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Seasonal Abundance, Zonation, and Migratory Behavior of Donax (Donacidae:  
Bivalvia) on Mustang and Northern Padre Island, Texas

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ABSTRACT

Donax variabilis roemeri Philippi and Donax texasianus Philippi populations were sampled for 14 months (May 1982- June 1983) to determine population density, zonation, migratory behavior, growth rates, spawning periods, and dispersion. These donacids overlapped spatially on south Texas barrier island sandy beaches. Intertidal and subtidal samples were taken monthly on Mustang Island and northern Padre Island along transects from the high intertidal zone to the third sand bar (200 m offshore). Both donacids were collected throughout the year at the two sampling sites but D. texasianus was most abundant from May-June, and D. v. roemeri reached peak numbers during August. Post-larvae were present 10 months out of the year and were most abundant from May to November. The donacid populations occupied separate habitats from February to April: D. v. roemeri occupied the intertidal zone and D. texasianus resided subtidally. The two donacids migrated with the tides in the intertidal zone during May to August. Growth rates were greatest for the two species during the spring and summer; D. v. roemeri ranged from 1.4 to 3.4 mm per month and D. texasianus ranged from 0.9 to 1.9 mm of growth per month (winter and spring). Spawning periods for the donacids extended from March to December.

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## INTRODUCTION

Bivalves of the genus Donax L. inhabit the intertidal-subtidal zones of exposed sandy beaches throughout the world. This is a harsh environment that is characterized by widely fluctuating physical conditions. Donax species tend to develop dense, resurgent populations that migrate with the tides, occur sympatrically in the sandy beach habitat, and subsequently crash.

The interesting attributes and accessibility of Donax have prompted many studies. Most of the early references were taxonomic descriptions, revisions, distributional ranges, annotated lists, and monographs. Orton (1929) was among the first to report on population fluctuations of Donax. He reported that an estimated 100 million D. vittatus da Costa died within a three-mile section of beach in Lancashire, England. Coe (1953, 1955, 1956, 1957) reported on the seasonal variability of D. Gouldii Dall populations along the coast at La Jolla, California. His results represented the culmination of 17 years of intermittent observations and indicated that Donax populations may vary from a few individuals in one year to thousands the next.

Others have studied population ecology. Loesch (1957), who conducted a study on the Donax populations of Mustang Island, Texas, estimated that there were about 70 Donax per linear yard of beach during September 1951, and more than 32,000 clams per linear yard during June 1952. Additional work was done on the California coast by Johnson (1966a, 1966b, 1968) who proposed that adverse environmental conditions such as those brought about by sudden temperature and salinity changes caused the population fluctuations. Wade (1964, 1967a, 1967b, 1968, 1969) made extensive contributions by studying populations of D. denticulatus L. and D. striatus L. along the coast of Jamaica. Wade showed that parameters such as beach profile, sand grain size, and wave energy influenced the abundance of Donax populations.

Mikkelsen (1981, 1985) compared two populations of D. variabilis Say from the southwest and central eastern coasts of Florida. The substantial difference in density between the populations was attributed to the physical differences of the beaches. Average summer growth rates of the two populations differed only by 0.7 mm. Sastre (1984) examined D. denticulatus populations from five Puerto Rican beaches. He concluded that nutrient availability was an important factor limiting Donax densities.

Numerous investigators have analyzed the tidal migratory behavior of Donax. Generally, the clams move shoreward during high tide and seaward during low tide. Mori (1938, 1950), who studied the tidal migrations of D. semigranosis Dunken along the coast of Okinosa, Japan, believed that the species possessed a biological clock that was synchronized with the tidal cycle. Donax migrations on Texas beaches have been reported by Hedgpeth (1953) and Loesch (1957). Hedgpeth noted that D. variabilis periodically emerge from the sand into the surf, and are carried up and down the beach by tides. Similar behavior was noted by Jacobson (1955) concerning the tidal migrations of D. fessor Say at Rockaway Beach, New York, but he believed that movement was caused by wave action. Turner and Belding (1957), Loesch (1957), and Tiffany (1971) have suggested that tidal migrations are initiated by the acoustic shock/stimulation produced by waves breaking on the beach.

In contrast, several other researchers have reported that Donax also exhibits nonmigratory behavior. Edgren (1959) observed that D. variabilis at Clearwater Beach, Florida, did not exhibit tidal migrations, but remained buried high in the intertidal zone during low tide. At Kure Beach, North Carolina the clam remained buried in the mid intertidal region during low tide (Aldrich, 1959). Donax variabilis populations at Sanibel Island, Florida, remained low in the intertidal zone during all tidal phases (Mikkelsen, 1981), and this behavior was the result of a population adapting to local environmental conditions. The tidal migrations of D. variabilis and D. parvula Philippi varied seasonally at Bogue Banks, North Carolina (Leber, 1982a) but both species migrated with the tides in the intertidal zone through the spring and early summer. During late summer and fall D. variabilis remained buried high in the intertidal regions at low tide, and D. parvula migrated subtidally.

Two species of Donax occur along the sandy barrier island beaches of south Texas (Abbott, 1974; Andrews, 1981): D. variabilis roemeri Philippi, 1849 (= D. roemeri roemeri) and D. texasianus Philippi, 1847 (= D. texasiana, and D. tumida). Morrison (1971) favored the division of D. variabilis Say, 1822, into western and eastern subspecific forms. However, he noted that the species name was preoccupied. Boss (1970) proposed the official conservation of the name D. variabilis Say, 1822, to the International Congress of Zoological Nomenclature, and it was subsequently conserved (Melville, 1976). The distributional range of D. variabilis roemeri extends from the Mississippi delta to Campeche, Mexico, and that of D. texasianus extends from the Louisiana-Texas border to Vera Cruz, Mexico.

The objectives of this study were: 1) to determine the seasonal abundance and zonation of *D. variabilis roemeri* and *D. texasianus* on Mustang Island and northern Padre Island; 2) to investigate the migratory behavior of *D. variabilis roemeri* and *D. texasianus* on northern Padre Island; 3) to compare present *Donax* population dynamics on Mustang Island to those reported by Loesch (1957); and to reveal new information regarding the growth, spawning, and dispersion (intertidal and subtidal) of those donacids at those localities.

### STUDY AREA

The south Texas coast is buttressed by a chain of barrier islands separating it from the Gulf of Mexico (Fig. 1). These barrier islands are long bars of sand characterized by exposed fore-island beaches, dunes, vegetated zones, and back-island lagoon shorelines. Disagreements exist concerning the origin and development of barrier islands (Leatherman, 1982); but, regardless of the mechanism by which the barrier islands were created, it is clear that the islands have undergone extensive morphological changes since their origin. This trend is expected to continue because of the dynamic nature of the building processes which involve longshore currents, waves, storm surges, wind, and slowly rising sea level.

The study area includes the sandy beaches of two barrier islands, Mustang and Padre Island. Mustang Island is located in Nueces County and extends southward about 26 km from Aransas Pass on the north to Corpus Christi Pass. The landward side of the island is bordered by Corpus Christi Bay and the seaward side faces the Gulf of Mexico. Padre Island extends some 177 km along the Texas coast, but only the northern section is included in this study. The northern portion of Padre Island is located in Nueces and Kleberg Counties and extends 28 km from Corpus Christi Pass to Malaquite Beach. Northern Padre Island is bordered by the Laguna Madre on the landward side, and the seaward side faces the Gulf of Mexico.

