuals is unknown, it is difficult to accurately determine when these individuals actually settled into the sediment. The short larval stage (36-48 hours) and rapid postlarval development of juveniles (Figure 11) suggests that individuals reenter the sediment soon after reaching the decapodid stage with carapace lengths of approximately 0.3-0.5 mm. At growth rates of 0.5 mm $month^{-1}$, individuals with carapace lengths of 3 to 4 mm may have actually settled into the sediment 5 to 6 months prior to their appearance in the population samples. Nothing is known about the factors influencing where and when juveniles settle into the sediment, although some juvenile *L. louisianensis* constructed burrows connected to adult burrows rather than the sediment surface (see Burrow Morphology, Chapter 4) suggesting that the presence of adults may facilitate juvenile settlement and/or survivorship. Connections between juvenile and adult burrows have also been observed in Callianassa kraussi (Forbes 1973) and Neotrypaea californiensis (Griffis pers. obs.). Intraspecific facilitation of juvenile settlement by adults has been suggested for the ghost shrimp *Callianassa japonica* (Tamaki and Ingole 1993). Intraspecific competition and predation may also be important mechanisms regulating population density in some populations of burrowing shrimp (Bird 1982, Griffis 1988, Posey 1986a). Further work is required to identify the role of these and other factors in determining the abundance and distribution of *L. louisianensis* in estuarine environments.

LEPIDOPTHALMUS LOUISIANENSIS GUT CONTENTS

Bacillariophyceae (Diatoms)

Centric: *Cyclotella*, *Actinoptychus*

Pennate: Amphora, Achnanthes, Nitzchia, Pinnularia, Gomphonema

Euglenophyceae

Trachelomonas hispida var. *punctata*

Sarcomastigophora

Granuloreticulosea: *Streblus* and others

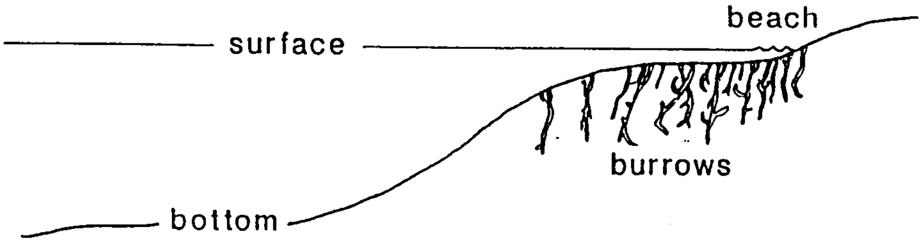


Figure 20. List of *L. louisianensis* gut contents.

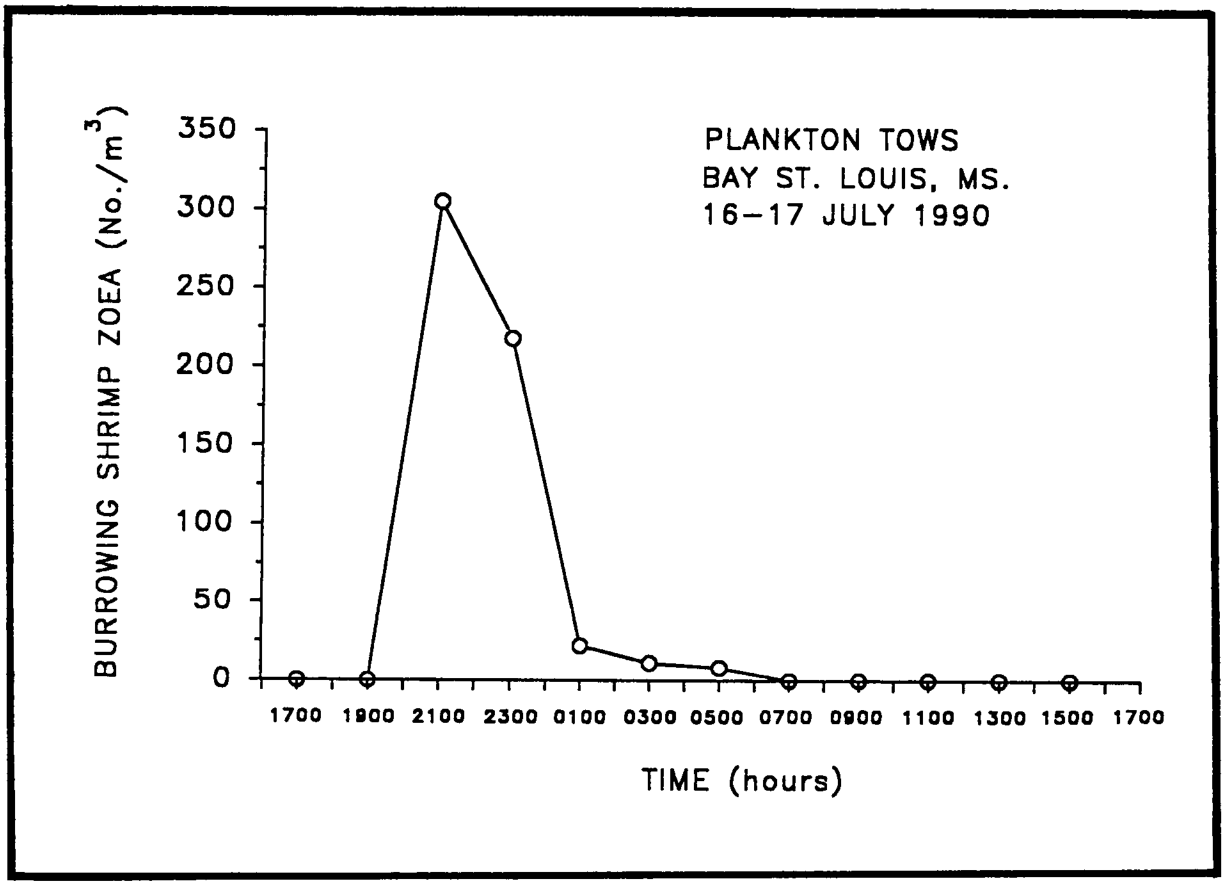


Figure 21. Number of *L. louisianensis* zoea larvae (No. m^{-3}) collected in plankton tows over a 24-hour period in July 1990.

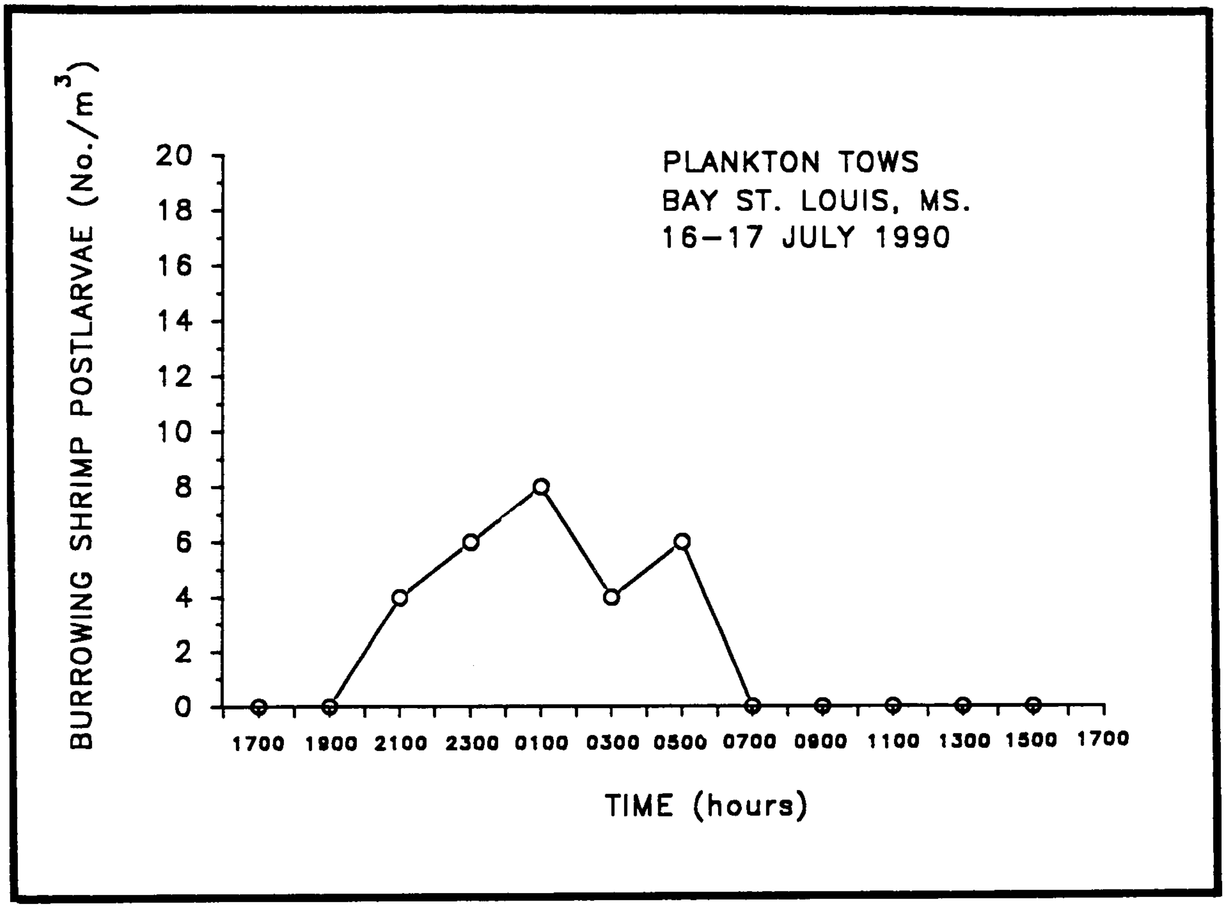


Figure 22. Number of *L. louisianensis* postlarvae (No. m^{-3}) collected in plankton tows over a 24-hour period in July 1990.

CHAPTER 3: POPULATION DYNAMICS OF THE BEACH GHOST SHRIMP, *CALLICHIRUS ISLAGRANDE*

INTRODUCTION

The beach ghost shrimp *Callichirus islagrande* and *Callichirus major* inhabit quartz sand beaches in the northern Gulf of Mexico (Phillips 1971, Hill and Hunter 1976, Britton and Morton 1989, Radocinski et al. 1991). *Callichirus islagrande* is common on foreshore beaches in general, and is frequently found on both the gulf (foreshore) and bay (backshore) beaches of barrier islands. *Callichirus major* is found less frequently in the northern Gulf and primarily inhabits bay side benthic habitats of barrier islands (Figure 23). Little is known about what determines the distribution of these species besides the fact that they appear to have less osmoregulatory capability than the estuarine ghost shrimp *Lepidophthalmus louisianensis*, and may be restricted from more estuarine habitats by lower salinities (Felder 1978). Both species construct burrows in intertidal and shallow subtidal sediments. The production and maintenance of these burrows may have significant effects on the flux of nutrients and the turnover of sediments (see Chapter 4). Given this potential ecological importance and the fact that ghost shrimp inhabit benthic environments that are susceptible to physical perturbations and/or chemical contamination associated with the nearshore oil industry, this study was designed to determine seasonal patterns of distribution, demographics, and reproduction in *C. islagrande*. Prior to this study, little population data was available for use in estimating the population-level responses of this species to habitat degradation.

METHODS

The distribution and population biology of *C. islagrande* was studied on beaches of the barrier island Isles Dernieres, Louisiana. Populations of *C. islagrande* were monitored on both the gulf (foreshore) and bay (backshore) sides of the island. *Callichirus major* populations were only present in the lowest intertidal and shallow subtidal zones of the bay side of the island. All distribution data and population samples were collected from these sites on semi-annual intervals from July 1989 through May 1993.

The density and distribution of ghost shrimp populations were determined by counting burrow openings on the sediment surface. The number of burrows per 0.5 or 1.0 m^2 quadrats were counted during low tide at 2-5 m intervals along permanent transects extending perpendicularly from the beach crest. Burrow densities on the gulf shore were counted on 20 transects, each 10 m apart, extending approximately 25 m from fixed points on the beach. Burrow densities in the bay habitat were counted on three transects, each 15 m apart and approximately 60 m in length. The distinctive burrow openings of these species are distinguishable from the relatively few other macrofaunal burrows (primarily polychaetes and hemichordates) present at this site. Where possible, surface sediment was excavated in order to count subsurface burrow openings and correlate the actual numbers of burrows to surface burrow openings. The relationship between surface and subsurface burrow openings was approximately 1:1. Polyester resin casts of *C. islagrande* burrows indicated that burrows typically have one opening to the surface, and that each burrow is usually occupied by a single

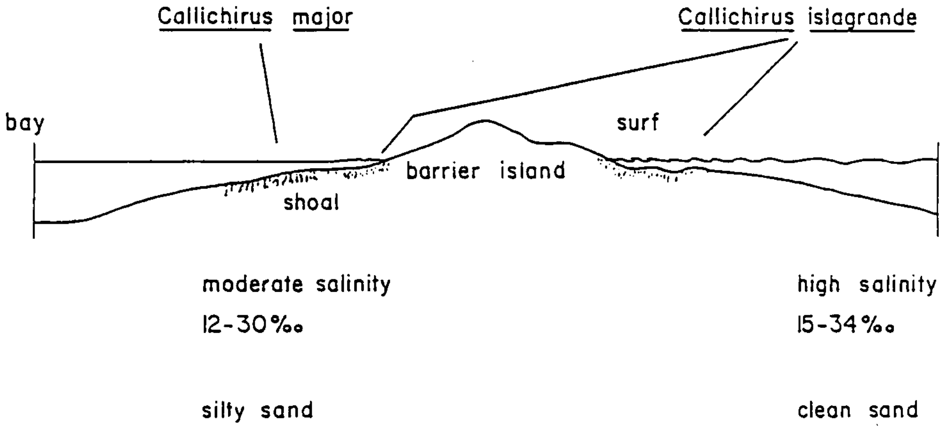


Figure 23. Typical distribution of *Callichirus islagrande* and *C. major* on gulf and bay beaches of barrier islands in the northern Gulf of Mexico.

individual (see Chapter 4). This information allowed direct estimates of population density from counts of surface burrow openings per unit area.

Individuals were collected during low tide using manual suction pumps (yabbie pumps) which permitted individuals to be collected live and undamaged. At each sampling period collections of *C. islagrande* were made from gulf and bay beach sites in order to determine within population variation based on beach location. Collections of *C. major* were made from the lower intertidal and subtidal bay shore habitat when tidal conditions permitted. Ghost shrimp were immediately placed in perforated individual plastic vials and then into large holding containers filled with local seawater for transport to the laboratory. At the laboratory, all individuals were sexed, weighed (WW; wet weight following blotting with tissue paper), and measured for carapace length (CPL) and total length (TL). Total length was measured as the distance from the tip of the rostrum to the posterior margin of the telson using a flat ruler to the nearest millimeter. All other morphometric measurements were made using dial calipers to the nearest 0.1 mm. Carapace length was measured as the distance between the tip of the rostrum and the posterior margin of the carapace. Chela measurements (made only on males) included chela height (ChH; maximum height of the propodus from ventral to dorsal margin), chela width (ChW; maximum width of the propodus) and chela length (ChL; maximum length of the propodus along ventral margin). Ovarian width (OW; width of right ovary visible dorsally within the third abdominal segment) was determined in females. After measurement, some population samples were lyophilized, weighed (DW; dry weight), and then ashed (480 °C for 6 hours) for calculation of ash-free dry weight (AFDW). Analysis of population data was primarily with regression techniques using carapace length as the metric of body size because it was less variable with changes in reproductive state and less susceptible to measurement error than other body measures.

RESULTS

Distribution and Abundance

The distribution and abundance of *Callichirus islagrande* varied spatially along the intertidal gradient and temporally between seasons in both the gulf shore and bay shore habitats. On the gulf beach population densities (as estimated from counts of surface burrow openings m^{-2}; see Methods) increased from a mean of 10 individuals m^{-2} (maximum 22) in January 1990 to a mean of 40 individuals m^{-2} (maximum 90) in October 1990 (Figure 24). These were the highest densities observed on the gulf shore during the course of the study. Population densities then decreased dramatically within one month to a mean of 4 individuals m^{-2} (maximum 10). Densities appeared to remain relatively low through Fall 1991 with slight increases in mean number of individuals m^{-2} in the spring and fall seasons. The data in Figure 23 also indicate that the distribution of the population changed concurrent with movement of the beach face as the island shifted or eroded inland over time. However, the population did not change in distribution relative to the beach crest and maintained the same position within the intertidal zone over time.