Mustang and northern Padre Island lie within the dry subhumid zone of Texas; and these islands have a subhumid to semiarid climate (Diener, 1975). Hill and Hunter (1976) report that rainfall averages 66.9 cm annually at Corpus Christi and that the mean annual air temperature is 22.1°C, but winter storms occasionally drop the temperature below 0°C and summer heat waves push it above 36°C. Water temperatures at Port Aransas have been reported to average a mean annual temperature of 22.7°C with a mean monthly low of 13.6°C and a

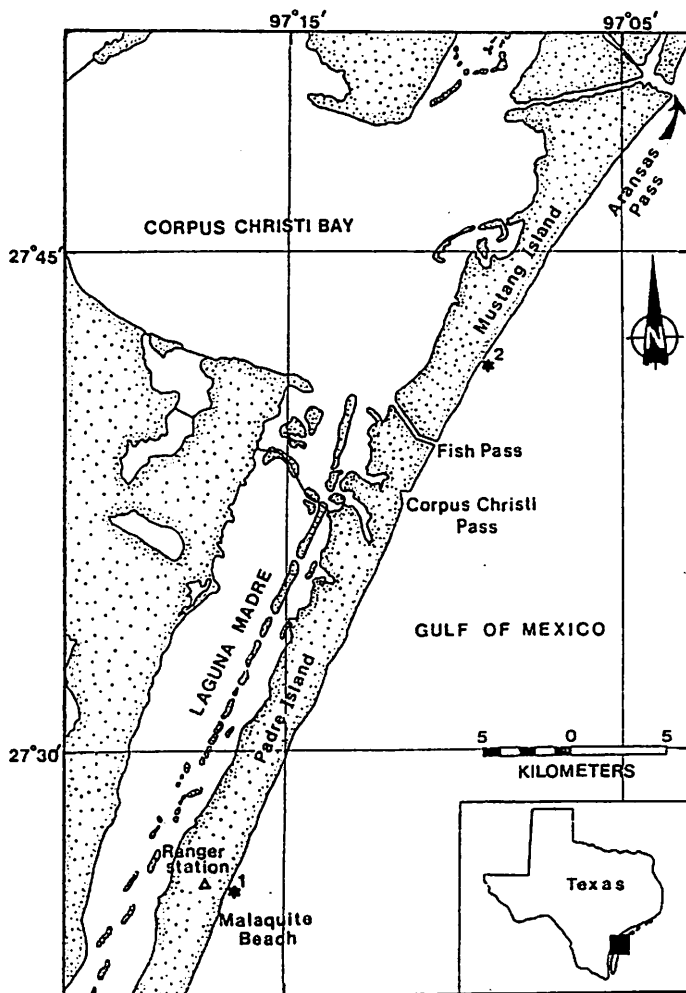


Figure 1. Map of the south Texas coast with locations of sampling sites (After Groat, 1975).



mean monthly high of 30.0°C (Hill and Hunter, 1976). Winds generally blow across the islands from the southeast. Winter storms usually cause the winds to blow from the north. Hill and Hunter also report that the mean annual wind speed is 5.3 m/sec.

Other physical parameters such as salinity, breaker size, and tidal ranges of the study area have been monitored on a seasonal basis. The mean annual salinity from Port Aransas was recorded by Hill and Hunter (1976) as 32 ‰. Breakers are normally less than 1 m, but greater heights occurred during inclement weather. The annual mean breaker height is about 0.6 m (Weise and White, 1980). Tides are diurnal, semidiurnal, and mixed, with a mean tidal range of 51.8 cm (Hill and Hunter, 1976).

The seaward side of these islands is characterized by a dune-beach-bar complex (Fig. 2). The foredunes are well developed and stabilized by vegetation in most areas. According to Hill and Hunter (1976) the backshore is about 65-115 m wide. The intertidal zone is about 25-45 m wide with a gentle slope (1°-5°). Beach sediment is composed of fine grained sand (0.125-0.25 mm) (Morton and Pieper, 1977). The subtidal zone features a bar-trough system. There are usually three sand bars and three troughs located parallel to the beach. The third bar was estimated to occur about 200 m from shore. Hedgpeth (1953) determined that the crest of the bar is about 2-3 m below the water surface, and its trough is 4-5 m deep. The other bars are closer to the shore and in water less than 2 m deep.

## METHODS AND MATERIALS

Two sample sites were selected for study (Fig. 1). One site was located on Mustang Island (27°45'N, 97°10'W) and the other was located on Malaquite Beach which is in the northern section of Padre Island (27°20'N, 97°20'W). The beaches on Mustang Island are popular tourist attractions that are open to vehicular traffic. Malaquite Beach is also frequently visited by beachgoers but it is located within the portion of Padre Island National Seashore that is closed to vehicular traffic. The sample sites were located approximately 34 km apart. The sites were visited monthly from May 1982 to June 1983.

Four transects (Fig. 3) were established at each sampling site. Transect A, designed for the study of the vertical distribution of *Donax*, consisted of a series of sampling stations arranged in a straight line which was orientated at 90° to the



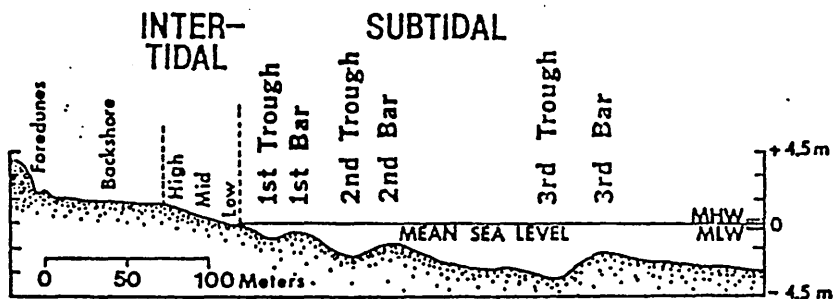


Figure 2. Profile of a typical Mustang and northern Padre Island Beach and bar-trough system (Hill and Hunter, 1976).

high tide line and extended from the top of the intertidal zone to the crest of the third sand bar. The intertidal zone was divided into high, middle, and low limits; and one sample was collected at each limit. The limits were established monthly at each site. The lower limit of the intertidal zone was determined by locating the greatest point of tidal recession during the low tide phase of the sampling day. The berm or beach drift line was located and used as the upper limit of the high intertidal zone. The area between these two points was divided evenly into three sections to represent each of the intertidal limits. One sample was also taken at each bar and trough. The deeper subtidal samples were collected by personnel equipped with snorkeling gear. They reached the sites by use of a three-person rubber raft. Transects B, C, and D, designed for study of the horizontal distribution of Donax, were parallel to the high tide line and were in the intertidal zone. One transect was established in each of the three intertidal limits. Each parallel transect extended to the north and south of transect A, and samples were taken at 2, 4, and 6 m intervals from it. A total of nine samples were collected from the perpendicular transect, and 18 samples were collected from the parallel transects.

Additional transects were established at the northern Padre Island site. Two transects (G and H) were designed to investigate the patchiness of Donax spp. populations. Three samples spaced approximately 1 km apart in the middle intertidal zone were collected from each transect (north and south of transect A). Monthly samples were taken on transects B, C, D, G, and H when the tide was advancing and had reached at least the mid-intertidal zone. The migratory behavior of Donax was determined by comparing samples collected at high and low tides (transects E and F) each month. The E and F transects extended across the intertidal zone from the high to low limits with one sample collected at each intertidal limit.

All samples were taken with an open steel 1.36 l can sampler. One sample (volume of 5,656 cm<sup>3</sup>) consisted of four 1.36 l subsamples. Samples were collected by pushing the sampler along the surface of the substrate to a depth of 10 cm. A scooping motion was used to fill the sampler with substrate. This sampling procedure was developed by Tunnell et al. (1981) for rapid collection of IXTOC 1 oil spill samples, and utilized in the present study because of the difficulties inherent to sampling subtidal stations (e.g., loose substrate and wave action). Each sample was washed through and retained in a 0.5 mm mesh saran "biobag". The bags were placed in a bucket with 10% formalin and rose bengal for

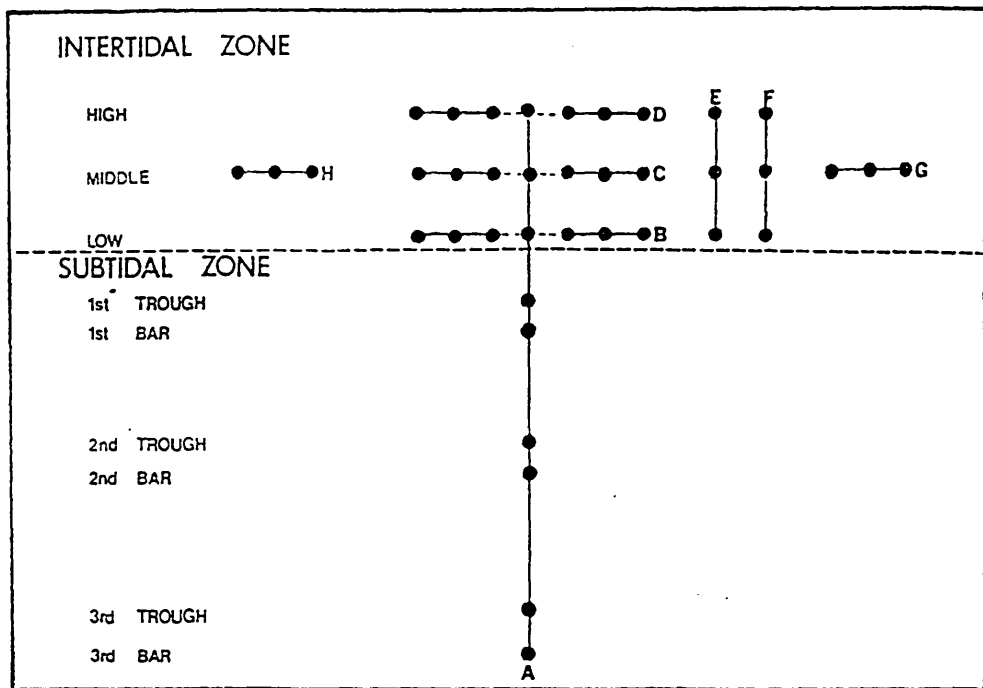


Figure 3. Transects established at the sampling sites. Samples were taken from Transects A-H on Malaquite Beach (northern Padre Island) and Transects A-D on Mustang Island

preservation and staining. The samples remained in the preservative for 7 to 10 days, then were transferred into containers filled with 45% isopropanol. The *Donax* specimens were identified to the species level (individuals less than 2.3 mm in length were not identifiable to species and categorized as post-larvae or spat), counted, and measured. Shell length (anterio-posterior axis) measurements were made using the micrometer of a Wild M-5 dissecting microscope. Individuals were measured to  $\pm 0.1$  mm. *Donax* density data was expanded to represent numbers of individuals per square meter ( $m^2$ ) by multiplying the number of specimens collected per sample by 17.3 (the sample volume was divided into a 10 cm deep square meter). Voucher specimens of the two species and post-larvae were deposited in the Corpus Christi State University Collection.

Physical parameters were recorded at each station. Water temperature was measured in the first trough, using a laboratory grade centigrade thermometer. Salinity was taken in the same area with a refractometer and recorded in parts per thousand. Beach profiles were determined using the method described by Emery (1961). Waves were measured using a graduated staff, and heights were determined by averaging the measurements of 10 consecutive waves. Tidal ranges, wind speed and direction, and ambient air temperature were obtained from daily weather reports dispatched by the Padre Island National Seashore Ranger Station.

Statistical analyses were applied to the data to determine differences between mean shell lengths, and non-random distributions. The mean shell lengths of the donacids were compared using the Student's t-test to determine if length differences existed between the sample stations (transect A) per month and site. The spatial distribution of the donacids along the B, C, D, G, and H transects were computed by the  $s^2/x$  ratio known as the Coefficient of Dispersion (CD) (Gage and Geekie, 1973; Botton, 1984). A random distribution is indicated when the value of the CD is one (the mean number of individuals per sample should equal the variance). An aggregated distribution is suggested by a CD significantly above one, and values less than one are indicative of even spacing. The significance of the departure from a random distribution was determined by the test of Clark and Milne (1955):  $1 \pm 2\sqrt{2n/(n-1)^2}$  where  $n$ =number of sample stations. Donacids with a CD within the limits of this test are considered to be randomly distributed. The Index of Dispersion (Chi-square distribution) was used to determine the significance of departure value for transects that had samples with less than five individuals (Gage and Geekie, 1973).

Length-frequency graphs were used to estimate monthly growth rates of the two species. The method described by Cassie (1954) was used to determine a set or size class of individuals. The mean shell length of each size class was calculated and the growth rate for the size class was estimated by determining monthly increases.

## RESULTS

### *Hydrographic Data*

Seasonal variations in salinity and water temperature were evident (Appendix A). Salinities and water temperatures did not differ between the two sample sites. Salinity ranged from 37<sup>0</sup>/oo on Mustang Island and 38<sup>0</sup>/oo on Malaquite Beach during June 1982 to 25<sup>0</sup>/oo at both sites during June 1983. Water temperatures at both sampling sites reached a high of 30°C during June 1983 whereas the lowest water temperatures were recorded during January with a reading of 14.8°C at Mustang Island and 15°C at Padre Island (Malaquite Beach). Wave heights ranged from 1 row/0.2 m on Malaquite Beach during August to 5 rows/1.2 m on Mustang Island during March. Width of the intertidal zone at both sampling sites averaged 29 m. The intertidal zones were widest from November-January.

### *Abundance*

A total of 74,451 specimens comprising 2 species and post-larvae were collected and analyzed from the two sample sites. The two species were evenly distributed between the two locations with 2,694 *D. variabilis roemeri* and 4,335 *D. texasianus* specimens taken from the A-D transects on Mustang Island, and 2,805 *D. v. roemeri* and 4,623 *D. texasianus* specimens were taken from the same transects on Padre Island. The post-larvae (individuals <2.3 mm) were not as evenly distributed, whereas 36,739 specimens were taken from the A-D transects on Mustang Island, and 26,091 post-larvae were collected from those transects on Padre Island. Post-larvae were collected in greater numbers from Mustang Island with 29% more specimens being taken.

Both species were collected throughout the year at the two sampling sites (Figures 4 and 5). Specimens of *D. v. roemeri* were collected in peak numbers

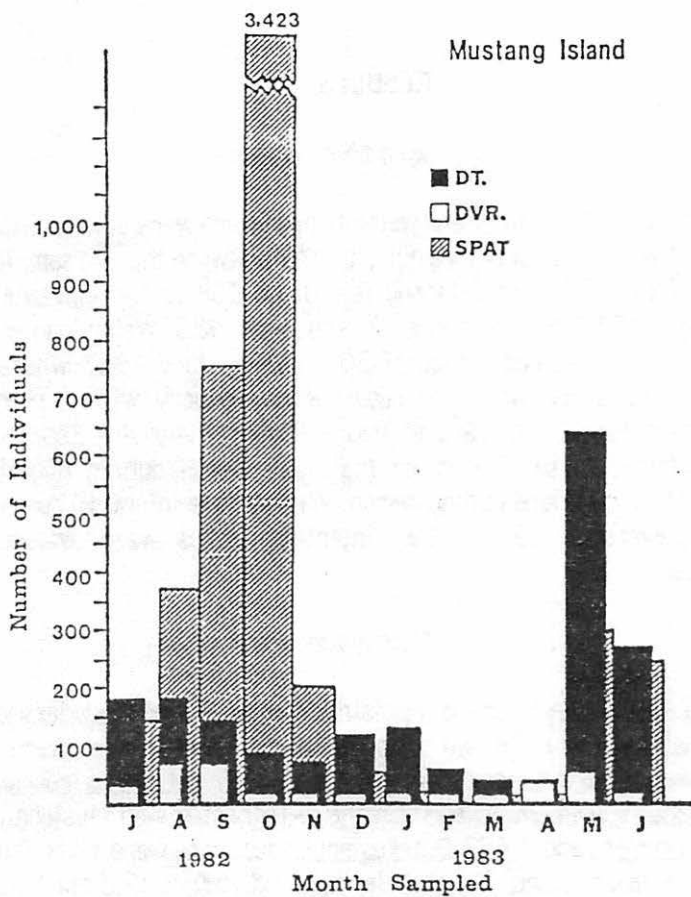


Figure 4. Total number of individuals collected from Transect A per month at Mustang Island. (Donax texasianus=DT; D. variabilis roemeri=DVR).





from April to September on Mustang Island, and from May, June, August, and September on Padre Island. The largest number of *D. texasianus* specimens were taken from Mustang Island during May–September. The clams were abundant on Padre Island during May–August. A second peak density was recorded in December and January at both sites. Lowest densities of the clams were recorded from February–April. Post-larvae were present throughout the year except for February on Mustang Island, and March on Padre Island. Post-larvae were most abundant during October on Mustang Island, and August on Padre Island.

### *Zonation*

Data compiled from samples collected on transect A were used to assess patterns of zonation (Figures 6 and 7). Specimens of *D. v. roemeri* were taken throughout the year at both sampling sites and primarily from the intertidal zone with 84% of the clams taken on Mustang Island, and 87% taken on Padre Island being collected intertidally. A peak density of *D. variabilis roemeri* was recorded in August on Padre Island with 2,128 individuals/m<sup>2</sup> taken from the mid-intertidal zone. The clams were taken in peak densities from the mid-intertidal zone at both sites. A peak density of *D. texasianus* was recorded in May 1983 on Mustang Island with 3,270 individuals/m<sup>2</sup> taken from the second trough. The majority of the population was collected from the subtidal zone throughout the year with 84% of the clams collected from Mustang Island and 81% of the clams from Padre Island being collected subtidally. Generally, the clams were most numerous beyond the first bar. Post-larvae were taken in large numbers from the intertidal zone with 71% of these individuals taken from the intertidal zone on Mustang Island. Post-larvae reached a peak density of 43,250 individuals/m<sup>2</sup> in the mid-intertidal zone during October on Mustang Island. The post-larvae on Padre Island were more evenly distributed throughout the transect with 57% of the population being taken from the intertidal limits. There was no apparent relationship between the width of the intertidal zone and the zonation or abundance of the donacids.