Population densities in the bay shore were much higher than on the gulf shore reaching a maximum of over 250 individuals m^{-2} in June 1990 and July 1991. Mean densities during these times were 100 to 150 individuals m^{-2}. Densities declined to lows of 15 to 30

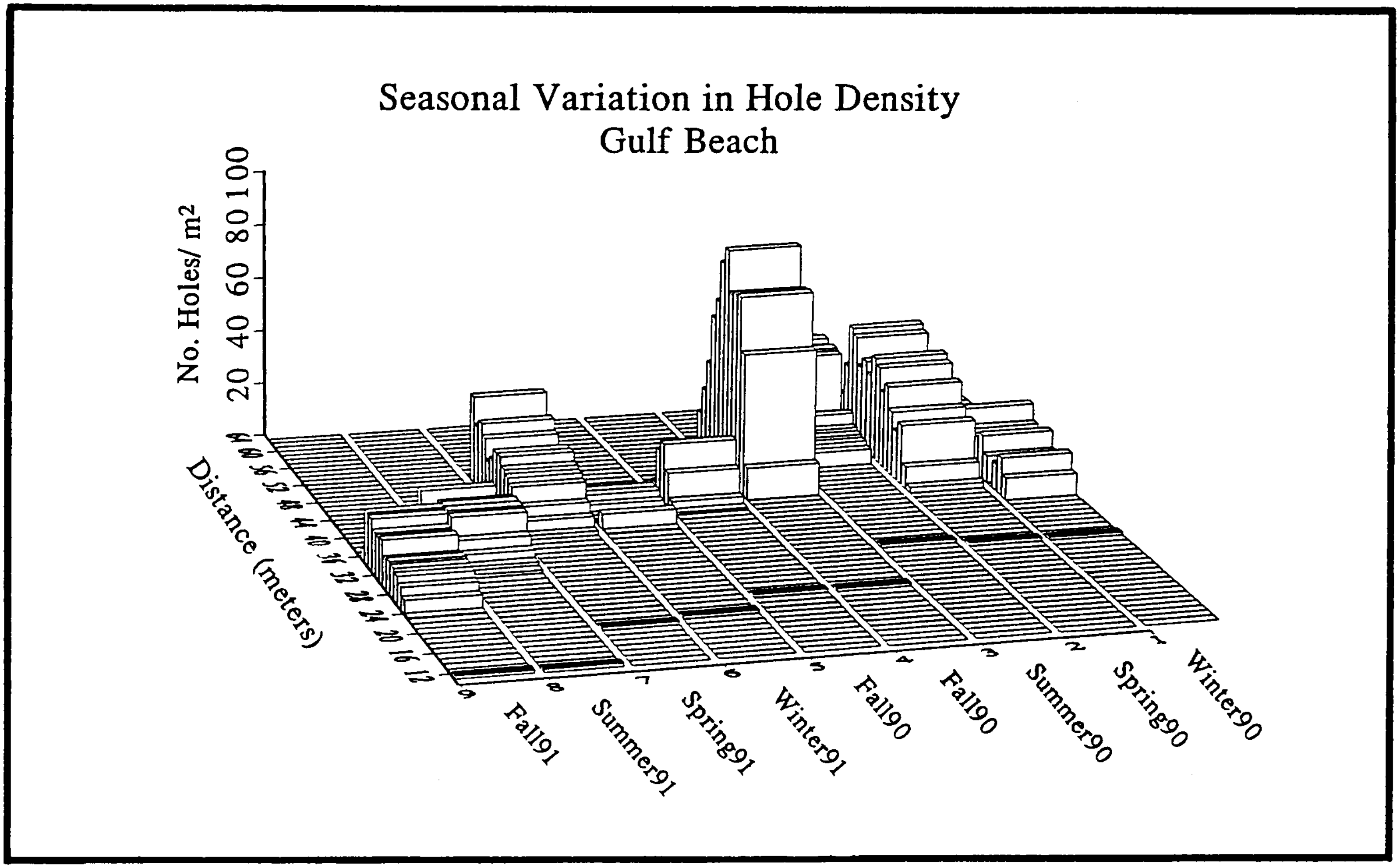


Figure 24. Variation in density (No. burrow openings m^{-2}) of *C. islagrande* on the gulf beach of Isles Dernieres, Louisiana. Plot shows changes in population density with season and distance from permanent beach marks (at 0 m) as well as the beach crest (black bar).

individuals m^{-2} during the fall 1990, winter 1991, and spring 1991. Densities remained relatively high into the fall 1991 (mean 100, maximum 220 individuals m^{-2}). The distribution of the population within the intertidal zone did not change during the sampling period from June 1990 to September 1991 (Figure 25). During the summer and fall sampling periods when densities were greatest, population densities increased gradually from the high to mid-intertidal (beach crest to 25 m; Figure 24), peaked at 25 to 30 m from the beach crest, and then declined rapidly at 30 to 35 m. Winter and spring distributions followed similar patterns but did not show the rapid decline in density after reaching peak levels. The bay population of *C. islagrande* appeared to extend to at least 40 m and at times 60 m into the intertidal zone from the beach crest.

Demographics

The size-frequency distributions of males, females, gravid females, and juveniles collected in population samples at the gulf and bay shore habitats are shown in Figures 26 and 27, respectively. The dates, sizes, and sex ratios of the population samples are shown in Table 3. A total of 1157 individuals were collected from the gulf (n = 735) and bay (n = 422) sites. Individuals ranged in size from 2 to 19 mm carapace length and 12 to 95 mm total length. Mean carapace length of individuals in the gulf beach population was slightly larger than mean carapace length of the bay population. Sex ratios at both sites were seasonally variable ranging from 0.71 to 3.00 females to males. Sex ratios were slightly female biased in the gulf populations (mean female:male ratio = 1.48) and equal in the bay populations (mean female:male ratio = 1.03). Multiple cohorts were distinguishable in the size-frequency plots and growth rates were estimated by visual inspection of shifts in mean carapace length of cohorts over time. Preliminary review of the data suggest that mean carapace length of smaller individuals (< 11 mm carapace length) increases at a rate of 0.5 to 0.6 mm month^{-1} or 6 to 7 mm year^{-1}. Larger, presumably older individuals appear to have slower growth rates ranging from 0.08 to 0.17 mm month^{-1} or about 1 mm year^{-1}. Growth rate estimates were similar for both the gulf and bay populations and lowest during the winter months. Further analysis of the data is required for more quantitative estimates of growth rates.

Reproduction

Ovary development, the frequency of gravid females, and the frequency of juveniles were monitored in both gulf and bay populations in order to determine characteristics of the reproductive cycle. Ovary development was observed in females with carapace lengths greater than 7 mm, suggesting that this may be the size at which females become sexually mature. Mean ovary width (mm) of females greater than 7 mm carapace length reached maximum levels in June and July in both gulf and bay populations (Figure 28). Ovary width declined in late summer and fall, then increased in January and February. Mean ovary width was higher in the bay than gulf shore population during maximum development and the subsequent decline in ovary width into the fall. Size specific ovary width (ratio of ovary width to carapace length) followed a similar pattern with a clear peak in July in both gulf and bay populations (Figure 29). Gravid females were collected in large numbers in May, June, July, September (1989-1993) during sampling from both the gulf and bay populations (Figures 26 and 27). The presence of gravid females in June, July, and September corresponds with the midsummer peak in ovary width. The presence of gravid females in May suggests that significant interindividual and between season variation exists in the timing of ovarian development.

Table 3. Summary of *Callichirus islagrande* population data collected from gulf (foreshore) and bay (backshore) beaches of the barrier island Isle Dernieres, Louisiana. Abbreviations are as follows: F = females, M = males, J = juveniles. Empty blocks indicate no data available.

	GULF BEACH					BAY BEACH				
Sampling Date	# F	# M	# J	Adult Total	Sex Ratio F:M	# F	# M	# J	Adult Total	Sex Ratio F:M
7-7-89	23	25	0	48	0.92					
1-26-90	46	42	0	88	1.10					
5-23-90	53	41	0	94	1.29					
6-22-90	51	39	0	90	1.31	22	23	0	45	0.96
7-31-90	26	17	0	43	1.53					
10-11-90	42	14	0	56	3.00					
11-18-90	22	12	0	34	1.83	34	49	0	49	2.27
2-24-91	30	12	5	47	2.50	18	34	0	34	1.13
6-20-91	26	26	0	52	1.00	29	55	0	55	1.12
7-22-91	21	25	1	47	0.84	20	48	0	48	0.71
9-2-91	28	16	8	52	1.75	28	56	7	56	1.33
7-24-92	31	23	5	59	1.35	28	55	5	55	1.27
9-8-92						16	52	4	52	0.5
5-22-93	40	14	0	54	2.86	19	44	0	44	0.76
TOTAL	439	296	19	735	1.48	214	208	16	422	1.03

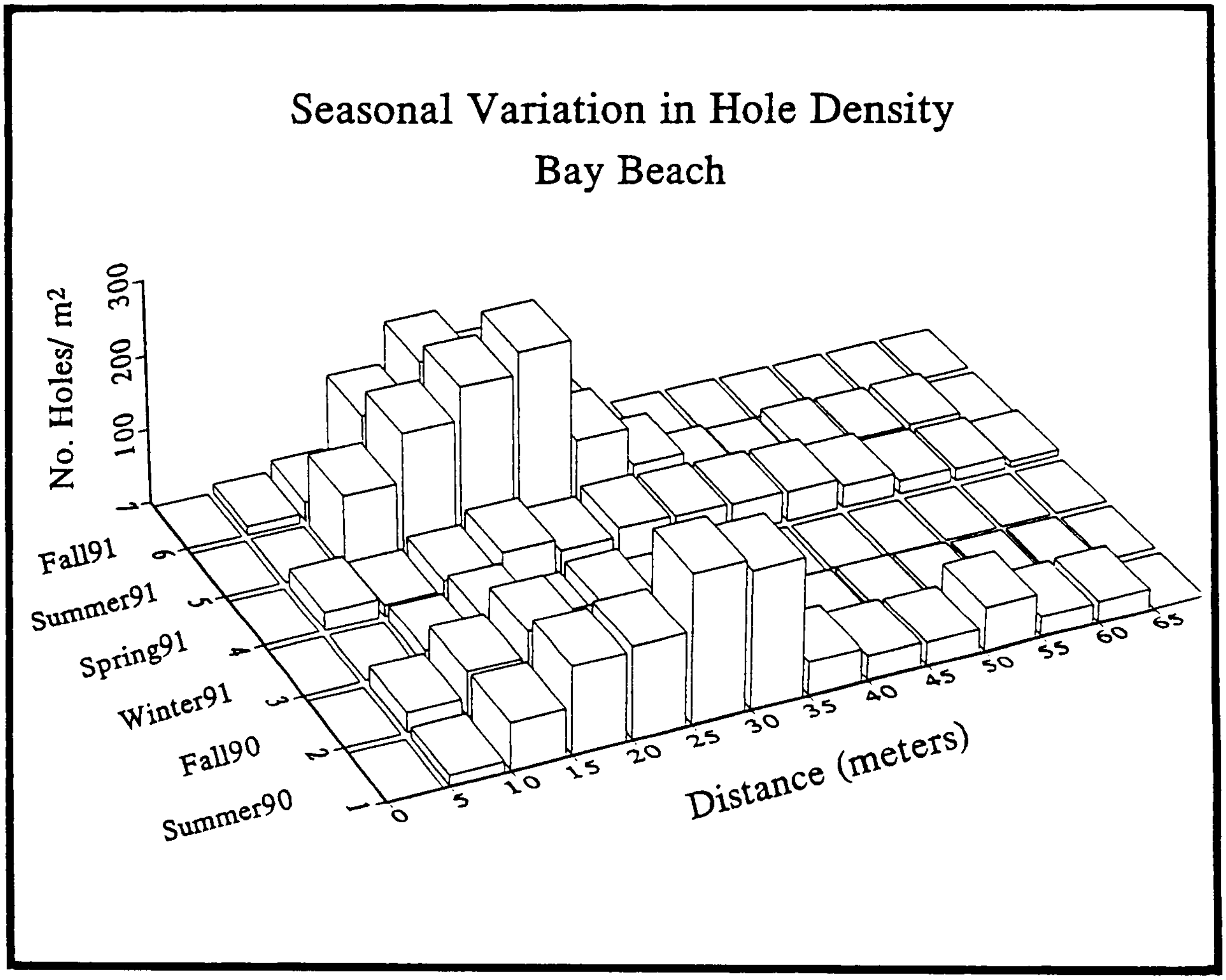


Figure 25. Variation in density (No. burrow openings m^{-2}) of *C. islagrande* on the bay beach of Isles Dernieres, Louisiana. Plot shows changes in population density with season and distance from the beach crest (at 0 m).

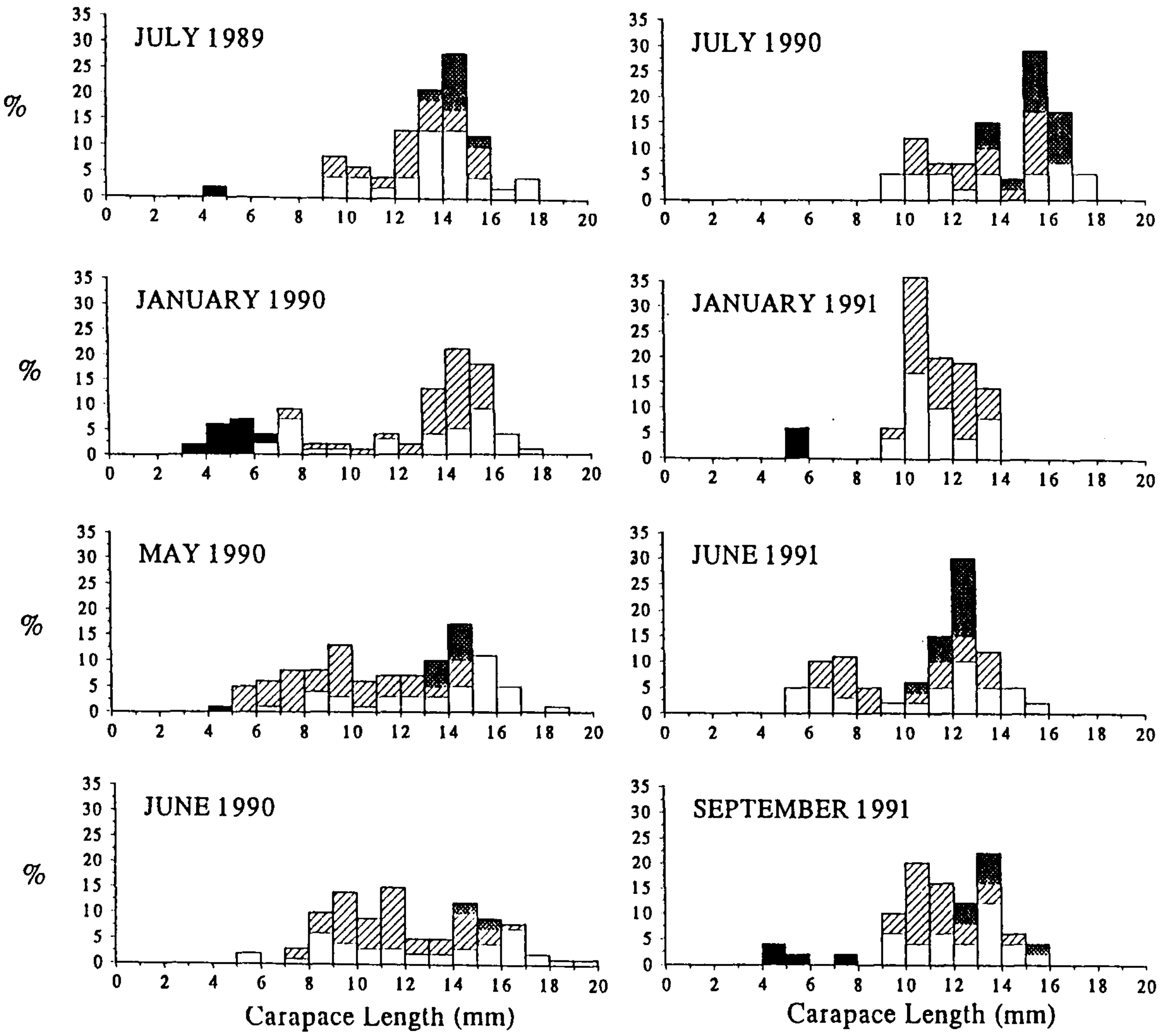


Figure 26. Size-frequency plots of monthly population samples of *C. islagrande* from gulf beach sites. Plots show the percent of sample in 0.5 mm carapace length size classes.