Large *D. v. roemeri* specimens (>10 mm) usually were taken from the low and mid-intertidal zones whereas large *D. texasianus* (>6 mm) generally were taken subtidally beyond the first sand bar (Table 1). During the months of January, February, and April a few large *D. texasianus* were taken from the intertidal zones at both sample sites. Young of both species and post-larvae were

Table 1. Combined monthly mean shell length of *Donax variabilis roemeri* and *D. texasianus* from each sample station on Mustang Island and northern Padre Island.

<u><i>Donax variabilis roemeri</i></u>	Mustang Island ( $\bar{x}$ in mm)	Padre Island ( $\bar{x}$ in mm)
Third Bar	0	0.3
Third Trough	0	0.5
Second Bar	1.1	0.4
Second Trough	0.8	0.8
First Bar	0.9	1.7
First Trough	2.0	2.8
Low Intertidal Zone	5.1	5.9
Mid Intertidal Zone	6.0	4.9
High Intertidal Zone	1.6	2.3

<u><i>Donax texasianus</i></u>	Mustang Island ( $\bar{x}$ in mm)	Padre Island ( $\bar{x}$ in mm)
Third Bar	4.7	4.9
Third Trough	4.8	5.0
Second Bar	4.8	3.9
Second Trough	5.2	4.7
First Bar	4.8	3.3
First Trough	4.1	3.9
Low Intertidal Zone	4.0	3.2
Mid Intertidal Zone	2.7	2.9
High Intertidal Zone	1.3	1.3

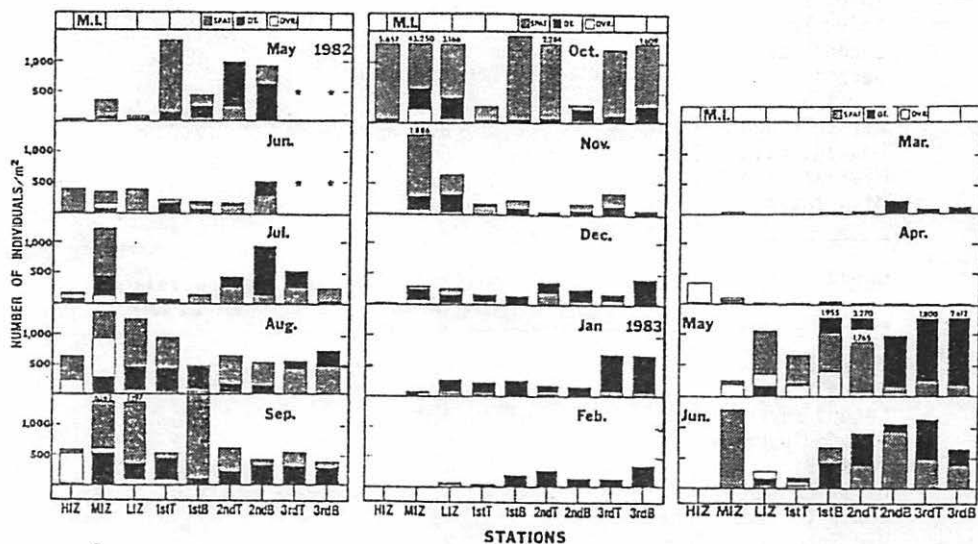


Figure 6. Monthly density fluctuations and zonation trends of *Donax texasianus* (DT), *D. variabilis roemeri* (DVR), and spat collected from Transect A on Mustang Island. (Stars indicate samples not taken).

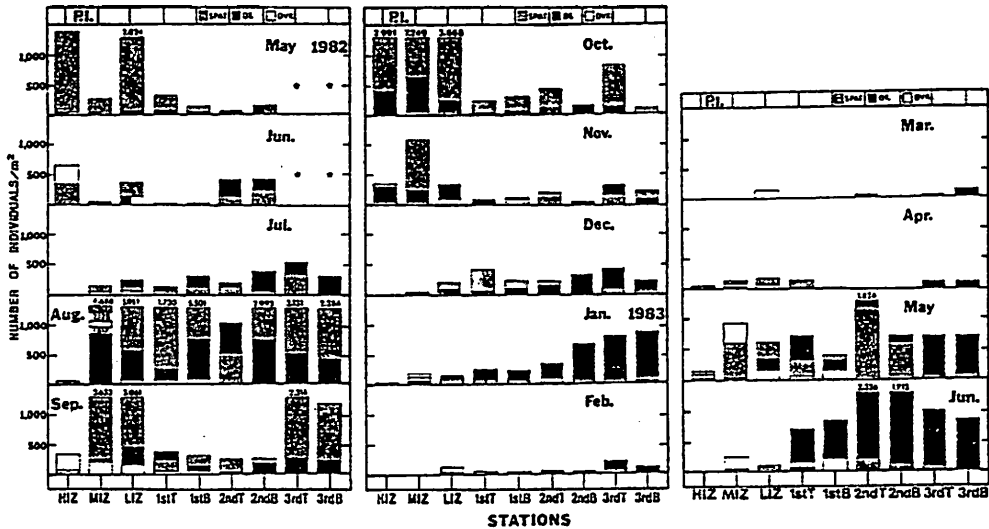


Figure 7. Monthly density fluctuations and zonation trends of *Donax texasianus* (DT), *D. variabilis roemeri* (DVR), and spat collected from Transect A on Malaquite Beach (Stars indicate samples not taken).

distributed throughout the A transects with no distinct size distribution or zonation. The largest *D. texasianus* (14 mm) and *D. v. roemerii* (27 mm) specimens were taken from Mustang Island. *Donax variabilis roemerii* and *D. texasianus* (Table 2) collected monthly from the two sample sites were similar in mean shell lengths. Significant differences in mean shell lengths of the donacids were noted primarily during the summer.

### *Migratory Behavior*

Tidal movements of *D. v. roemerii* and *D. texasianus* were monitored on transects E and F. Data for the two species were combined and their movements plotted on Figure 8. Both species migrate with the tides during the months May–August. During the period September–February the donacids migrational activities were reduced or ceased with the clams congregating in the mid and low intertidal limits. Migration activities slowly resumed during March and April, and were in full rhythm by May 1983. Post-larvae did not regularly follow the tides and remained distributed throughout the intertidal zone.

### *Growth Rates*

Growth rates for the two species collected from transects A–D were estimated by determining monthly mean shell length increases for each recruitment (Figures 9, 10, 11, and 12). Growth rates are presented by species, season, and sampling site on Table 3. Both donacids exhibited the greatest growth during the spring and summer. A maximum growth rate of 3.4 mm per month was estimated during the spring on Mustang Island for *D. v. roemerii*. Summer growth rates of *D. v. roemerii* averaged from 3.3 mm per month on Mustang Island to 2.1 mm per month on Padre Island. Higher growth rates were recorded from Mustang Island than on Padre Island (Table 3) for both species. Spring and summer *D. texasianus* growth rates ranged from 1.9 mm to 1.7 mm respectively on Mustang Island, to 1.7 mm to 1.0 mm on Padre Island.

### *Spawning*

Spawning periods were extrapolated from Figures 9, 10, 11, and 12 by using the abundances and mean lengths of young donacids as indicators of spawns. The

Table 2. Results of the Student's t-test comparing mean shell lengths of *Donax variabilis roemeri* and *D. texasianus* collected monthly from the two sampling sites (Transect A).

Month/Year	<i>Donax variabilis roemeri</i>		<i>Donax texasianus</i>	
	Degrees of freedom	t-value	Degrees of freedom	t-value
May 1982	3	0.44 NS	71	0.17 NS
June 82	11	2.21 *	139	0.01 NS
July 82	18	0.85 NS	293	2.10 *
Aug. 82	91	3.88 **	290	4.98 **
Sept. 82	112	3.75 **	264	2.25 *
Oct. 82	16	0.57 NS	205	1.43 NS
Nov. 82	11	0.15 NS	176	1.07 NS
Dec. 82	4	0.62 NS	208	0.49 NS
Jan. 83	5	1.15 NS	344	0.06 NS
Feb. 83	10	1.46 NS	53	0.32 NS
Mar. 83	9	0.08 NS	44	0.44 NS
Apr. 83	40	2.43 *	32	1.49 NS
May 83	151	0.02 NS	765	9.24 **
June 83	45	5.79 **	689	2.78 *

\*\*=P 0.01

\*=P 0.05

NS=Not significant at P=0.05

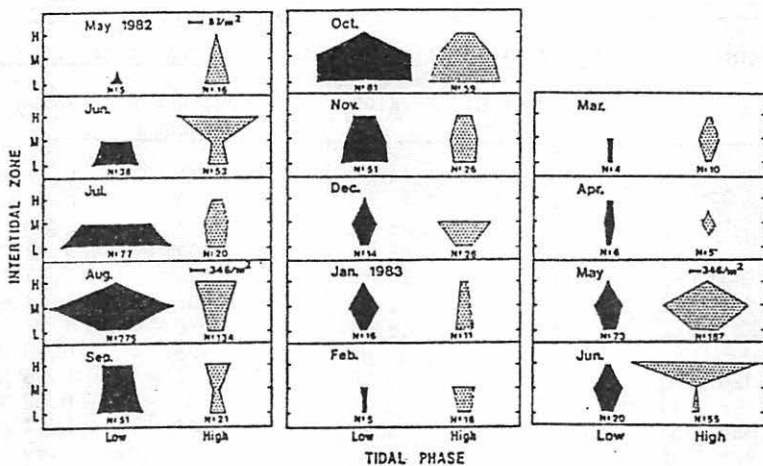


Figure 8. Monthly intertidal migrations at low and high tides (Transects E and F) of *Donax variabilis roemeri* and *D. texasianus* on Malaquite Beach. Density (no./m<sup>2</sup>) is given by 87 scale line except where indicated. (N=number of specimens).



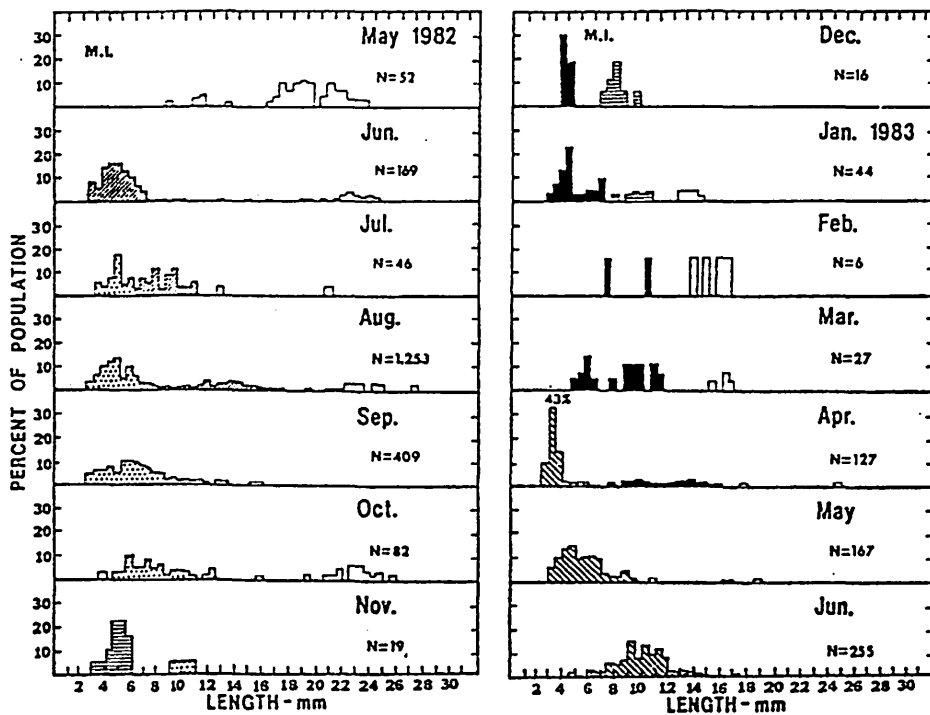


Figure 9. Length-frequency graphs of *Donax variabilis roemeri* from Mustang Island. (N=number of specimens collected from Transects A-D). Sets are represented by shaded areas.

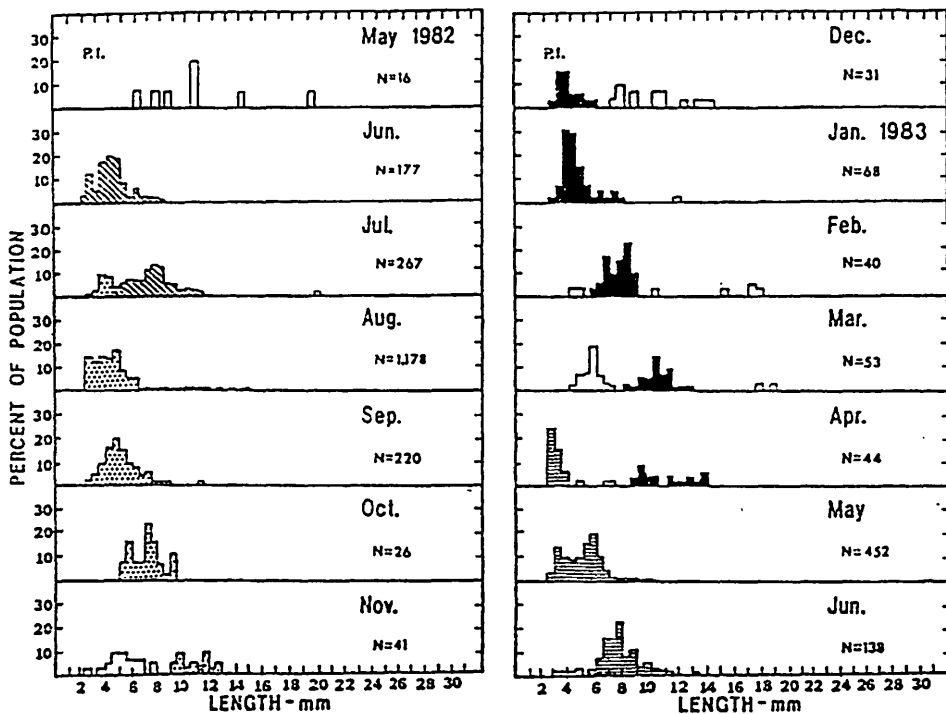


Figure 10. Length-frequency graphs of *Donax variabilis roemeri* from Malaquite Beach (northern Padre Island). (N= number of specimens collected from Transects A-D). Sets are represented by shaded areas.

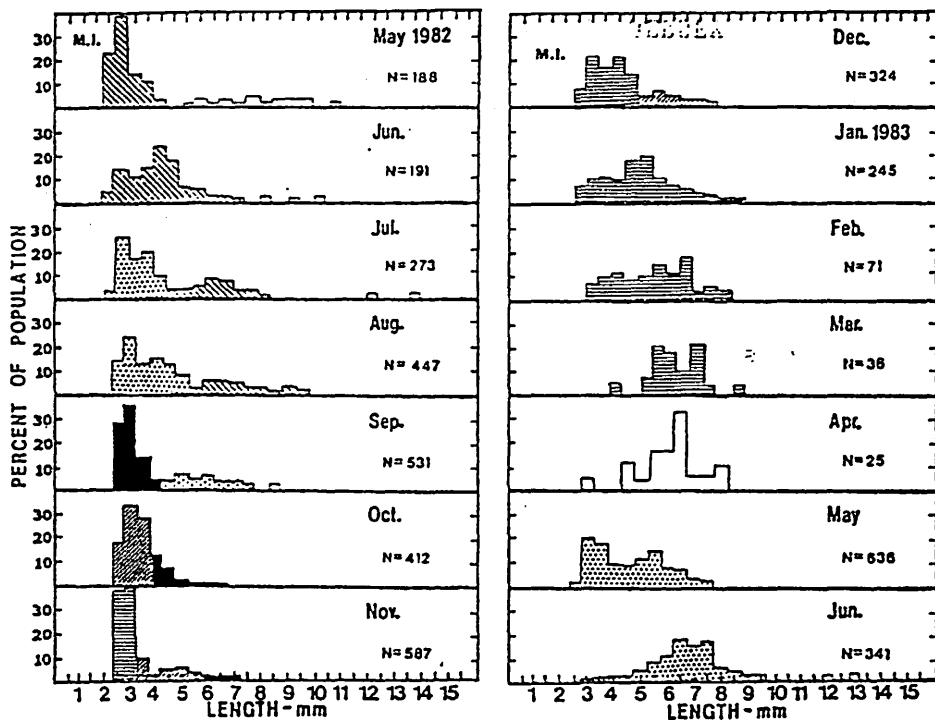


Figure 11. Length-frequency graphs of *Donax texasianus* from Mustang Island. (N=number of specimens collected from Transects A-D). Sets are represented by shaded areas.