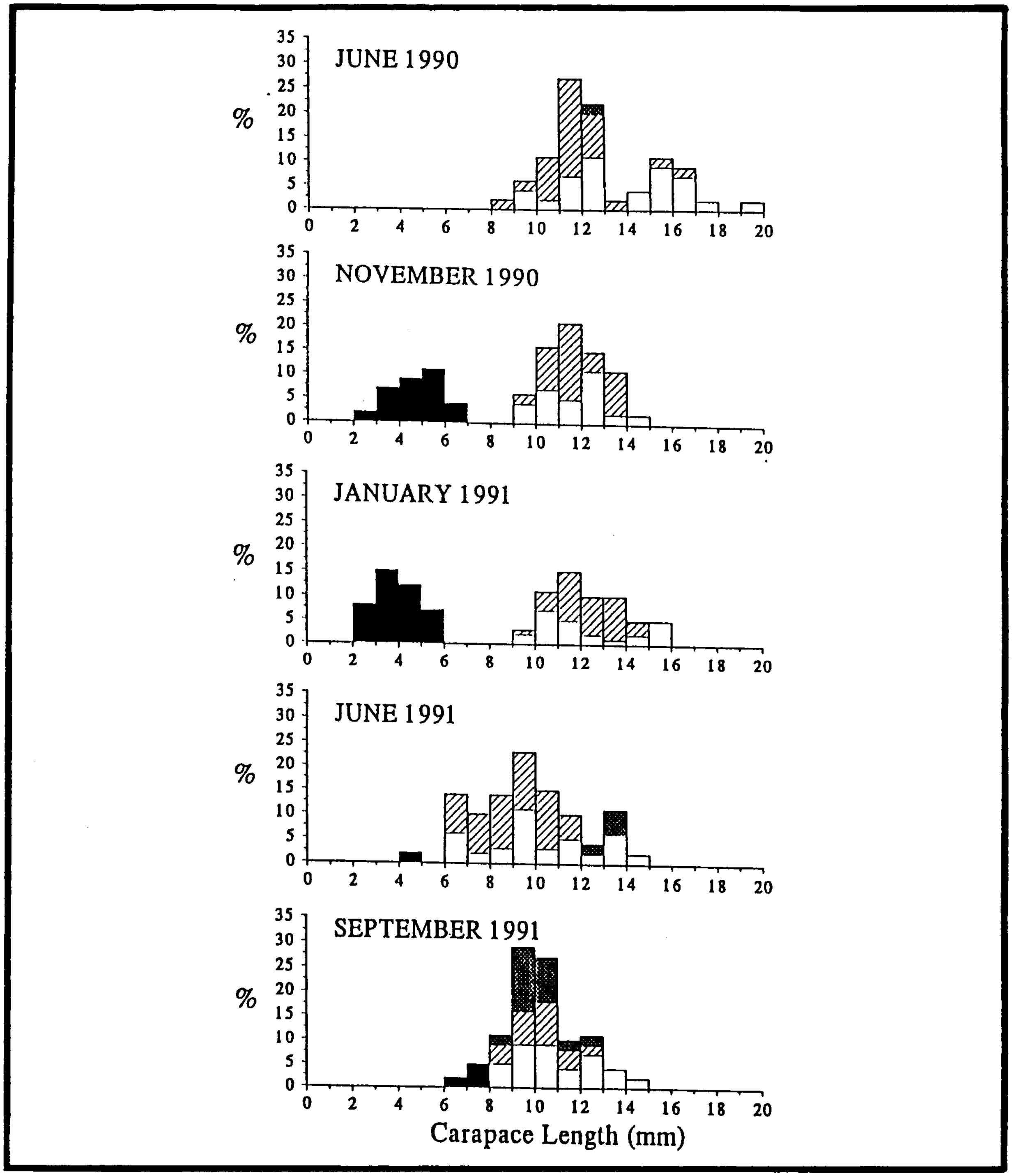


Figure 27. Size-frequency plots of monthly population samples of *C. islagrande* from bay beach sites. Plots show the percent of sample in 0.5 mm carapace length size classes.

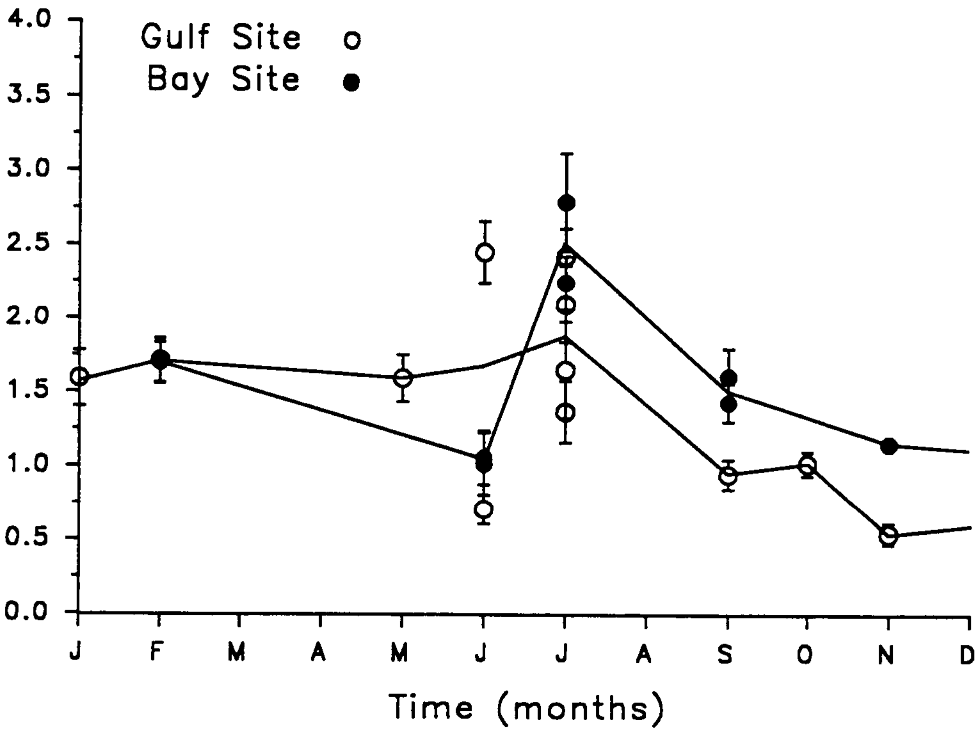


Figure 28. Changes in mean ovary width (mm) with time (months) for *C. islagrande* females with carapace lengths > 7.0 mm. Individuals collected in population samples from 1989 to 1993. Values from multiple years are plotted along a single year period for both inner and outer beach sampling sites. Lines connect average monthly values for each sampling site.

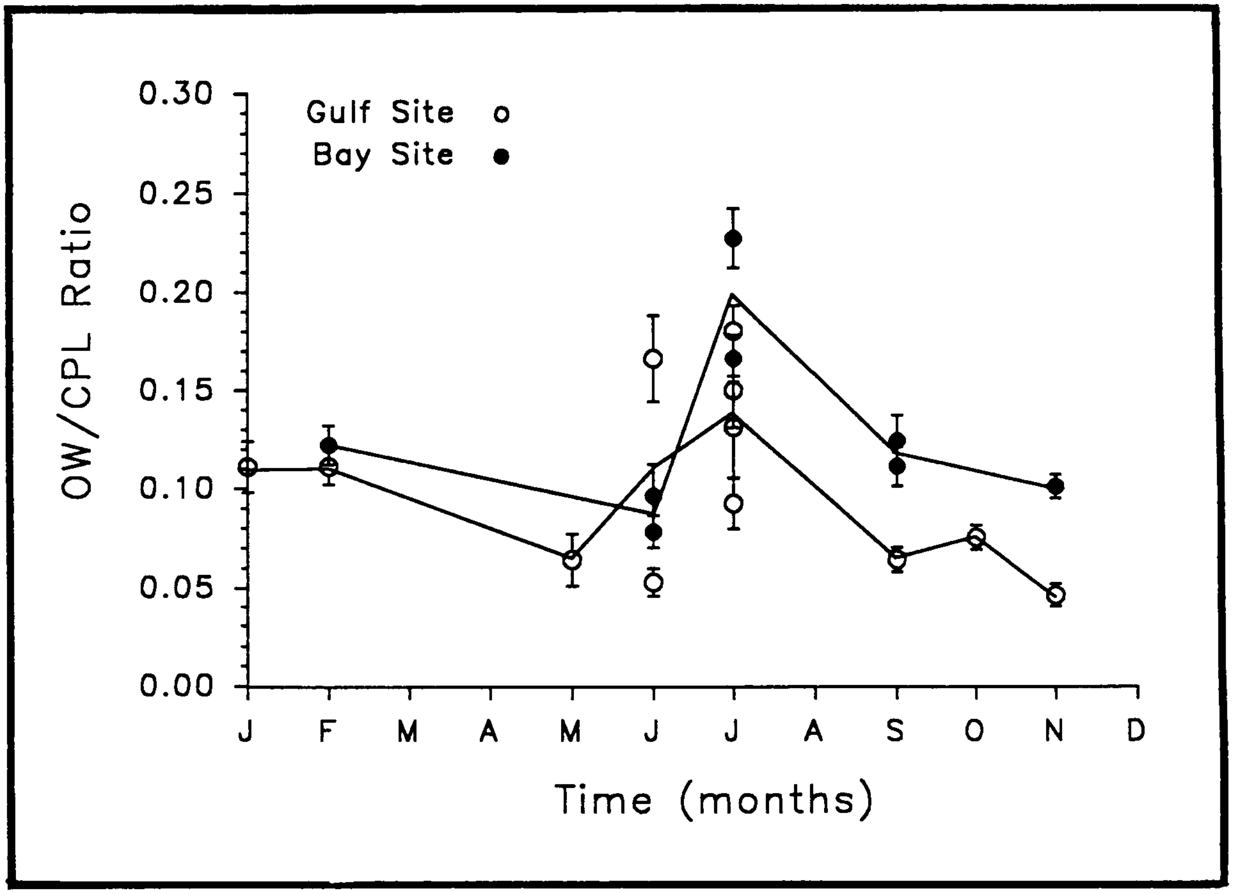


Figure 29. Changes in mean ovary width (mm): carapace length (mm) ratio with time (months) for *C. islagrande* females with carapace lengths > 7.0 mm. Individuals collected in population samples from 1989 to 1993. Values from multiple years are plotted along a single year period for both inner and outer beach sampling sites. Lines connect average monthly values for each sampling site.

Recruitment of new individuals into the population appeared to occur twice per year in the gulf site and once per year in the bay site based on the appearances of new cohorts of individuals with carapace lengths less than 4 mm (juveniles) in population samples. Juveniles appeared in the population samples from the gulf shore in July 1989, January 1990 and 1991, and September 1991 (Figure 26). Juveniles were present in the bay population in November 1990 and January 1991 (Figure 27).

Biomass

Population biomass was estimated from the relationship between wet weight (g) and ash-free dry weight (AFDW)(g) and carapace length (mm) for a total of 116 individuals collected from the gulf and bay sites during the 1990 sampling year. The relationship between carapace length and biomass (wet weight or AFDW) was similar for both males and females from the gulf (Figure 30) and bay (Figure 31) populations, so the sexes were pooled for comparisons between sampling sites. There was a significant positive correlation between carapace length and individual wet weight ($R=0.85$, $n=116$) and carapace length and AFDW ($R=0.87$, $n=116$) for both gulf and bay sites (Figure 32). Individuals from both the gulf and bay populations had similar relationships between carapace length and biomass variables. Estimates of population biomass (biomass m^{-2}) were made by calculating the wet weight (or AFDW) for an average individual from the mean carapace length for each population sample and the regression equations relating carapace length and the biomass variables. This produced an estimate of the mean biomass per individual for each sampling period, which was then multiplied by the mean number of individuals m^{-2} to produce estimates of biomass m^{-2}. Figures 33 and 34 show estimates of wet weight (g m^{-2}) and AFDW (g m^{-2}) along intertidal transects for both the gulf and bay sites, respectively. Wet weight biomass reached a maximum of 270 g m^{-2} in gulf populations and over 700 g m^{-2} in bay populations. Ash-free dry weight biomass reached a maximum of 70 g m^{-2} in gulf and 248 g m^{-2} in bay populations. Average wet weight estimates varied seasonally through 1990 and 1991 exhibiting peaks in midsummer in the bay site and November in the gulf site (Figure 35). Average population estimates of AFDW followed a pattern similar to that of the wet weight estimates (Figure 36).

DISCUSSION

Callichirus islagrande is an abundant macrofaunal burrower on gulf (foreshore) and bay (backshore) beaches of barrier islands in the northern Gulf of Mexico. The results of this study indicate that at Isles Dernieres, individuals are less dense in gulf shore populations (maximum density 90 individuals m^{-2}) than in bay populations (maximum 750 individuals m^{-2}). Densities at both sites exhibited considerable seasonal variation and maximum densities were observed during fall at the gulf site and during the summer in the bay population. The gulf shore population declined dramatically from 40 to 4 individuals m^{-2} over a one month period in fall 1990 coincident with storm activity in the area. This suggests that storm induced high seas and wave energy may play an important role in determining the abundance and distribution of the gulf shore populations. The gulf population shifted in distribution as the beach front changed position suggesting that these individuals may be mobile enough to maintain or regain their position in the lower intertidal zone relative to a moving beach crest. In contrast, the bay population did not appear to change in distribution along the tidal transects during this study. In spite of the apparent differences in storm induced habitat stability between the gulf and bay sites, individuals from the two populations had nearly identical size-biomass relationships and followed similar seasonal patterns of ovary development with a mid-summer maximum. The gulf population differed from the bay population

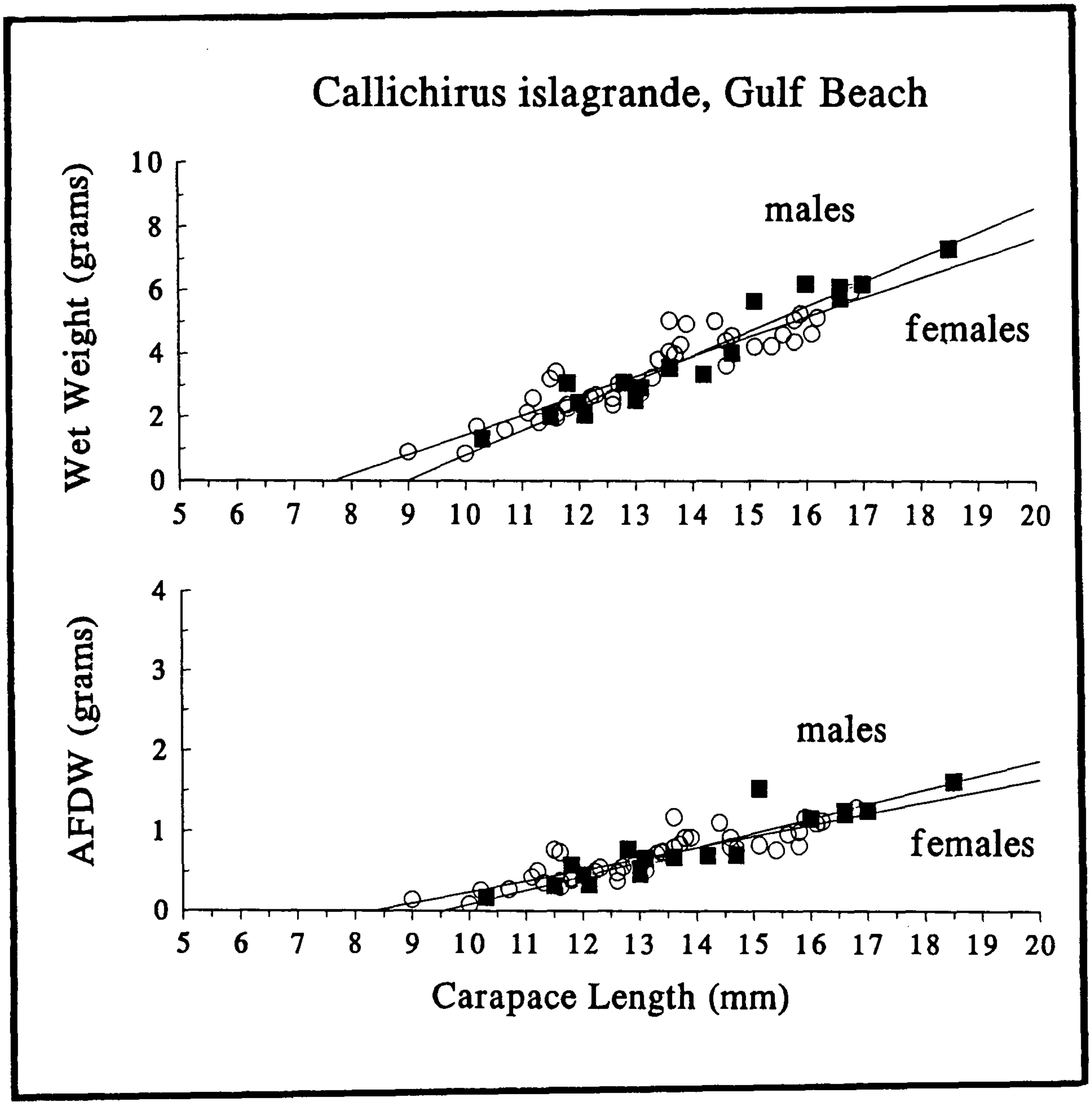


Figure 30. Relationship between carapace length (mm) and wet weight (g), and carapace length (mm) and ash-free dry weight (AFDW)(g) for female and male *C. islagrande* from gulf beach populations.

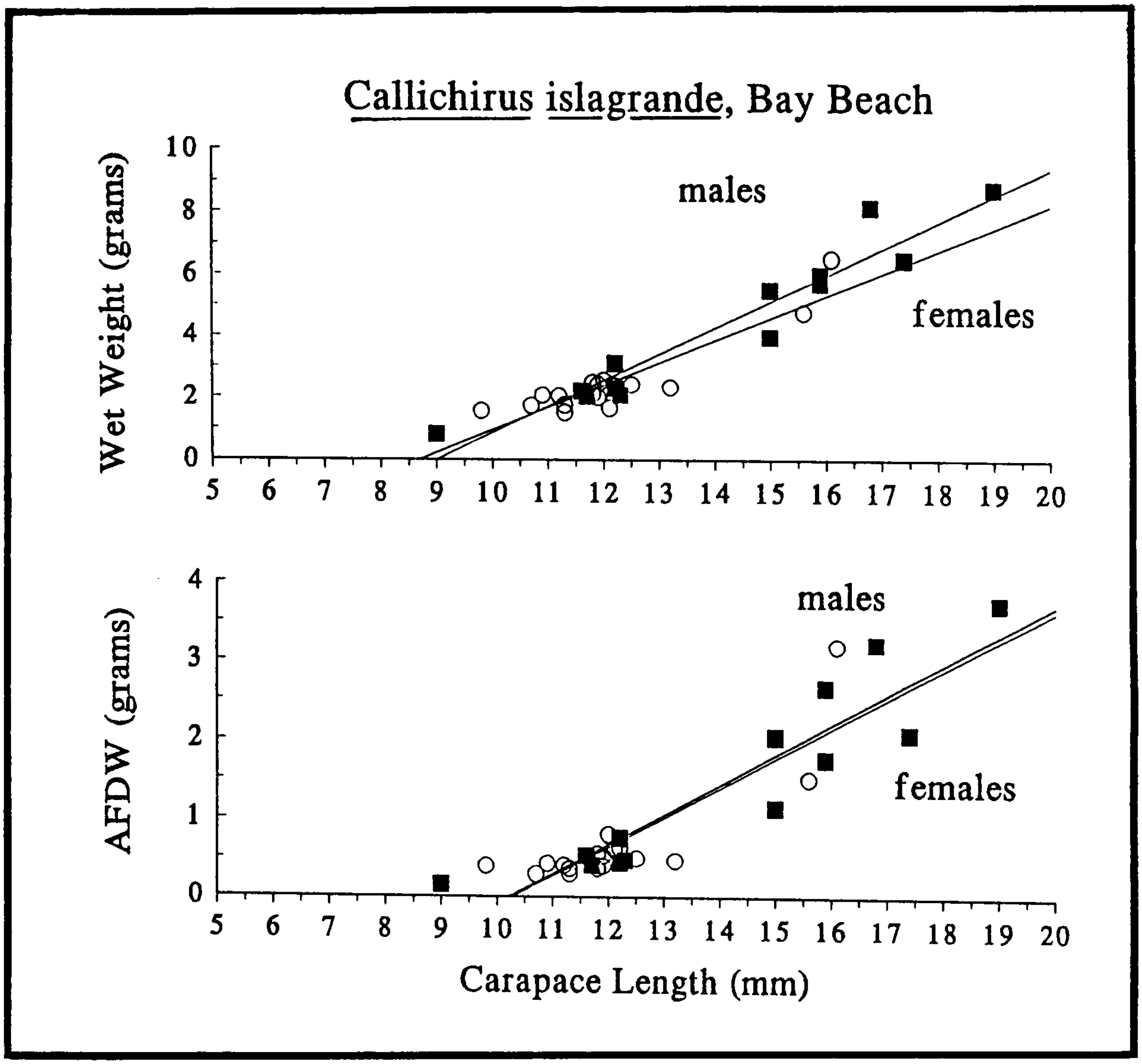


Figure 31. Relationship between carapace length (mm) and wet weight (g), and carapace length (mm) and ash-free dry weight (AFDW)(g) for female and male *C. islagrande* from bay beach populations.

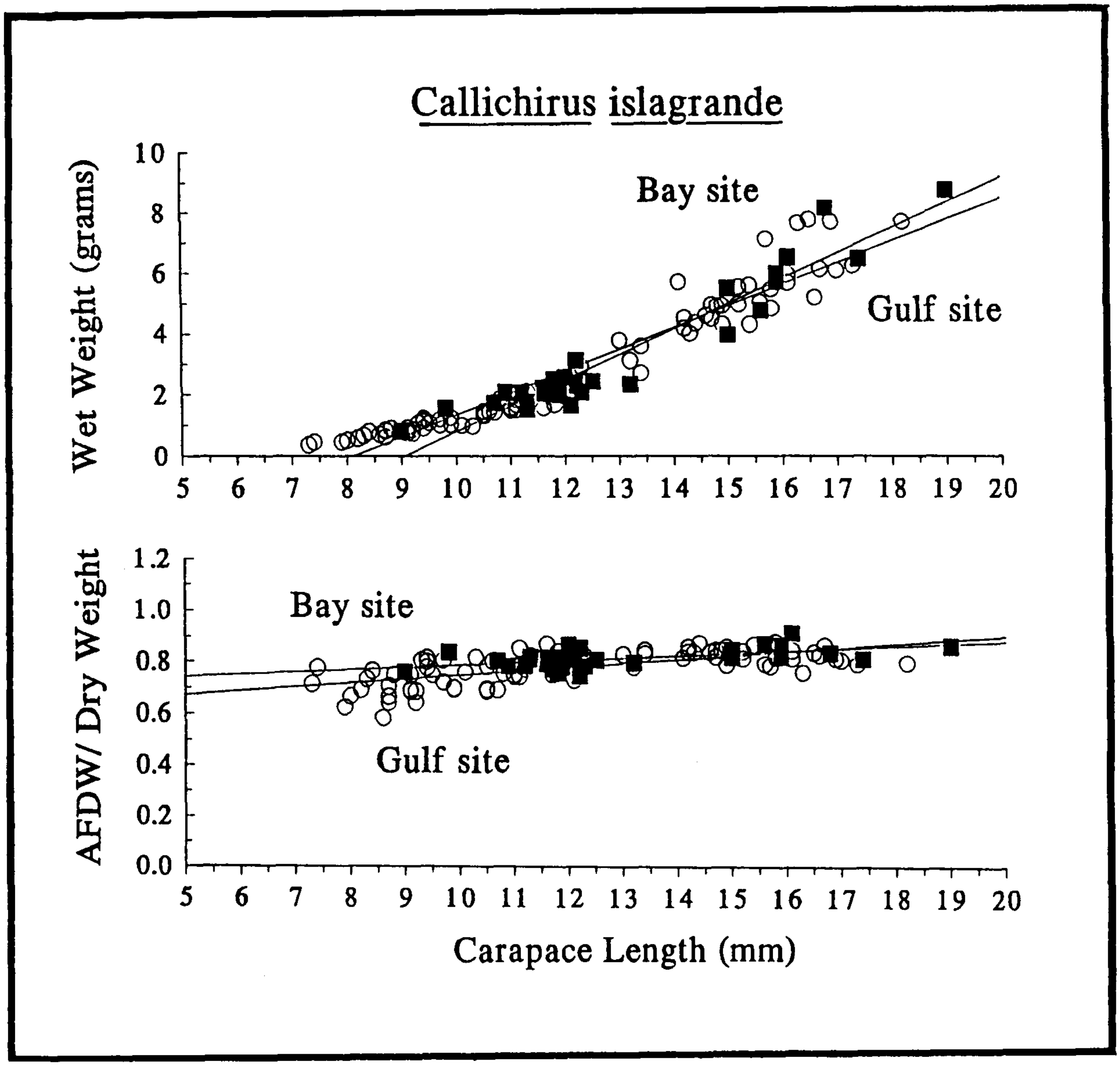


Figure 32. Relationship between carapace length (mm) and wet weight (g), and carapace length (mm) and ash-free dry weight (AFDW)(g) for *C. islagrande* from bay beach populations.

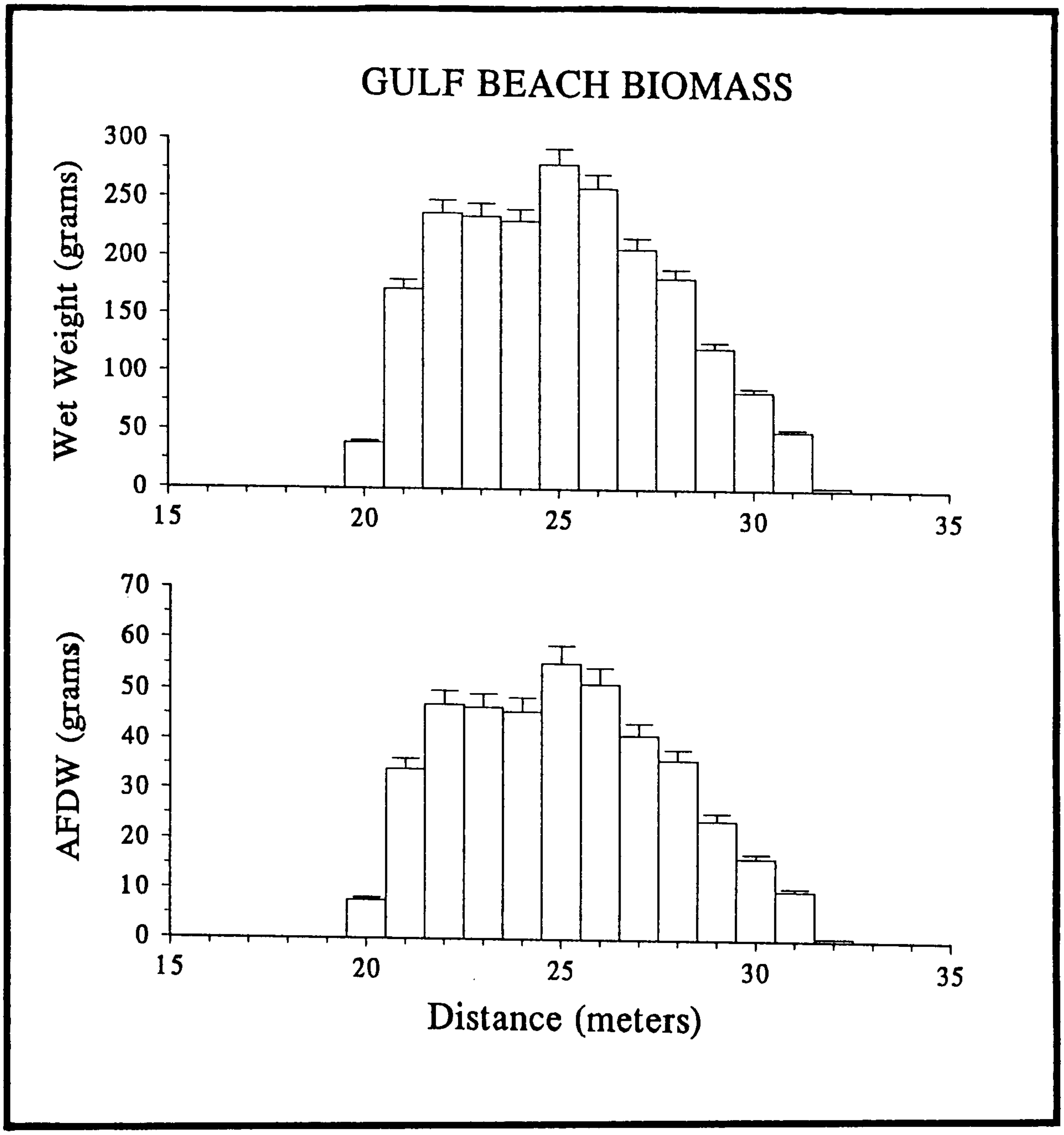


Figure 33. Mean (+ std. error) population biomass (wet weight (g) and ash-free dry weight (AFDW)(g)) of *C. islagrande* along a gulf beach transect.

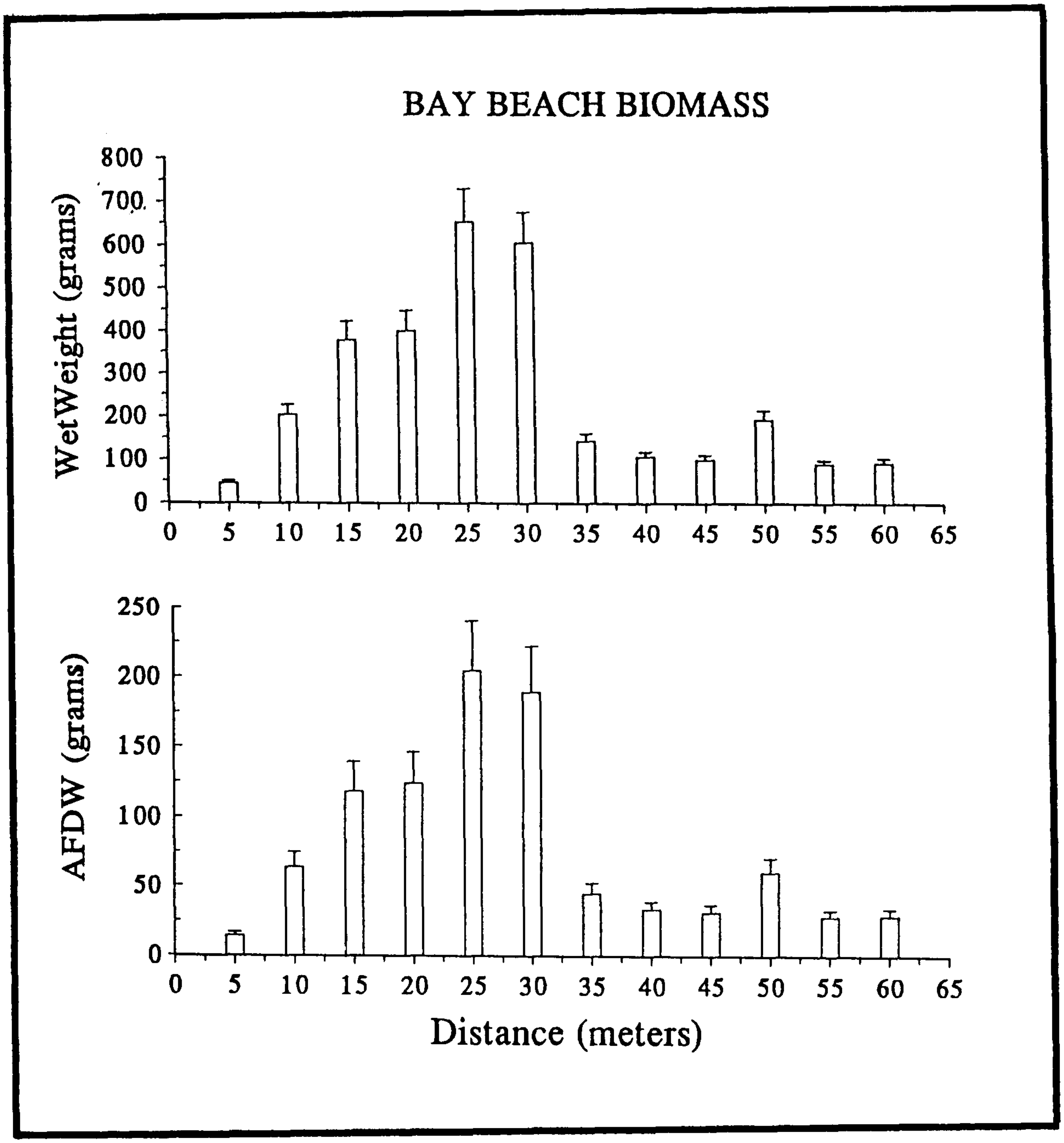


Figure 34. Mean (+ std. error) population biomass (wet weight (g) and ash-free dry weight (AFDW)(g)) of *C. islagrande* along a gulf beach transect.

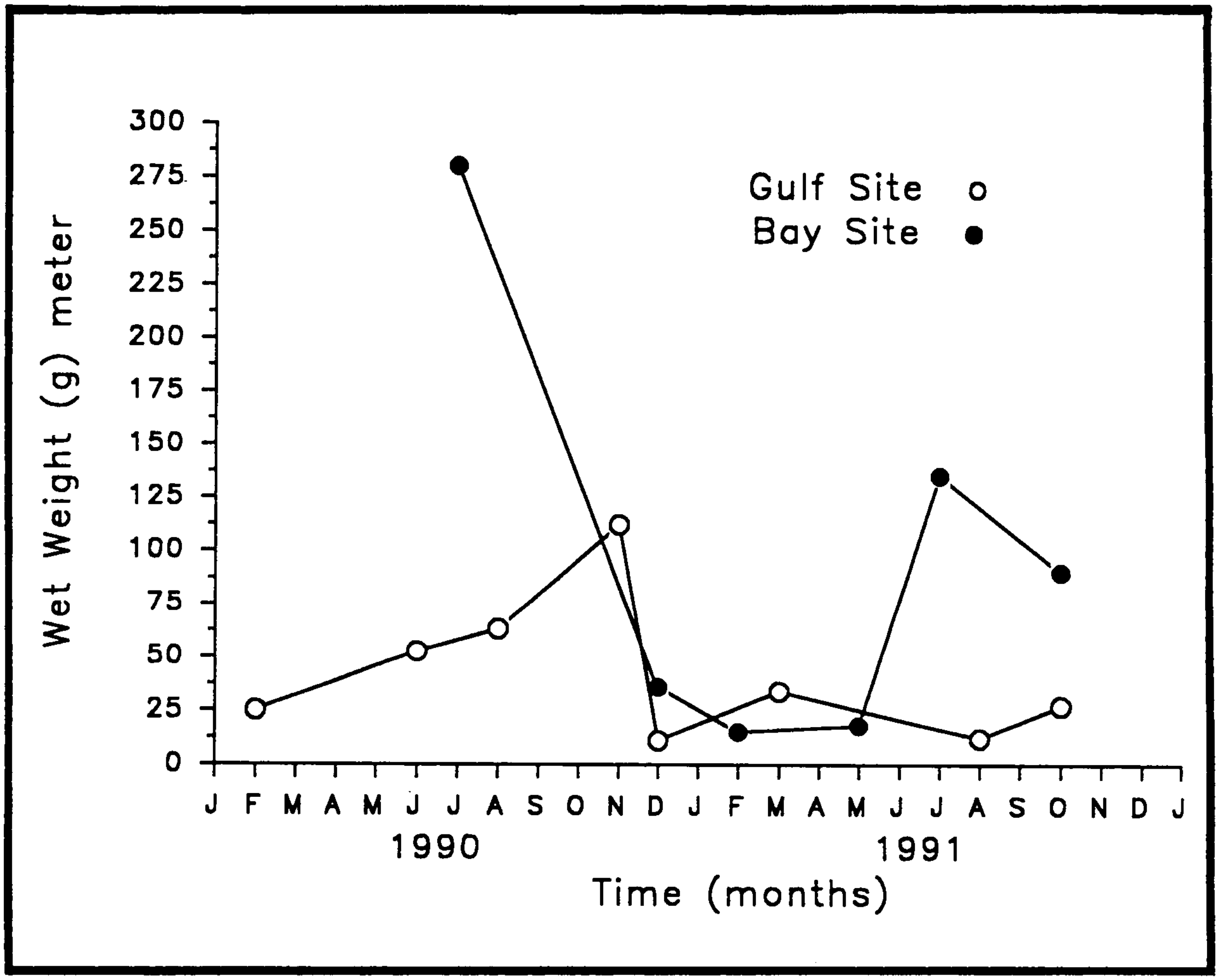


Figure 35. Changes in *C. islagrande* population biomass (wet weight (g) m^{-2}) with time at gulf and bay beach sampling sites.