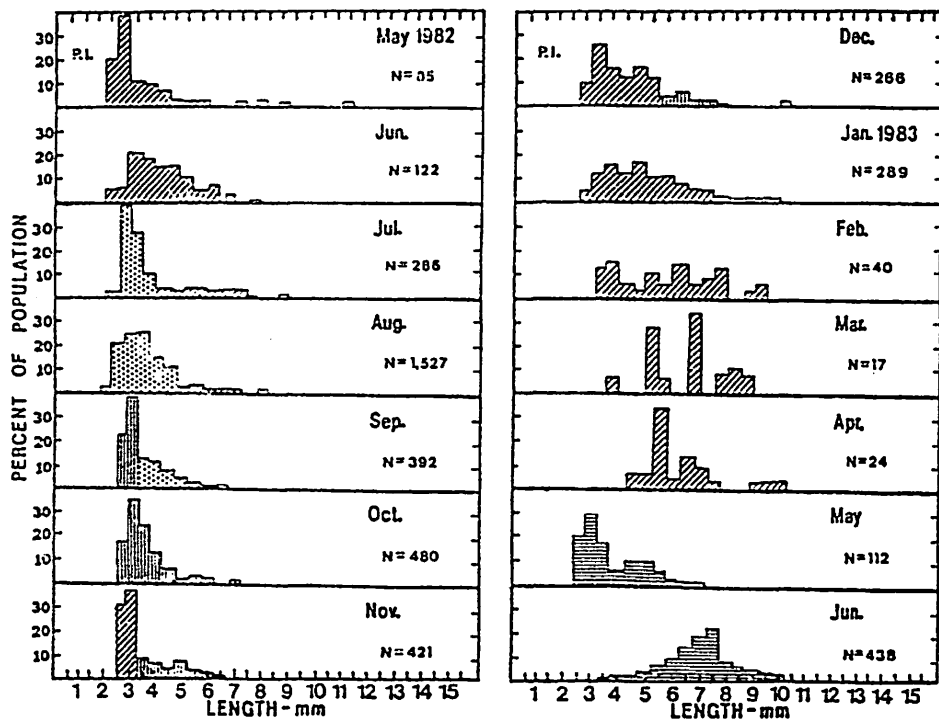


Figure 12. Length-frequency graphs of *Donax texasianus* from Padre Island. (N=number of specimens collected from Transects A-D). Sets are represented by shaded areas.

Table 3. Average monthly seasonal growth rates ( $\pm 1$  standard deviation) of Donax variabilis roemeri and D. texasianus on Mustang and northern Padre Island. The collecting period was divided into seasons: Summer (June-August), Fall (September-November), Winter (December-February), and Spring (March-May).

Seasons	Mustang Island	Padre Island
<u>Donax variabilis roemeri</u>		
Summer	3.3 mm ( $\pm 1.9$ )	2.1 mm ( $\pm 1.1$ )
Fall	2.3 mm ( $\pm 0.6$ )	2.7 mm ( $\pm 1.0$ )
Winter	1.4 mm ( $\pm 0.7$ )	1.9 mm ( $\pm 1.3$ )
Spring	3.4 mm ( $\pm 1.3$ )	1.9 mm ( $\pm 0.9$ )
$\bar{x}$	2.6 mm	2.2 mm
<u>Donax texasianus</u>		
Summer	1.7 mm ( $\pm 0.6$ )	1.0 mm ( $\pm 0.6$ )
Fall	1.2 mm ( $\pm 0.2$ )	1.2 mm ( $\pm 0.2$ )
Winter	0.9 mm ( $\pm 0.2$ )	1.1 mm ( $\pm 0.5$ )
Spring	1.9 mm ( $\pm 0.4$ )	1.7 mm ( $\pm 1.3$ )
$\bar{x}$	1.4 mm	1.3 mm

larval development period, settlement size, and growth rate of each size class were assumed to be constant. The donacids spawned ten months out of the year (March-December). Peak spawning months were noted for each species. Young *D. y. roemerii* (2.3 - 7.5 mm) were collected in greatest numbers from both sample sites during August. Young *D. texasianus* (2.3-5.0 mm) were most numerous on the two sampling sites during different months. These clams were abundant on Mustang Island during May 1983, and during August on Padre Island.

A total of five recruitments of young *D. y. roemerii* and six recruitments of young *D. texasianus* were collected on Mustang Island during the course of the study. Four recruitments of young *D. y. roemerii* and five recruitments of young *D. texasianus* were taken from Padre Island. Recruitments of young *D. y. roemerii* occurred at both sampling sites in June, July, December, and April. A small number of young *D. y. roemerii* were collected from Mustang Island during November. Young *D. texasianus* were collected at both sites during May, July, September, November, and May. An additional recruitment that may belong to the September group was collected during October on Mustang Island.

### *Distribution*

Patterns of spatial dispersion along the beach were examined from samples collected (post-larvae included) on transects B, C, and D (Tables 4 and 5). Coefficient of dispersion values predominantly indicated an aggregated pattern of distribution. Random distributions were infrequent along the shoreline, and seemed to be correlated to low population densities. The donacids did not exhibit a preference for the northern or southern portions of the transects and were predominantly distributed in an aggregated manner at both sites throughout the sampling period.

The donacids also displayed an aggregated distribution along the length of beach north and south (transects G and H) of transect A on Padre Island (Table 6). The monthly total number of specimens taken from the transects were similar. There was no obvious preference for one section of beach by the donacids.

### DISCUSSION

The total number of *D. variabilis roemerii* and *D. texasianus* specimens collected at each sampling site was similar with slightly more specimens of both

Table 4. Mean ( $\bar{x}$ ) and coefficient of dispersion (CD) for the donacids collected by station on Transects B, C, and D per month from Mustang Island. An aggregated distribution is indicated by A, whereas a random distribution is represented by R (Clark and Milne, 1955). Each mean and CD is based on 6 samples per transect (Table adapted after Botton, 1984).

Month/Year	Transect	$\bar{x}$	CD	Month/Year	Transect	$\bar{x}$	CD
May 1982	B	22.3*	29.8 A	Dec. 1982	B	51.3	0.8 R
	C	19.3	7.1 A		C	37.0	1.4 R
	D	∅			D	∅	
	B-C	20.8*	17.7 A		B-C	44.2	2.2 A
June 82	B	35.2	5.6 A	Jan. 83	B	21.8	0.4 R
	C	62.8	82.0 A		C	7.2*	2.9 A
	D	4.5			D	∅	
	B-C	49.0	53.9 A		B-C	14.5*	5.0 A
July 82	B	11.5	0.5 R	Feb. 83	B	1.3	
	C	34.0	10.6 A		C	∅	
	D	∅			D	∅	
	B-C	22.8	13.4 A				
Aug. 82	B	98.7	2.9 A	Mar. 83	B	4.0*	0.5 R
	C	375.8	171.0 A		C	1.0	
	D	7.6*	3.8 A		D	∅	
	B-D	161.0*	279.5 A		B-C	2.5	
Sept. 82	B	190.0	48.9 A	Apr. 83	B	11.7*	4.5 A
	C	466.0	36.7 A		C	11.7*	3.1 A
	D	149.0	101.7 A		D	∅	
	B-D	268.6	123.8 A		B-C	11.7*	3.4 A
Oct. 82	B	341.0	43.2 A	May 83	B	51.2	7.4 A
	C	1634.0	120.0 A		C	10.8	0.2 R
	D	587.0	53.5 A		D	∅	
	B-D	854.1	473.4 A		B-C	31.0	19.9 A
Nov. 82	B	164.0	1.3 R	June 83	B	27.8	8.0 A
	C	187.7	2.4 A		C	59.7	55.6 A
	D	5.2*	1.6 R		D	∅	
	B-D	126.1*	52.9 A		B-C	43.8	43.1 A

A=Aggregated

R=Random

\*\*Some samples in the transect have less than 5 individuals thus the  $\chi^2$  distribution test (P=0.05) was applied (Gage and Geekie, 1973).