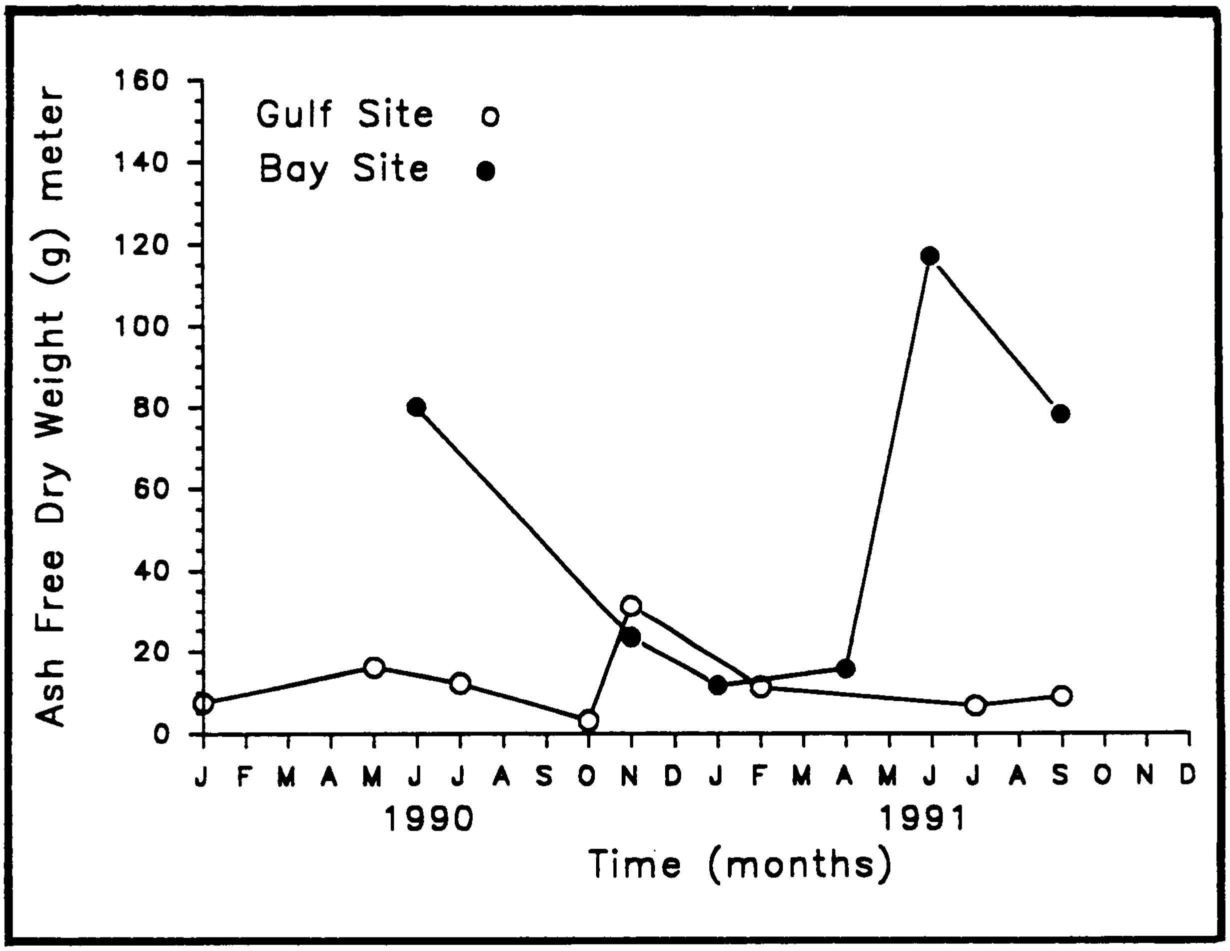


Figure 36. Changes in *C. islagrande* population biomass (ash-free dry weight (g) m^{-2}) with time at gulf and bay beach sampling sites.
]

by having a slightly female biased sex ratio, reaching slightly larger body sizes, having fewer individuals and less biomass m^{-2}, and having two recruitment events $year^{-1}$ instead of one as in the bay population.

CHAPTER 4: ECOLOGICAL EFFECTS OF INTERTIDAL AND SHALLOW SUBTIDAL THALASSINID INFAUNA

INTRODUCTION

Thalassinid shrimp are macrofaunal burrowers common in intertidal and subtidal soft sediments worldwide (Griffis and Suchanek 1991, Felder and Rodrigues 1993). They have been characterized as ecologically important members of these communities because their size, burrowing activity, and high densities can significantly modify the physical characteristics of the habitat, thereby influencing the productivity and composition of the benthic community (Branch and Pringle 1987, Posey 1990). Much of this habitat modification is due to the high levels of bioturbation associated with the burrowing and feeding of the shrimp. Bioturbation may have many different effects on benthic habitats including increasing oxygenation and mineralization (Kristensen et al. 1985), modifying sediment geochemistry and sediment transport (Aller et al. 1983, Jumars and Nowell 1984), and inhibiting or stimulating the growth and/or survivorship of certain organisms (Rhodes and Young 1970, Moriarty et al. 1985). Bioturbation and burrowing by thalassinid shrimp has been implicated with the inhibition of suspension-feeders, corals, seagrasses, benthic bivalves, and meiofauna (Aller and Dodge 1974, Peterson 1977, Suchanek 1983, Buchanan et al. 1985, Murphy 1985, Colin et al. 1986, Posey 1986b, Branch and Pringle 1987). The burrowing activity of thalassinid shrimp has also been associated with increases in sediment bacterial biomass (Branch and Pringle 1987, Dobbs and Guckert 1988), and nutrient fluxes from the sediment (Aller et al. 1983, Koike and Mukai 1983). This study was designed to investigate the ecological effects of *Lepidophthalmus louisianensis* and *Callichirus islagrande*, two species of thalassinid shrimp found abundantly in intertidal sediments of the northern Gulf of Mexico. Some effects of a third species, *Lepidophthalmus sinuensis*, were also included for comparative purposes because of the ecological similarity between this species and *L. louisianensis.*

METHODS

The ecological effects of burrows and burrowing by the ghost shrimp *Lepidophthalmus louisianensis* and *Callichirus islagrande* were studied in intertidal habitats of the northern Gulf of Mexico. *Lepidophthalmus louisianensis* was studied at an intertidal sandflat on the western shore of Bay St. Louis, Mississippi. The primary study sites for *Callichirus islagrande* were gulf (foreshore) and bay (backshore) beaches of the barrier island Isles Dernieres, Louisiana. *Lepidophthalmus sinuensis* was studied where it was found in association with penaeid shrimp farms in Colombia, South America (Lemaitre and Rodrigues 1991). Chapters 2 and 3 of this report describe these sites and the population dynamics of the first two species in detail. This report is divided into three parts to describe (1) burrow morphology, (2) bioturbation, and (3) nutrient flux from burrows of the burrowing shrimp.

Burrow Morphology

Polyester resin casts of burrows were made by adding resin to hardener and pouring the mixture into open burrows. The resin hardened in several hours and the burrow cast was removed by digging and washing away sediments with water from a gasoline-driven water pump. The shape, depth, mean diameter, and occupant characteristics of each burrow were recorded in order to calculate surface area and total volume of burrows from each species. Calculations of burrow surface area and volume were made using burrow diameter in equations for cylinder wall area and volume. In the field, samples of burrow walls were collected and frozen in liquid nitrogen or fixed in 10% formalin for laboratory analysis of grain size distribution, organic content, chlorophyll levels, and carbon-nitrogen ratios using standard analysis techniques. Changes in the reduction-oxidation (redox) potential of burrow wall and non-burrowed sediments was recorded in the field using platinum-copper and calomel reference probes attached to a pH-millivolt meter.

Bioturbation

Bioturbation was measured as the amount of sediment ejected from shrimp burrows per unit time. Ejected sediment was collected in sediment traps made from large plastic petri plates (15 cm diameter x 5 cm height) with a 3 cm diameter hole in one side placed over the burrow opening on the sediment surface. The traps were anchored and left for 24 hours before the contents were collected and weighed. Sediment traps were also anchored over nonburrowed sediment to act as controls for the collection of nonbioturbated sediment, and the mean sediment collected in these traps was subtracted from bioturbation trap values. The rate of fecal pellet production was also recorded in the field by counting pellets around burrow openings after exposure during low tide. Although this method quantifies only those pellets ejected during the low tide period, field observations of these species over full tidal cycles indicates that most pellets are ejected just prior to exposure and that these data are conservative estimates of fecal pellet production.

Nutrient Flux From Burrows

The exchange of nutrients between burrows and the overlying water column was measured by quantifying the nutrient content in water within the burrows and estimating pumping rates out of the burrows from literature values. Nutrient content of the burrow water was compared to nutrient levels in pore water at various depths and the overlying water column. Water samples were collected from burrows by inserting small diameter tubing at least 20 cm into recently exposed burrows and slowly drawing water into a 60 ml syringe. Pore water was also sampled through plastic tubing with a 60 ml syringe after insertion into the sediment to the appropriate depth (0, 10, 20, or 40 cm).

RESULTS

Burrow Morphology

Resin casts of burrows of *Lepidophthalmus louisianensis*, *L. sinuensis*, and *Callichirus islagrande* were generally similar in overall morphology. All three species produced burrows with narrow, circular, smooth-walled shafts leading straight down from 5 to 15 cm from the sediment surface to the main burrow. The main burrow consisted of a single shaft that led downward and branched to various degrees into short, dead end tunnels typical of the Type 4 burrows described by Griffis and Suchanek (1991). The burrows differed in depth and number of surface openings among the three species. *Lepidophthalmus louisianensis* constructed long burrows with single openings that extended deep into the sediment for 40 to 200 cm with little branching. Juvenile *L. louisianensis* burrows were observed branching off adult burrows. The burrows of *L. sinuensis* were shallower (30-50 cm depth), more branched, and averaged 3 holes per burrow in the commercial ponds. *Callichirus islagrande* made simple burrows with one surface opening and usually one side branch that extended to depths of 30-50 cm. Burrow diameters were highly correlated with the carapace length of the occupant, and both burrow surface area (Figure 37) and burrow volume (Figure 38) increased linearly with burrow diameter over the range of sizes collected. Burrow surface area and volume were highest in burrows of *L. louisianensis* due primarily to their greater length.

The significant relationship between burrow characteristics and carapace length permitted the calculation of mean burrow surface area and volume from mean carapace length in population samples (see Chapters 2 and 3). These values multiplied by average population densities produce and estimate of the average burrow wall surface area (m^2) and average burrow volume (liters) created by burrowing shrimp beneath each square meter of sediment surface. These values are listed in Table 4 for the three species in this study and others cited in the literature. At average densities of 90 burrows m^{-2}, *L. louisianensis* constructs 2.10 m^2 of burrow surface area and 4.77 liters of burrow volume beneath each square meter of sediment surface. At maximum densities of 400 burrows m^{-2}, these values are 9.33 m^2 m^{-2} and 21.20 liters per m^2 sediment surface. At average densities of 100 burrows m-2, L. sinuensis produces 1.61 m^2 burrow wall surface area and 2.6 liters of burrow volume per m^2 sediment surface. At maximum densities of 220 burrows m^{-2}, *C. islagrande* constructs 5.25 m^2 burrow surface area and 16.72 liters burrow volume per m^2 sediment surface.

Lepidophthalmus louisianensis and *Callichirus islagrande* differed in the construction of the burrow wall. *Lepidophthalmus louisianensis* constructed a thick burrow wall composed of two parts, a thin (@ 1-2 mm) inner lining and a thicker (@ 2-3 mm) outer matrix. The burrow lining and matrix have significantly higher carbon, nitrogen, and overall organic content than ambient non-burrowed sediment and the sediment surface (Table 5). The burrow wall is primarily composed of silt and clay particles (mean 8-10 % by weight) which are uncommon in surface or non-burrowed sediment (mean 0.6-0.8 % by weight) surrounding the burrow walls. These results suggest that *L. louisianensis* is actively concentrating fine particles in the burrow walls and constructing organically enriched burrow environments as observed in the burrowing shrimp *Neocallichirus trilobata* (Dobbs and Guckert 1988). The walls of *C. islagrande* burrows are not lined with fine particles and do not differ in sediment grain size or organic content from ambient, nonburrowed sediment. However, the burrows of both species oxygenate the sediment surrounding the burrow walls for one to two centimeters as indicated by decreasing redox potential values with increasing distance from the burrow wall (Figure 39).

Bioturbation

All three species of burrowing shrimp ejected sediment from burrows onto the sediment surface. Mean bioturbation rates were 10 (+ 1.3 SE) g wet sediment $burrow^{-1}$ day^{-1} for *L. louisianensis* and *L. sinuensis*, and 51 (+ 20 SE) g wet sediment $burrow^{-1}$ day^{-1} for *Callichirus islagrande* during summer sampling periods. Estimates of bioturbation m^{-2} were calculated by multiplying the mean bioturbation rate $burrow^{-1}$ day^{-1} by the mean number of burrows m^{-2}. *Lepidophthalmus* species at a mean density of 100 burrows m^{-2} eject approximately 1080 g wet sediment m^{-2} day^{-2} (Figure 40). At maximum densities the bioturbation would be

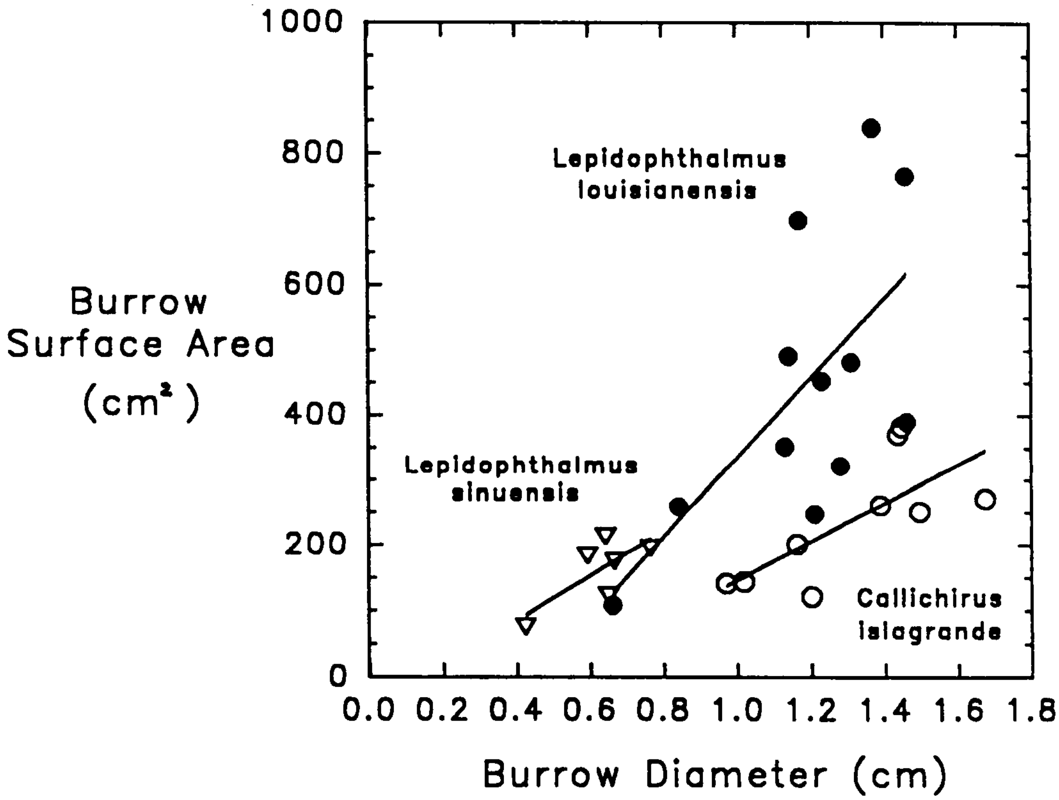


Figure 37. Relationship between burrow diameter (cm) and burrow surface area (cm^2) for *L. louisianensis*, *L. sinuensis*, and *C. islagrande*. Values calculated from burrow resin casts.

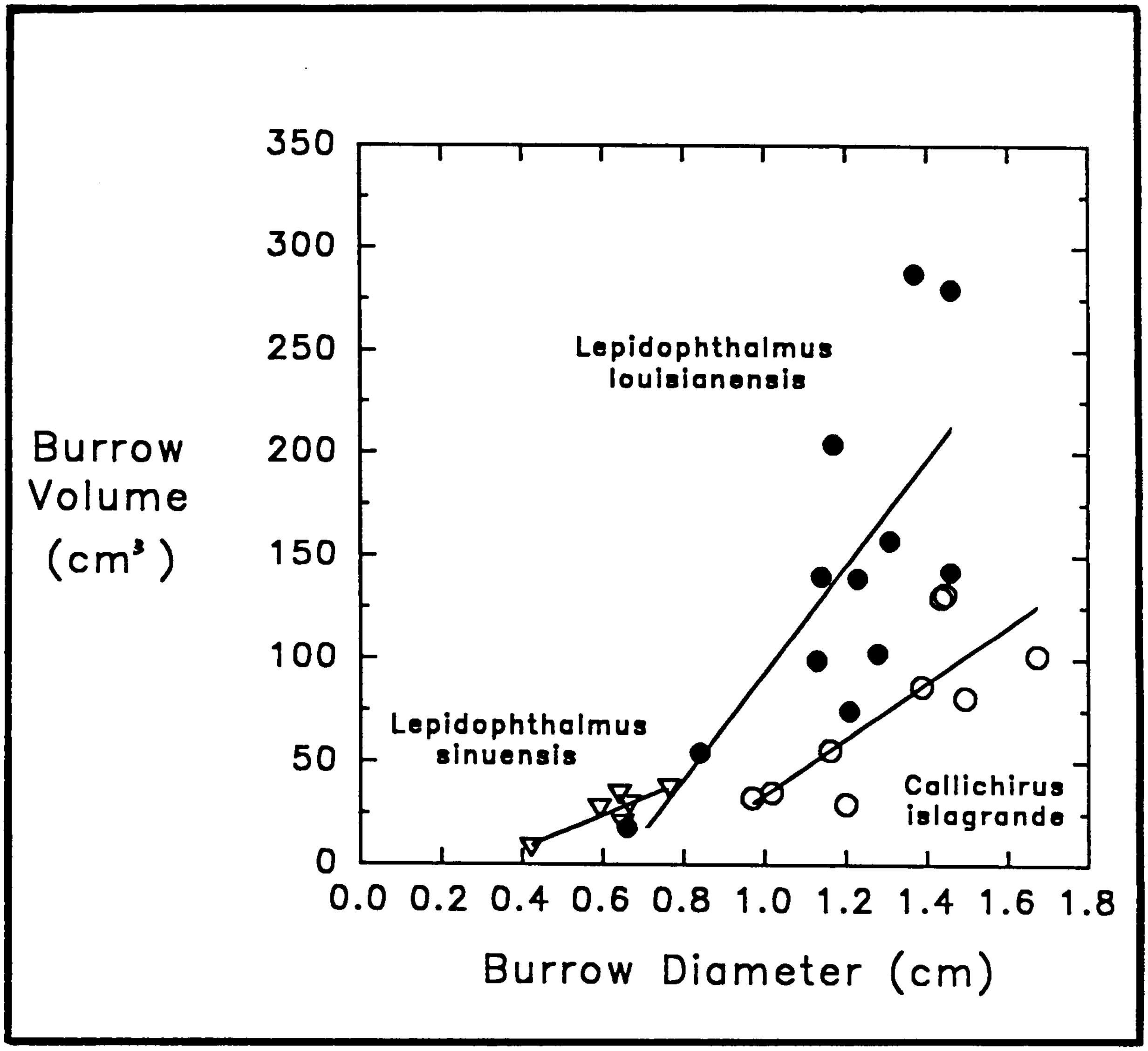


Figure 38. Relationship between burrow diameter (cm) and burrow volume (cm^3) for *L. louisianensis*, *L. sinuensis*, and *C. islagrande*. Values calculated from burrow resin casts.

Table 4. Summary of population densities and burrow characteristics for thalassinid shrimp.

Species	Average Population Density (# burrows m-2)	Estimated Burrow Surface Area (m2 m^{-2})	Estimated Burrow Volume (L m^{-2})	Reference
Callianassa bouvierei	450	2.6	3.2	Dworschak and Pervesler 1988
Callianassa californiensis	78-170	1.2 - 2.7	3.1-6.7	Miller 1984
	50-100	0.7 - 1.4	1.6-3.2	Griffis and Chavez 1988
	100-180	1.9 - 3.4	5.6-10.2	Swinbanks and Murray 1981
Callianassa gigas	50-100	1.6 - 3.1	3.9-7.8	Griffis and Chavez 1988
Callianassa subterranea	50	1 - 2	6	Witbaard and Duineveld 1989
Callichirus islagrande	70	1.7	5.3	this study
Lepidophthalmus louisianensis	90	2.1	4.8	this study
Lepidophthalmus sinuensis	100	1.6	2.6	this study
Upogebia littoralis	200-250	7 - 9	NA	Ott et al. 1976
Upogebia pugettensis	10-40	0.3 - 1.2	1.2-4.8	Swinbanks and Murray 1981
Upogebia pusilla	30-80	1 - 3	5 - 11	Dworschak 1983

Table 5. Summary of burrow wall characteristics of *Lepidophthalmus louisianensis* from Bay St. Louis, Mississippi.

		Sediment Sample			
Variable		Burrow Lining	Burrow Matrix	Ambient Sediment	Surface Sediment
% Organics	mean	3.657	2.467	0.508	0.522
	sd	0.349	0.971	0.248	0.037
	n	6	6	6	6
% Carbon	mean	0.775	0.677	0.085	0.05
	sd	0.187	0.220	0.029	0.01
	n	4	6	4	4
% Nitrogen	mean	0.095	0.042	0.055	0.018
	sd	0.056	0.02	0.019	0.009
	n	4	6	4	4
% Silt + Clay	mean	10.76	8.15	0.67	0.74
	sd	3.37	1.3	0.01	0.86
	n	8	4	0.01	3

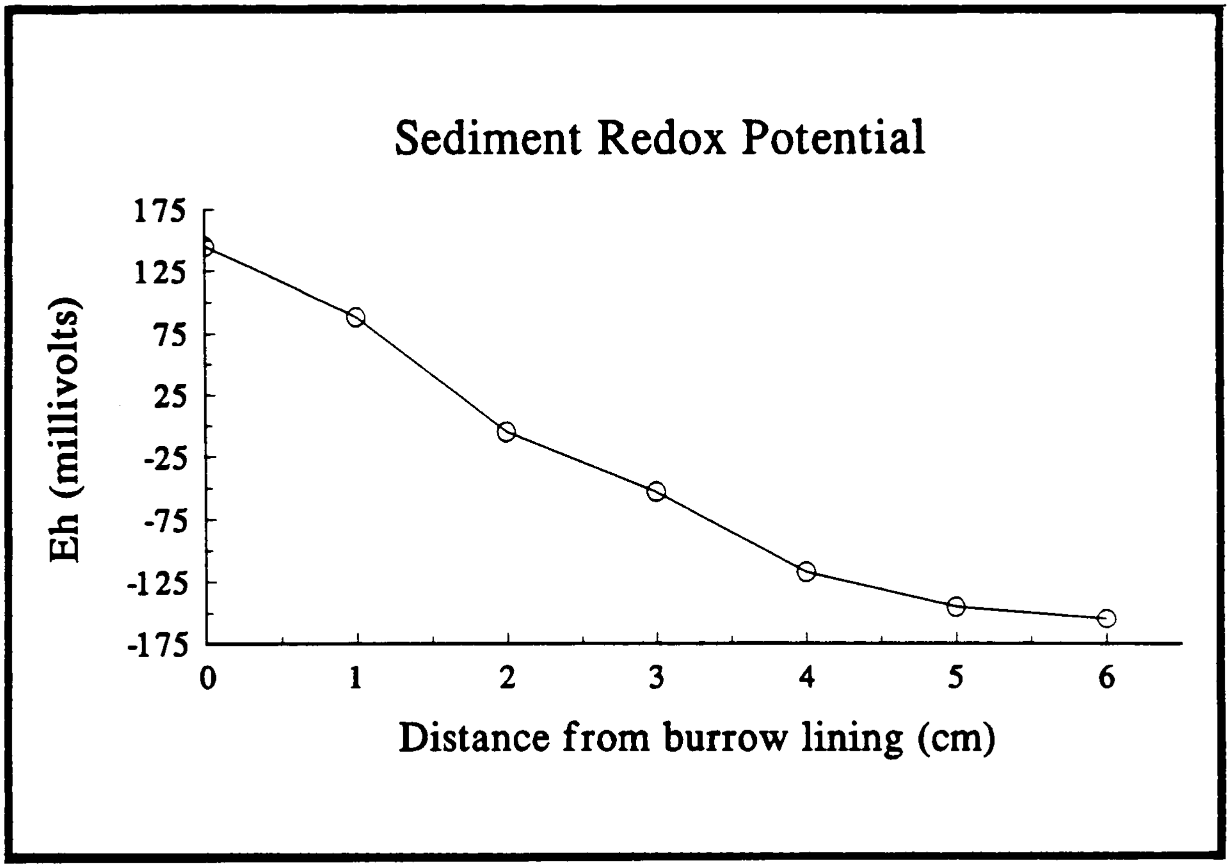


Figure 39. Changes in mean redox potential (millivolts) with distance from the burrow lining of *C. islagrande* during summer at the bay beach site, Isle Dernieres, Louisiana.

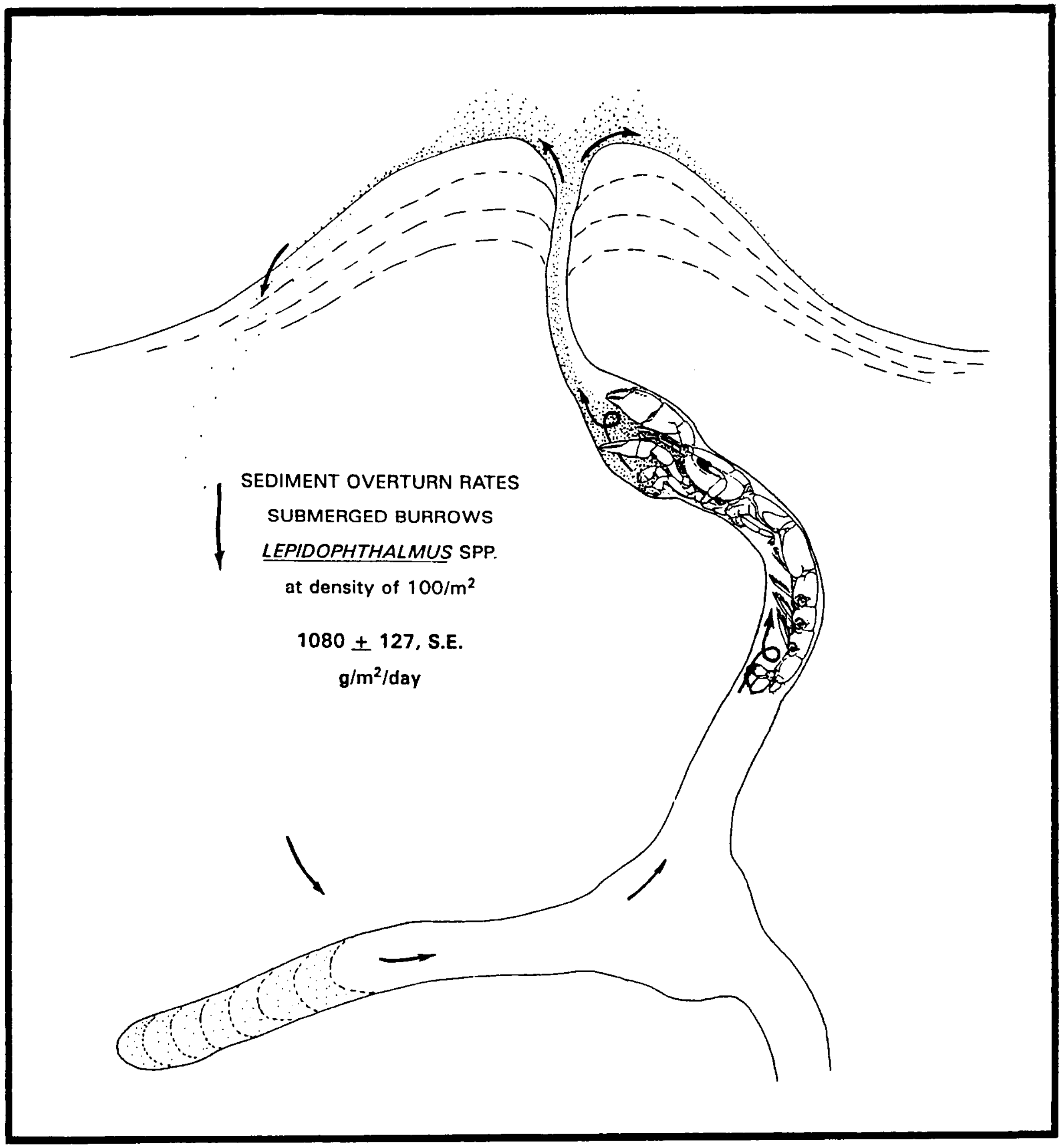


Figure 40. Illustration of bioturbation rates and sediment turnover by *Lepidophthalmus* species.

approximately 4320 g wet sediment m^{-2} day^{-1}. At a mean density of 70 burrows m^{-2}, *Callichirus islagrande* eject approximately 3574 g wet sediment m^{-2} day^{-1}. At maximum densities of 220 burrows m^{-2}, the bioturbation would be approximately 11.2 kg wet sediment m^{-2} day^{-1}. Bioturbation by the *C. islagrande* population across a typical bay beach tidal gradient is shown in Figure 41. Table 6 lists mean bioturbation values for these species and other thalassinid shrimp.

Fecal pellets were produced from approximately 30 % of the *C. islagrande* burrow openings and 70 % of the *L. louisianensis* burrow openings as water receded during summer low tides (Figure 42). The number of fecal pellets ejected from the burrows was highly variable ranging from 2 to 60 in both species. Fecal pellets also varied in size. Mean pellet weight was 0.006 g (wet) for *L. louisianensis* and 0.01 (wet) for *C. islagrande*. At average densities of 100 burrows m^{-2}, *L. louisianensis* produces a minimum of 0.4 g fecal pellets m^{-2} day^{-1}. At average densities of 70 burrows m^{-2}, *C. islagrande* produces a minimum of 0.2 g fecal pellets m^{-2} day^{-1}. Fecal pellets of both species were primarily composed of fine sediments (silts and clays) and some diatoms.

Nutrient flux from burrows

Water ejected from *Callichirus* and *Lepidophthalmus* burrows by organism pumping had lower redox levels than ambient surface water (Figure 43). The nutrient composition of *L. louisianensis* burrow water was similar to deep pore water collected from 40 cm depth (Figure 44). Burrow water and deep pore water had ten times the ammonia (@ 20 uM $liter^{-1}$), about twice the nitrate + nitrite (@ 1.0 uM $liter^{-1}$), almost twice the silicate (@ 59 uM $liter^{-1}$), and twice the phosphate (0.75 uM $liter^{-1}$) levels in surface water samples. Nitrate + nitrite levels were highest (8.4 uM $liter^{-1}$) in the 10 cm pore water samples (ten times burrow water values). The concentration of ammonia and silicate in burrow water of *L. sinuensis* was also higher than surface water concentrations (Figure 44). Burrow water phosphate and nitrate + nitrite were lower than surface water concentrations. The concentration of nutrients in *C. islagrande* burrow water was similar to surface water concentrations for nitrate, nitrite, silicate, and phosphate (Figure 45). Burrow water samples from this species had twice the ammonia concentration of surface water samples.

In order to estimate the flux rates of nutrients from shrimp burrows, the rate at which water was pumped out of the burrow was assumed to be 0.038 liters $burrow^{-1}$ $hour^{-1}$ based on pumping rates measured in similar species of burrowing shrimp (Koike and Mukai 1983, Mukai and Koike 1984). At this rate, populations of *L. louisianensis* at mean densities of 100 burrows m^{-2} would contribute approximately 85 uM ammonia, 3.0 uM nitrate + nitrite, 262 uM silcates, and 3.6 uM phosphate m^{-2} $hour^{-1}$ or 10 to 40 times the concentration present per liter in the water column (Figure 46). At this pumping rate both *L. sinuensis* and *C. islagrande* would also transfer high levels of nutrients from sediment pools into the overlying water column.