Table 5. Mean ( $\bar{x}$ ) and coefficient of dispersion (CD) for the donacids collected by station on Transects B, C, and D per month from Padre Island. An aggregated distribution is indicated by A, whereas a random distribution is represented by R (Clark and Milne, 1955). Each mean and CD is based on 6 samples per transect (Table adapted after Botton, 1984).

Month/year	Transect	$\bar{x}$	CD	Month/Year	Transect	$\bar{x}$	CD
May 1982	B	42.8	58.6 A	Dec. 1982	B	72.7	10.5 A
	C	18.7	0.7 R		C	15.5	13.0 A
	D	37.5	55.6 A		D	$\emptyset$	
	B-D	33.0	44.5 A		B-C	44.1	30.1 A
June 82	B	28.3	6.1 A	Jan. 83	B	23.3	8.9 A
	C	52.2	24.6 A		C	12.0*	3.8 A
	D	28.2	53.0 A		D	0.7	
	B-D	36.2	27.7 A		B-C	20.5*	6.3 A
July 82	B	21.2	9.1 A	Feb. 83	B	5.2*	1.8 R
	C	63.5	22.5 A		C	0.7	
	D	0.2			D	$\emptyset$	
	B-C	42.3	29.0 A				
Aug. 82	B	456.0	82.0 A	Mar. 83	B	6.3*	1.0 R
	C	731.0	186.7 A		C	$\emptyset$	
	D	133.0*	332.7 A		D	0.7	
	B-D	495.0*	233.6 A				
Sept. 82	B	149.0	46.6 A	Apr. 83	B	24.3	8.1 A
	C	280.0	39.8 A		C	13.8	2.0 R
	D	48.7	60.8 A		D	$\emptyset$	
	B-D	159.2	98.5 A		B-C	19.1	6.9 A
Oct. 82	B	220.0	7.6 A	May 83	B	49.2	4.5 A
	C	440.8	6.2 A		C	71.3	14.6 A
	D	8.2	4.4 A		D	5.8*	3.7 A
	B-D	250.7	126.0 A		B-D	53.3*	17.1 A
Nov. 82	B	26.5	5.4 A	June 83	B	3.2*	0.9 R
	C	91.0	5.9 A		C	15.0*	10.2 A
	D	51.0	2.4 A		D	3.3*	0.7 R
	B-D	56.2	17.5 A		B-D	7.2*	11.0 A

A=Aggregated

R=Random

\*=Some samples in the transect have less than 5 individuals thus the  $\chi^2$  distribution test ( $P=0.05$ ) was applied (Gage and Geekie, 1973).

species, 4% and 6% respectively, being taken from the Padre Island site. A large oil spill, referred to in the literature as IXTOC I, impacted south Texas beaches in 1979. Kindinger (1981) and Tunnell et al. (1981) compared pre- and post-IXTOC I oil spill samples taken from sites near the sites discussed in the present study. Kindinger's (1981) pre-spill (August) *Donax* sp. mean density estimations from Mustang Island was 410 individuals/m<sup>2</sup> and 479 individuals/m<sup>2</sup> from Padre Island. These numbers compare well to mean density estimates determined for transect A in the present study with 507 individuals/m<sup>2</sup> from Mustang Island and 856 individuals/m<sup>2</sup> from Padre Island during August 1982 (excluding post-larvae).

Rabalais and Flint (1983) reported on the effects of an IXTOC I tar reef situated in the first trough of a Padre Island sandy beach located approximately 105 km south of Malaquite Beach. The authors determined from samples taken July 1980 that intertidal and most subtidal densities of infaunal organisms away from the tar reef had recovered and surpassed pre-spill densities reported by Kindinger (1981) and Tunnell et al. (1981). However, densities of infaunal organisms in the tar reef area had not returned to pre-spill numbers.

Post-spill density by Kindinger (1981) was considerably lower, which was believed to be a direct result of the oil on the beaches. Impacted oil effected the oxygen content of the sandy sediment, and thereby reduced the amount of habitat space available to infaunal organisms (Kalke et al., 1982). Comparison of pre-spill and post-spill IXTOC I (Kindinger, 1981) data to data from the present study indicates that donacid populations along the south Texas coast have returned to pre-spill abundances within a three year period.

Post-larvae were collected in greater numbers from Mustang Island than on Padre Island. Particulate organic matter outflow from the Corpus Christi Bay estuary passes through Aransas Pass and settles along the Mustang Island shoreline (McFarland, 1963). This constant nutrient source may provide favorable conditions for larvae settlement. In contrast, the Padre Island collecting site has no intervening riverine-estuarine outflow within close proximity, and may be a less suitable area for larvae settlement. The ecological conditions which were apparently more advantageous for larval settlement at Mustang Island may have become less important as the post-larvae matured because approximately equal densities of more mature individuals occurred at both collecting sites.

Vehicular traffic on Mustang Island could have been one of the neutralizing factors causing proportional population densities at the two sampling sites. However, Wolcott and Wolcott (1984) conducted a study investigating the impact

Table 6. Mean ( $\bar{x}$ ) and coefficient of dispersion (CD) for the donacids collected by station on Transects G and H per month. An aggregated distribution is indicated by A, whereas a random distribution is represented by R (Clark and Milne, 1955). Each mean and CD is based on 6 samples (3 samples from each transect) (Table adapted after Botton, 1984).

Month/Year	$\bar{x}$	CD
May 1982	32.2	26.5 A
June 82	85.7	8.7 A
July 82	80.5	34.3 A
Aug. 82	414.0	48.3 A
Sep. 82	76.7	8.5 A
Oct. 82	112.5	6.0 A
Nov. 82	137.0	49.4 A
Dec. 82	34.8	0.6 R
Jan. 83	14.5	3.5 A
Feb. 83	2.5*	1.2 R
Mar. 83	5.5	2.8 A
Apr. 83	6.0	3.4 A
May 83	54.5	21.8 A
Jun. 83	6.5	1.5 R

A=Aggregated distribution

R=Random distribution

\*=Some samples in the transect have less than 5 individuals thus the  $\chi^2$  distribution test ( $P=0.05$ ) was applied (Gage and Geekie, 1973).

of off-road vehicles on the macroinfauna of a North Carolina sandy beach. They believed that the noncompressible quality of the sand substrate combined with the shell morphology of donacids prevents the clams from being crushed in the foreshore zone by passing vehicles and concluded that macroinfauna can tolerate moderate levels of diurnal off-road vehicle traffic. Loesch (1957) estimated densities from 32,000 (June) to 70 (September) Donax per linear yard of beach on Mustang Island. Donax densities on Mustang Island have declined since Loesch's survey. A long term monitoring program is necessary to determine if the decline is cyclic or permanent.

The majority of D. v. roemeri specimens remained in the intertidal zone throughout most of the sampling period at both sampling sites. No seaward migration, as suggested by Loesch (1957), from the intertidal zone to subtidal regions was noticed any time during the year. However, during May 1983 D. v. roemeri specimens were collected from the intertidal zone out to the second bar at both sampling sites. The dispersed distribution of the clams may have been the result of above normal tides, and large breakers caused by a weather disturbance.

The two species were reduced in densities and essentially separated in distribution and habitat from February-April with D. v. roemeri occupying the intertidal zone, and D. texasianus remaining subtidally. This may be a consequence of spawning activities because post-larval recruitments, young D. v. roemeri and D. texasianus began to appear during May 1983 (Figures 4 and 5). Donax variabilis roemeri and D. texasianus were abundant intertidally during August-October. Shelton and Robertson (1981) also reported that the two donacids were abundant intertidally during this period. Loesch (1957) concluded, however, that the two species separate in habitat (intertidal vs. subtidal) during the summer.

Leber (1977, 1982a, and 1982b) and Mikkelsen (1981) mentioned the sympatric distribution of D. variabilis and D. parvula from the North Carolina and Florida coasts. Donax variabilis occurs in shallower water than D. parvula, much the same as the two donacids from the south Texas coast. However, Leber (1977) stated that the two east coast species remain separated in distribution from the late summer to March, and D. variabilis remained stranded high in the intertidal zone during this period. The separation may be necessary for the two species to fulfill some aspect of their life histories such as reproductive isolation (Leber, 1982b).