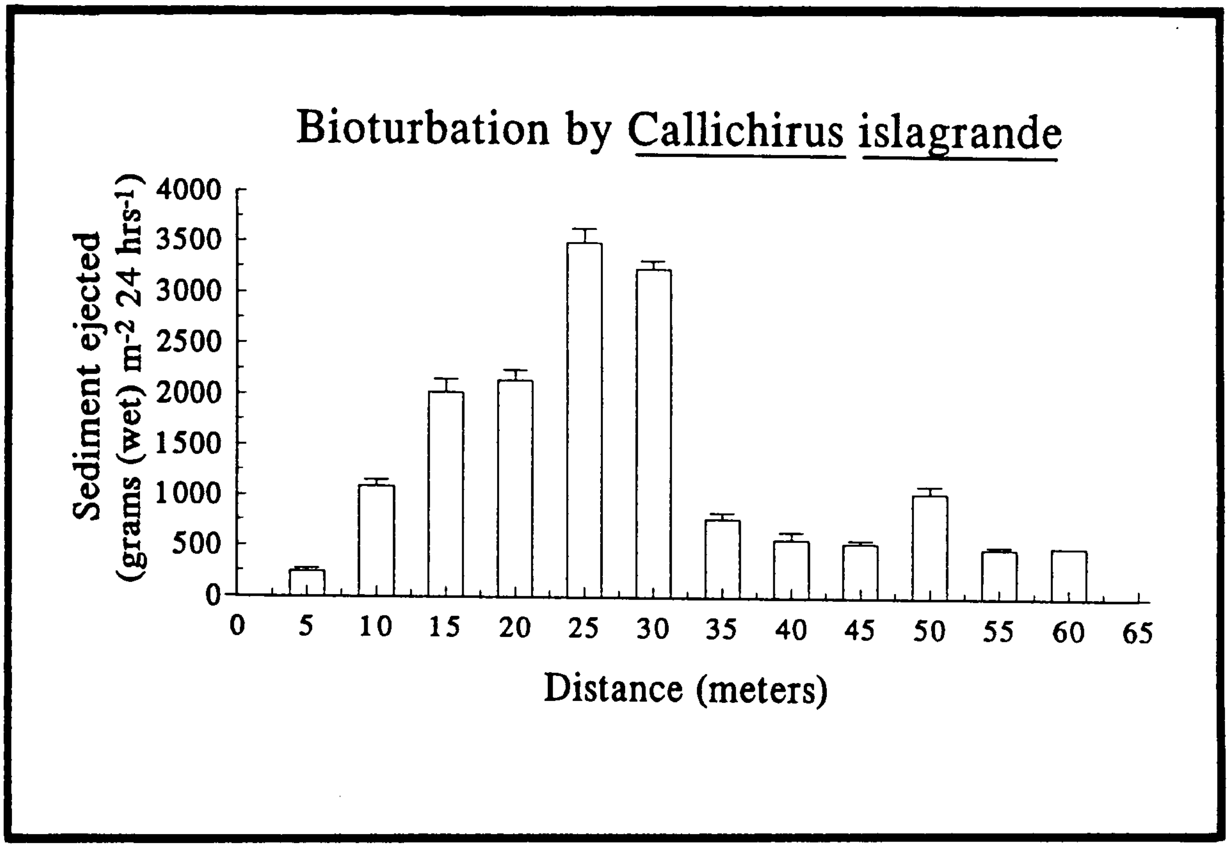


Figure 41. Bioturbation rates of a population of *C. islagrande* along a typical intertidal transect at the bay beach study site, Isles Dernieres, Louisiana.

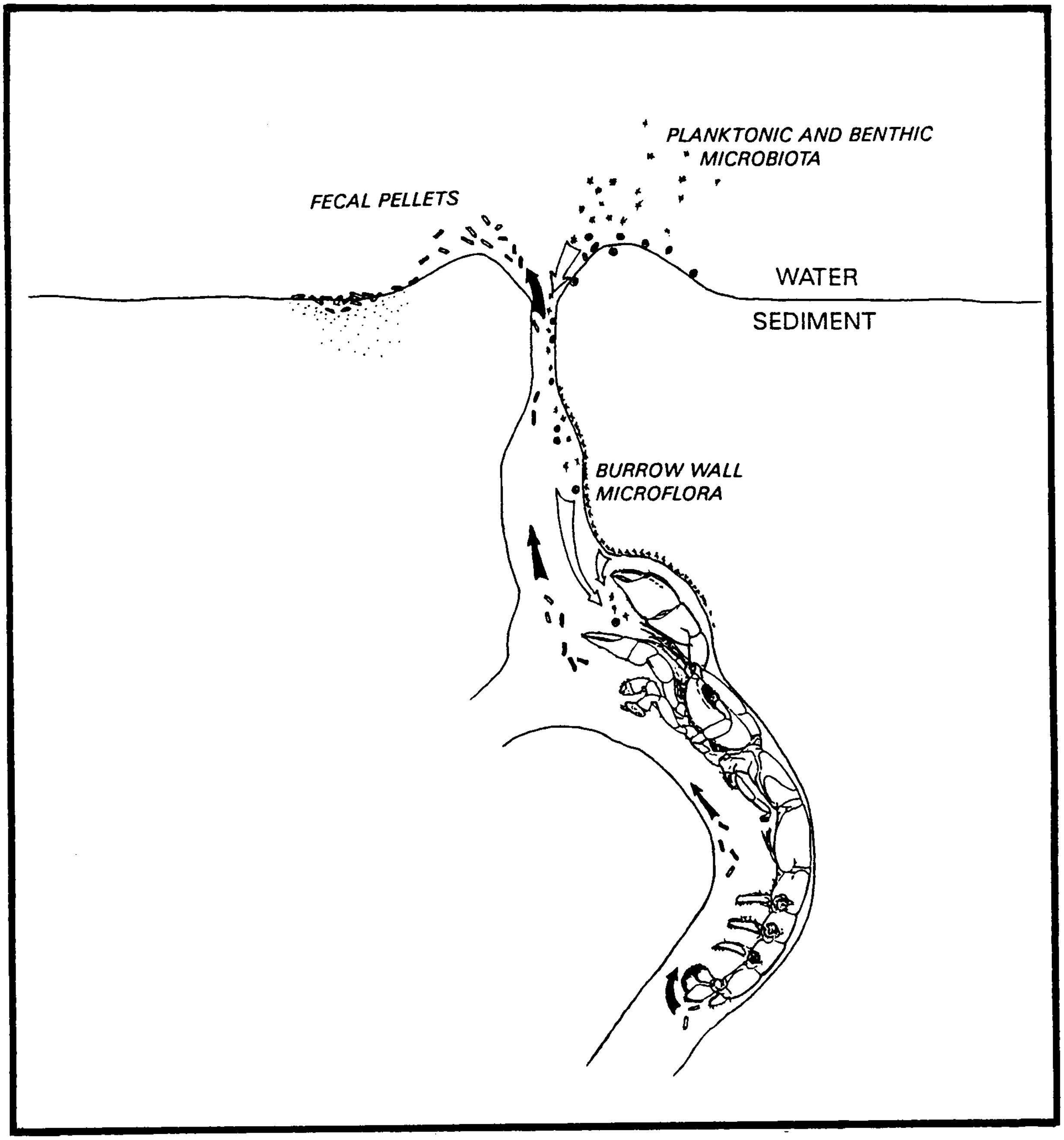


Figure 42. Illustration of fecal pellet production and microbial utilization by *L. louisianensis*.

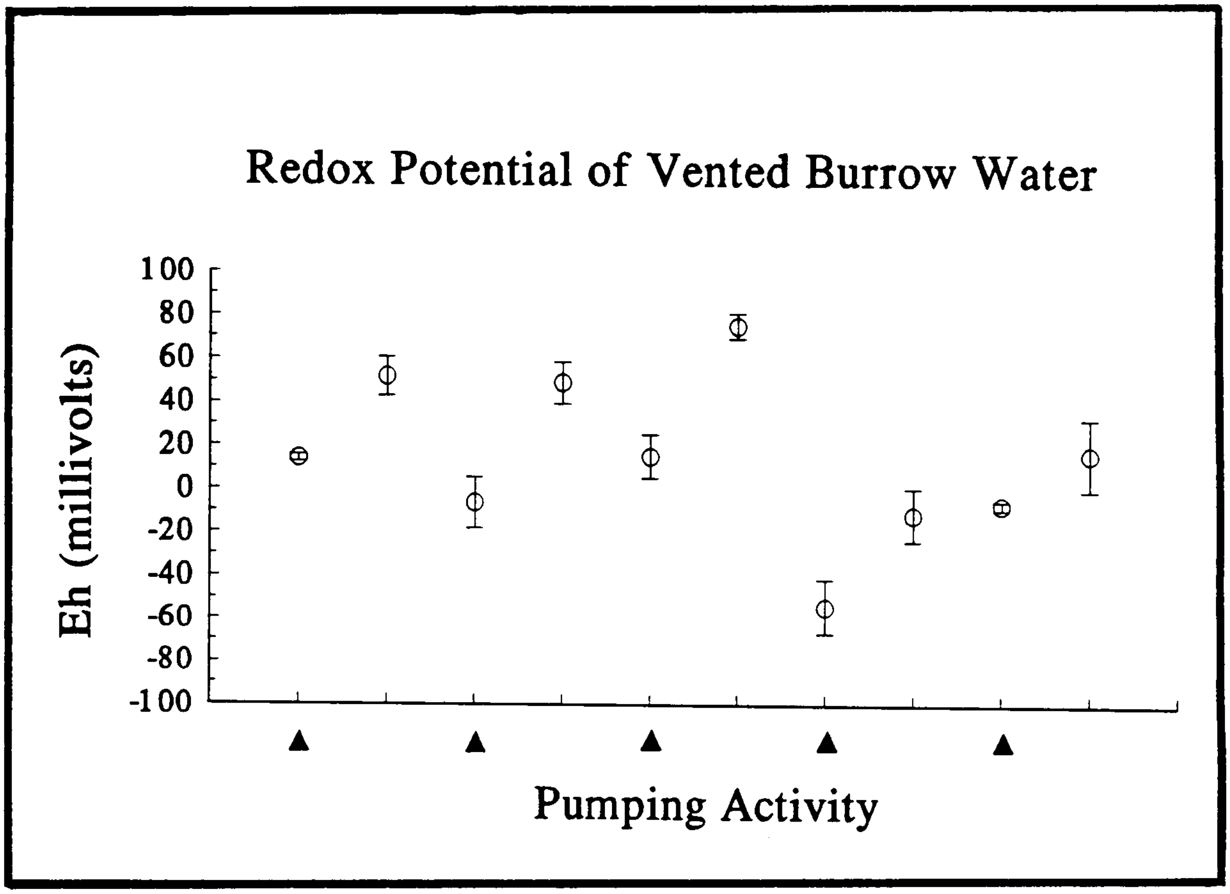
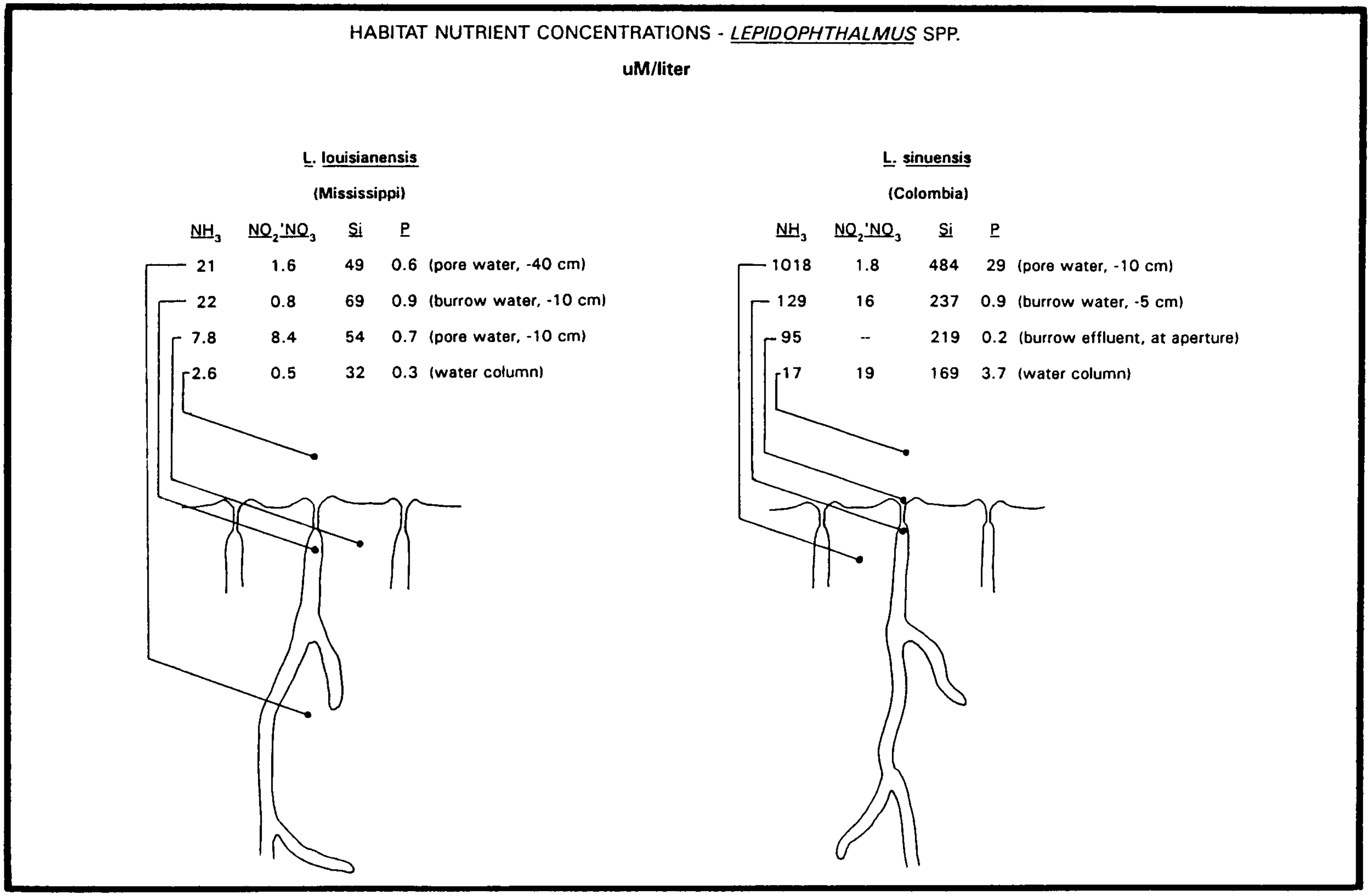


Figure 43. Changes in redox potential (millivolts) of water pumped from burrows of *C. islagrande*. Dark triangles indicate periods of pumping activity.



HABITAT NUTRIENT CONCENTRATIONS - *LEPIDOPHTHALMUS* SPP.

uM/liter

L. louisianensis

(Mississippi)

NH_3	NO_2+NO_3	Si	P	
21	1.6	49	0.6	(pore water, -40 cm)
22	0.8	69	0.9	(burrow water, -10 cm)
7.8	8.4	54	0.7	(pore water, -10 cm)
2.6	0.5	32	0.3	(water column)

L. sinuensis

(Colombia)

NH_3	NO_2+NO_3	Si	P	
1018	1.8	484	29	(pore water, -10 cm)
129	16	237	0.9	(burrow water, -5 cm)
95	--	219	0.2	(burrow effluent, at aperture)
17	19	169	3.7	(water column)

Figure 44. Illustration showing nutrient concentrations (uM liter^{-1}) in the water column, pore water at 10 cm depth, pore water at 40 cm depth, and burrow water of *L. louisianensis* and *L. sinuensis*. Data are presented for ammonia (NH4), nitrate+nitrite (NO2+NO3), silicates (Si), and phosphates (P).

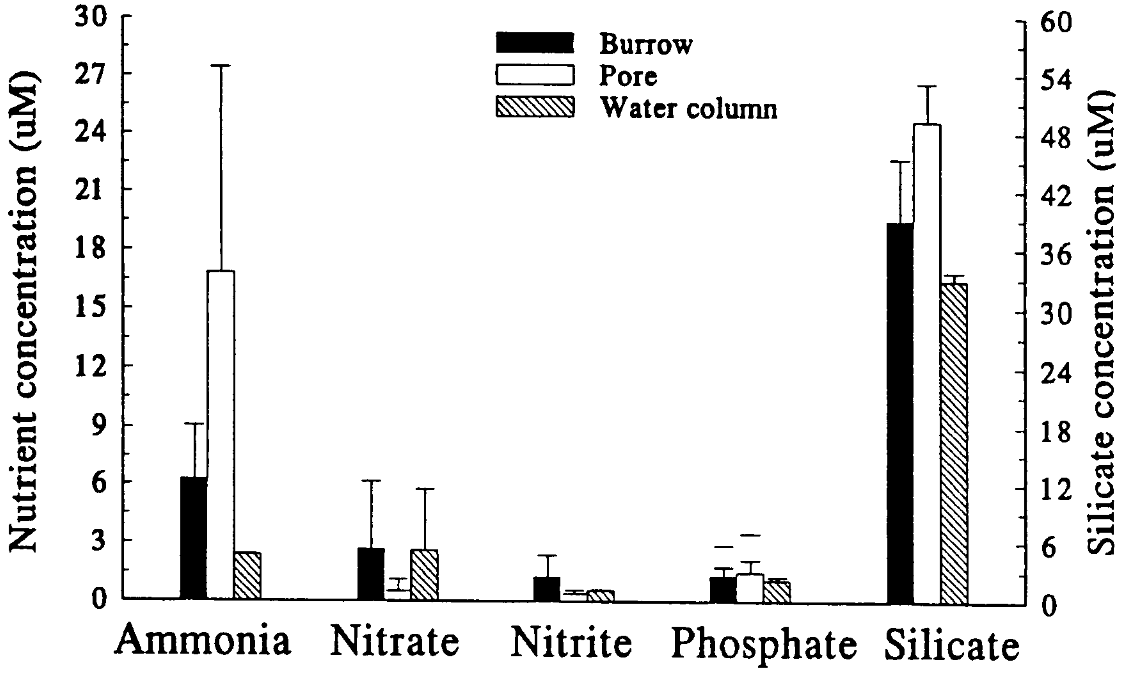


Figure 45. Nutrient concentrations (uM liter^{-1}) in the water column, pore water at 40 cm depth, and burrow water of *C. islagrande* during summer at the bay beach study site, Isle Dernieres, Louisiana.

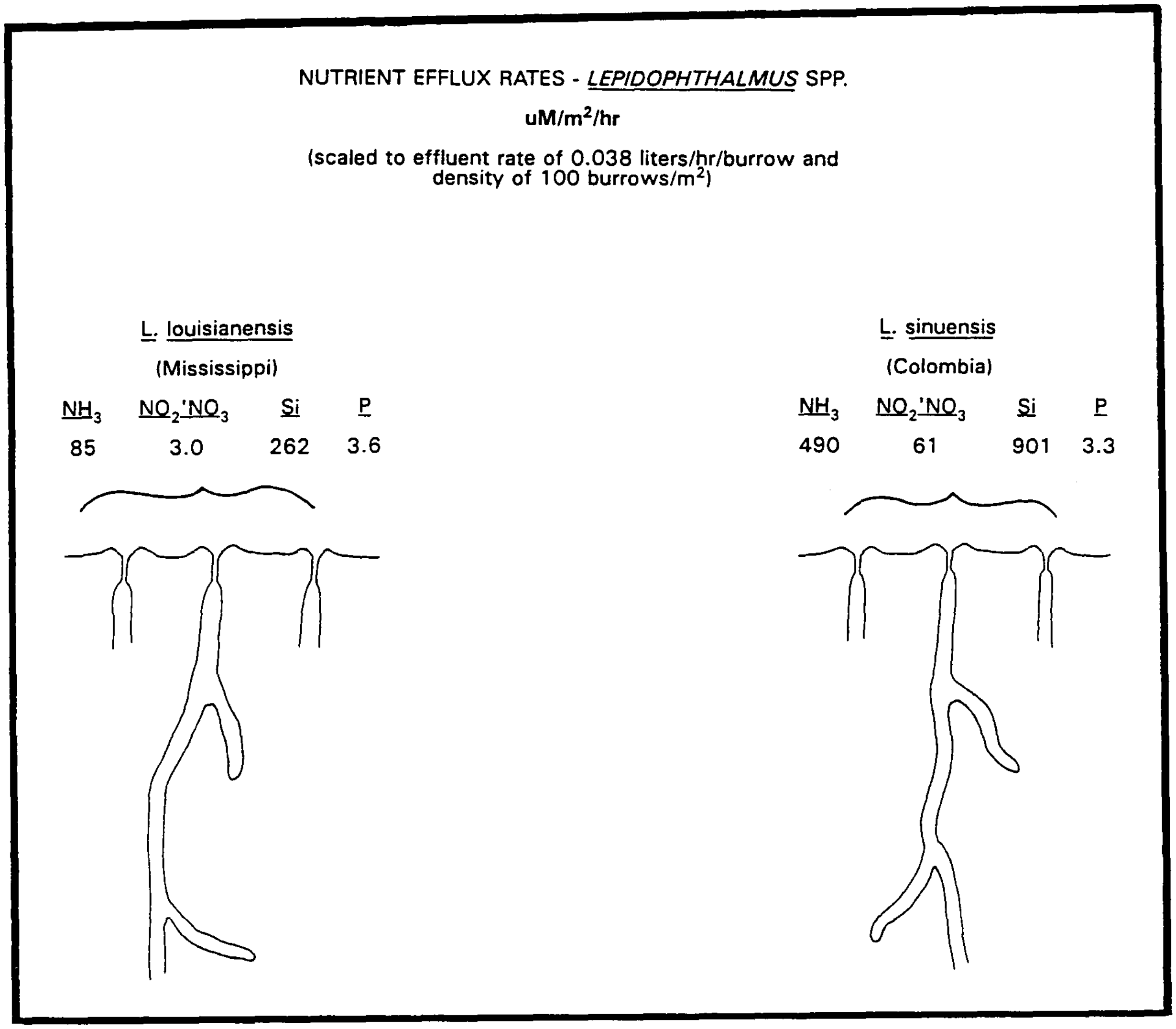


Figure 46. Illustration showing rates of nutrient efflux (uM m^{-2} $hour^{-1}$) from *L. louisianensis* and *L. sinuensis* burrows. Data are presented for ammonia (NH4), nitrate + nitrite (NO2 + NO3), silicates (Si), and phosphates (P).

Table 6. Summary of sediment bioturbation by burrowing shrimp.

Species	Estimated Sediment Bioturbation	Reference
Callianassa californiensis	2700 ml (wet) m^{-2} day^{-1}	Swinbanks and Lutermauer 1987
Callianassa kraussi	12.14 kg (wet) m^{-2} day^{-1}	Branch and Pringle 1987
Callianassa subterranea	3.5 kg (dry) m^{-1} yr^{-1}	Witbaard and Duineveld 1989
Callichirus islagrande	3574 g (wet) m^{-2} day^{-1}	this study
Glypterus armatus	3.3 kg (wet) m^{-2} yr^{-1}	Vaugelas 1984
Glypterus laurea	156 kg (wet) $burrow^{-1}$ yr^{-1}	Vaugelas 1984
Lepidophthalmus spp.	1080 g (wet) m^{-2} day^{-1}	this study

DISCUSSION

The results of this study indicate that all three species of burrowing shrimp construct branched burrows connected to single or multiple openings to the sediment surface by a narrow, circular shaft (often referred to as the chimney). The burrows of *L. louisianensis* and *C. islagrande* appear to have a single opening to the sediment surface while *L. sinuensis* has and average of three openings per burrow.

All three species add large amounts of burrow wall surface area and burrow volume beneath each m^2 sediment surface. The interface between the water and sediment surface is generally considered to be a highly productive zone. By increasing the surface area of this region, the burrowing shrimp may increase both the flux of nutrients from the sediments and the productivity of the benthic community. *Lepidophthalmus louisianensis* may have the greatest effect on productivity of the burrow wall sediments by concentrating organic matter and fine particles in the burrow lining and matrix. All three species appear to add organic matter, nutrients, and fine particles to the sediment surface by ejecting large numbers of fecal pellets from burrow openings (see cover diagram). The fate of the fecal material is unknown but may be an important source of organic matter and nutrients for other species as suggested by Frankenberg et al. (1967) for Atlantic populations of *Callichirus major*. In addition, all three species appear to enrich the overlying water column with nutrients by pumping nutrient-rich water from burrows to the sediment surface. The high levels of nutrients (particularily ammonia) in burrow water samples suggests that the burrow walls may provide exchange surfaces for nutrient movement between sediment and water pools. At least some of the ammonia enrichment of burrow water is derived from metabolic wastes of the shrimp themselves. The loss of burrowing shrimp populations from nearshore environments due to physical or biological disturbances would probably decrease the rate of sediment turnover and nutrient flux by terminating bioturbation and the maintenance of burrow wall exchange sites. Further experimental work is recommended to determine the quantitative effects of burrowing shrimp removal from nearshore environments.

LITERATURE CITED

Aller, R.C. and R.E. Dodge. 1974. Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res. 32:209-232.

Aller, R.C., R.E. Yingst, and W.J. Ullman. 1983. Comparative biogeochemistry of water in intertidal *Onuphus* (Polychaeta) and Upogebia (Crustacea) burrows: temporal patterns and causes. J. Mar. Res. 41:571-604.

Bird, E.M. 1982. Population dynamics of thalassinidean shrimps and community effects through sediment modification. Ph.D. Dissertation. Univ. of Maryland. College Park, MD. 150 pp.

Branch, R.M. and G.M. Pringle. 1987. The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna, and benthic microflora. J. Exp. Mar. Biol. Ecol. 107:219-235.

Buchanan, D.V., D.L. Bottom, and D.A. Armstrong. 1985. The controversial use of the insecticide Sevin in Pacific Northwest estuaries: Its effects on Dungeness crab, Pacific oyster, and other species. Proceedings of the Symposium on Dungeness Crab Biology and Management. Alaska Sea Grant Rep. 85-3: 401-417.

Britton, J.C. and B. Morton. 1989. Shore ecology of the Gulf of Mexico. University of Texas Press. Austin.

Colin, P.L., T.H. Suchanek, G. McMurtry. 1986. Water pumping and particulate resuspension by callianassids (Crustacea:Thalassinidea) at Enewetak and Bikini Atolls, Marshall Islands. Bull. Mar. Sci. 38:19-24.

Dobbs, F.C. and G.B. Guckert. 1988. *Callianassa trilobata* (Crustacea: Thalassinidea) influences abundance of meiofauna and biomass, composition, and physiologic state of microbial communities within its burrow. Mar. Ecol. Prog. Ser. 45:69-79.

Dworschak, P.C. 1983. The biology of *Upogebia pusilla* (Petagna)(Decapoda, Thalassinidea) I. The burrows. P.S.Z.N.I.: Mar. Ecol. 4(1):19-43.

Dworschak, P.C. and P. Pervesler. 1988. Burrows of *Callianassa bouvieri* Nobili 1904 from Safaga (Eqypt, Red Sea) with some remarks on the biology of the species. Senckenberg. Maritima 20:1-17.

Felder, D.L. 1973. An annotated key to crabs and lobsters (Decapoda) from coastal waters of the northwestern Gulf of Mexico. Publications of The Center for Wetland Resources, LSU-SG-73-02: 103 pages, 179 figures.

Felder, D.L. 1978. Osmotic and ionic regulation in several western Atlantic Callianassidae (Crustacea, Decapoda, Thalassinidea). Biol. Bull. 154(3):409-429.

Felder, D.L. 1979. Respiratory adaptations of the estuarine mud shrimp, *Callianassa jamaicense* (Schmitt, 1935)(Crustacea, Decapoda, Thalassinidea). Biol. Bull. 157:125-137.

Felder, D.L., D.L. Lovett. 1989. Relative growth and sexual maturation in the estuarine ghost shrimp *Callianassa louisianensis* Schmitt, 1935. J. Crust. Biol. 9(4):540-553.

Felder, D.L. and S.A. Rodrigues. 1993. Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to L. siriboia, new species, from Brazil (Decapoda: Thalassinidea: Callianassidae). J. Crust. Biol. 13(2):357-376.

Forbes, A.T. 1973. An unusual abbreviated larval life in the burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). Mar. Biol. 22:361-365.

Forbes, A.T. 1976. Breeding and growth of the burrowing prawn *Callianassa kraussi* Stebbing (Crustacea: Decapoda: Thalassinidea). Zool. Afr. 12(1):149-161.

Forster, S. and G. Graf. 1992. Continuously measured changes in redox potential influenced by oxygen penetrating from burrows of *Callianassa subterranea*. Hydrobiologia 235/236:527-532.

Frankenberg, D., S.L. Coles and R.E. Johannes. 1967. The potential trophic significance of *Callianassa major* fecal pellets. Limnol. Oceanogr. 12:113-120.

Griffis, R.B. 1988. Behavioral interactions between burrowing shrimp: effects on distribution of sympatric thalassinids. Am. Zool. 28(4):179A.

Griffis, R.B. and F.L. Chavez. 1988. Effects of sediment type on burrows of *Callianassa californiensis* Dana and *C. gigas* Dana. J. Exp. Mar. Biol. Ecol. 117:239-253.

Griffis, R.B. and T.H. Suchanek. 1991. A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea). Mar. Ecol. Prog. Ser. 79:171-183.

Hedgpeth, J.W. 1950. Notes on the marine fauna of salt flat areas in Aransas National Wildlife Refuge. Publications of the Institute of Marine Science, University of Texas 1:103-119

Hill, G.E. and R.E. Hunter. 1976. Interaction of biological and geological processes in the beach and nearshore environments, northern Padre Island, Texas. Soc. Econ. Paleontol. Mineralog., Special Publ. 24:169-187.

Jumars, P.A. and A.R.M. Nowell. 1984. Effects of benthos on sediment transport: difficulties with functional grouping. Continental Shelf Res. 3:115-130.

Koike, I. and H. Mukai. 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. Mar. Ecol. Prog. Ser. 12:185-190.

Kristensen, E., M.H. Jensen, and T.K. Anderson. 1985. The impact of polychaete (*Nereis virens* Sars) burrows on nitrification and nitrate reduction in estuarine sediments. J. Exp. Mar. Biol. Ecol. 85:75-91.

Lemaitre, R. and S. de A. Rodrigues. 1991. *Lepidophthalmus sinuensis*: a new species of ghost shrimp (Decapod: Thalassinidea: Callianassidae) of importance to the commercial culture of penaeid shrimps on the Caribbean coast of Colombia, with observations on its ecology. Fishery Bulletin, United States 89:623-630.

Lovett, D.L. and D.L. Felder. 1989. Application of regression techniques to studies of relative growth in crustaceans. J. Crust. Biol. 9:529-539.

Manning, R.B. and D.L. Felder. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). Proc. Biol Soc. Wash. 104:764-792.

Miller, M.F. 1984. Bioturbation of intertidal quartz-rich sands: A modern example and its sedimentologic and paleoecologic implications. J. Geology 92:201-216.

Moriarty, D.J.W., P.C. Pollard, W.G. Hunt, C.M. Moriarty and T.J. Wassenberg. 1985. Productivity of bacteria and microalgae and the effect of grazing by holothurians in sediments and a coral reef flat. Mar. biol. 85:293-300.

Mukai, H., Koike, I. 1984. Pumping rates of the mud shrimp *Callianassa japonica*. J. Oceanogr. Soc. Japan 40:243-246.

Murphy, R.C. 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon- the importance of bioturbation. J. Mar. Res. 43:673-692.

Murphy, R.C. and J.N. Kremer. 1992. Benthic community metabolism and the role of deposit-feeding callianassid shrimp. J. Mar. Res. 50:321-340.

Ott, J.A., Fuchs, B., Fuchs, R., Malasek, A. 1976. Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso and their effect on sediment. Senckenbergiana Marit. 8:61-79.

Peterson, C.H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43:343-359.

Phillips, P.J. 1971. Observations on biology of mudshrimps of the genus *Callianassa* (Anomura: Thalassinidea) in Mississippi Sound. Gulf Research Reports 3:165-196.

Posey, M.H. 1986a. Predation on a burrowing shrimp: distribution and community consequences. J. Exp. Mar. Biol. Ecol. 103:143-161.

Posey, M.H. 1986b. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. Mar. Ecol. Prog. Ser. 31:15-22.

Posey, M.H. 1990. Functional approaches to soft-substrate communities: how useful are they? Reviews in Aquatic Science 2:343-356.

Radocindki, C., R.W. Heard, T. Simons and D. Gledhill. 1991. Macroinvertebrate associations from beaches of selected barrier islands in the northern Gulf of Mexico: Important environmental relationships. Bull. Mar. Sci. 48(3):689-701.

Rhodes, D.C. and D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.

Roberts, R.R., T.H. Suchanek and W.J. Wiseman. 1982. Lagoon sediment transport: the significant effect of *Callianassa* bioturbation. Proc. 4th Int. Coral Reefs Symp. Manila.

Staton, J.L. and D.L. Felder (a). Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea: Decapoda: Thalassinoidea) in the western Atlantic and Gulf of Mexico. Bull. Mar. Sci. In press.

Staton, J.L. and D.L. Felder (b). Genetic variation in populations of the ghost shrimp genus *Lepidophthalmus* (Crustacea: Decapoda: Thalassinoidea). Mar. Biol. Submitted.

Suchanek, T.S. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. J. Mar. Res. 41:281-298.

Suchanek, T.H., P.L. Colin, G.M. McMurty and C.S. Suchanek. 1986. Bioturbation and redistribution of sediment radionuclides in Enewetak Atoll lagoon by callianassid shrimp: biological aspects. Bull. Mar. Sci. 38(1):144-154.

Swinbanks, D.D. and J.M. Murray. 1981. Biosedimentological zonation of Boundary Bay tidal flats, Fraser River Delta, British Columbia. Sedimentology 28:201-237.

Swinbanks, D.D. and J.L. Luternauer. 1987. Burrow distribution of thalassinidean shrimp on a Fraser delta tidal flat, British Columbia. J. Paleont. 61(2):315-332.

Tamaki, A. and B. Ingole. 1993. Distribution of juvenile and adult ghost shrimps, *Callianassa japonica* Ortmann (Thalassinidea), on an intertidal sand flat: Intraspecific facilitation as a possible pattern-generating factor. J. Crus. Biol. 13(1):175-183.

Vaugelas, J. de. 1984. Preliminary observations on two types of callianassids (Crustacea, Thalassinidea) burrows in the Gulf of Aqaba (Red Sea). Proc. 1st Int. Symp. Coral Reef Envts. Red Sea 1:520-539.

Waslenchuk, D.G., E.A. Matson, R.N. Zajac, F.C. Dobbs and J.M. Tramontano. 1983. Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. Mar. Biol. 72:219-225.

Wass, M.L. 1950. The decapod crustaceans of Alligator Harbor and adjacent inshore areas of northwestern Florida. Quart. J. Florida Acad. Sci. 18:129-176.

Willis, E.R. 1942. Some mud shrimps of the Louisiana coast. Occasional Papers of the Marine Laboratory, Louisiana State University 2:1-6.

Witbaard, R. and G.C.A. Duineveld. 1989. Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu)(Thalassinidea) from the southern North Sea. Sarsia 74:209-219.

MARCH 3, 1849

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Minerals Revenue Management** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.