Leber (1982a) noted that the tidal migrations of D. variabilis and D. parvula vary seasonally. Donax parvula migrates in the intertidal zone from February to

July, and *D. variabilis* migrates through August. *Donax v. roemeri* and *D. texasianus* actively migrated in the intertidal zone from May-August on south Texas beaches; the remainder of the year only sporadic or limited migrations were observed. Reduced intertidal migrations during the winter was also reported by Loesch (1957). Laboratory observations by McLachlan and Young (1982) indicate that donacids are more apt to initiate migratory movements during summer months. At low temperatures the clams are not able to burrow rapidly, and thus unable to maintain a position on the beach.

Post-larvae did not regularly migrate with the tides. Limited tidal movements of small donacids (7-8 mm) were reported by Marsh (1962); and he believes that the smaller clams remain in the sand substrate throughout the tidal cycle.

Growth rate estimates were determined by means of length-frequency graphs. Loesch (1957) indicated that problems exist with their usage, and estimations obtained from such graphs may not be based on growth alone. Physical factors such as predators and longshore currents may influence monthly growth rates.

The growth rates of the two donacids varied per sampling site with predominantly greater rates being recorded from Mustang Island (Table 3). Larger individuals of both species were consistently taken from Mustang Island and this may have been the result of, as with the post-larval abundances, available particulate organic matter in the water. Wade (1968) and Sastre (1984) believe that *D. denticulatus* populations reach maximum length on beaches with high organic matter levels in the water.

The average growth rate of 2.8 mm per month (summer-fall) for *D. v. roemeri* on Mustang Island was greater than the rate determined by Loesch (1957). Loesch calculated the growth rate from June-December to be 1.7 mm per month. Estimates were made from mean shell lengths of recruitments of individuals usually smaller than 15 mm in this study, whereas Loesch may have used larger individuals. Donacids have higher growth rates during post-larval and juvenile life stages (Alagerswami, 1966). Size classes of individuals with mean lengths larger than 15 mm were not abundant and thus more difficult to monitor.

Mikkelsen (1985) determined that *D. variabilis* from southwest Florida and central eastern Florida have average summer growth rates of 3.0 mm and 3.7 mm per month. These estimates are similar to the values determined for *D. v. roemeri* on Mustang Island. Average seasonal growth rates of *D. texasianus* (1.4 mm per month) from Mustang Island compared well to the rates determined for this species by Loesch (1957) of 1 mm per month.

Peak spawning periods were determined for both donacids. Donacids have an embryonic and larval stage (planktonic) of about 3 weeks average duration followed subsequently by settlement (Nayar, 1954; Chanley, 1969). Settlement of *D. variabilis* occurs when the larvae reach a length of 275  $\mu\text{m}$  to 340  $\mu\text{m}$  (Chanley, 1969). *Donax texasianus* is assumed to settle on the sand substrate at approximately the size reported for *D. variabilis*.

Peak numbers of young *D. v. roemeri* (2.3-7.5 mm) were present at both sampling sites during August. Settlement of these individuals may have occurred about early July and spawning from late May to early June. There were two recruitments of young *D. v. roemeri* collected from each sampling site during the summer. Mikkelsen (1985) also indicated that two recruitments of young *D. variabilis* were taken from Sanibel Island, Florida during the summer. Specimens of *D. texasianus* (2.3-5.0 mm) were numerous at both sampling sites during May 1983 (Mustang Island) and August (Padre Island). The May group probably settled in early April and were spawned in mid March. The August group may have been spawned in late May and settlement occurred in mid June. Peak periods of recruitment and the sites of settlement for both species may vary annually depending on the physical parameters that influence the success of each settlement. Wade (1964) attributed the variable settlement locality of *D. denticulatus* to the prevailing currents that carry the planktonic larvae away from the parent population.

Most species of *Donax* have a short (1-2 years) life span (McLachlan, 1979). Loesch (1957) determined that *D. v. roemeri* has a life span of approximately 1 year, and *D. texasianus* between 6 months to 1 year. Mikkelsen (1985) also estimated that *D. variabilis* lives approximately 1 year with a small percentage of the population lasting 2 years. Large (>10mm) *D. v. roemeri* were absent or scarce from November-March (Fig. 9) and September-February (Fig. 10) which indicated that most of these individuals had died or buried themselves deeper than 10 cm; they had not migrated subtidally. Large individuals were more numerous in late spring suggesting that another size class (May-June spawn) was completing the growth cycle. Thus, *D. v. roemeri* has a life expectancy of 1 year with a small portion of the population existing for longer spans.

The mean length rates of *D. texasianus* size classes increased for 5 to 6 months before becoming indistinguishable (Figures 11 and 12). Hence, *D. texasianus* has a lifespan of at least 5 months, and a portion of the population may live 1 year as determined by Loesch (1957).

There were two primary spawning periods (May-June and July-November) (Figures 4 and 5) for the donacids. Although, periods of peak post-larval recruitments were apparent, distinct spawning periods for each species could not be determined. The November decline in the survival of post-larvae may have been correlated with plankton production. Shaver (1984) determined that plankton production from the surf zone on Padre Island peaked during September and October, whereas it steadily declined from November to April. Plankton serve as a primary food source for the donacids (McFarland, 1963). A four degree drop in the water temperature (October-November) may have been a contributing factor to the post-larval decline. Wade (1964, 1968) mentioned the high mortality rate of D. denticulatus the first four months after settlement, and attributed the decline to changes in environmental parameters such as salinity. Also, the November decline of post-larvae could have marked the close of the primary spawning season, with sporadic spawns occurring the remainder of the year.

The donacids generally exhibited an aggregated spatial distribution in the intertidal zones of both sampling sites. Smith (1971) described a similar pattern of distribution for donacids on the sandy beaches of West Africa. Donax denticulatus may occur in aggregates because of its preference for a particular type of substrate (Sastre, 1985). Interspecific competition with other members of the sandy beach community may cause the clams to be distributed in an aggregated manner (Leber, 1982b). Sastre (1985) believes that some mechanism in the sandy beach environment promotes the aggregated distribution. Donn et al. (1986) propose that D. serra Roding aggregates in the flatter areas of the sandy beach intertidal zone to enhance filter feeding capabilities. Other possible reasons for the aggregated distributions of donacids on south Texas beaches may be the involvement of biochemical factors for sensing of metabolites, or it may increase the success rate of the fertilization process.

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Appendix A. Sampling data from Mustang and northern Padre Island, Texas, barrier island sandy beaches.

Data	Collecting Site	Salinity (o/oo)	Air Temp. (°C)	Water Temp. (°C)	Beach Slope	Wind Direction (mph)	Wave Height
5-31-82	PI	35	32	28	4°	SE 10-15	3R*/2ft.
5-31-82	MI	35	29.5	28	N/A	SE 10-15	3R/1ft.
6-26-82	PI	38	31	29	N/A	SE 8-10	3R/1ft.
6-26-82	MI	37	31	29	N/A	SE 10-15	3R/2ft.
7-16-82	PI	36	31.5	28	N/A	SE 10-20	2R/2ft.
7-17-82	MI	36	32	29	N/A	SE 15-20	3R/2ft.
8-19-82	PI	36	32	29	5	NE 10-15 knots	1R/0.5ft.
8-20-82	MI	35	32	29	5	SE 10-15 knots	2R/1ft.
9-25-82	PI	32	31.5	29	2.5	E 5 knots	2R/2ft.
9-26-82	MI	30	31.5	28	5	E 10-15 knots	3R/2ft.
10-23-83	PI	32	22	21	3	NE 10-20 knots	3R/4ft.
10-24-82	MI	30	23	22	4	NE 10-15 knots	3R/2ft.
11-20-82	PI	31	26	18	4	SE 10-15 (6 knots)	3R/2.8ft.
11-21-82	MI	31	25.5	18	5	E-SE 5-10 (8 knots)	3R/2ft.
12-18-82	PI	32	24	15	2	S 15-20 (8 knots)	3R/2ft.
12-19-82	MI	33	22	16	5	N-NE 15-20 (14-20 knots)	3R/3ft.
1-15-83	PI	30	17	15	4	N-NW 9 knots	3R/2.5ft.
1-16-83	MI	30	17	14.8	5	E-NE 5-10	2R/2ft.
2-19-83	PI	32	20	16	5	SE 15-20	2R/2ft.
2-20-83	MI	33	22	16	5	SE 15-20	4R/4ft.
3-19-83	PI	30	25	16	5	SE 15-20	4R/2ft.
3-20-83	MI	30	26	16	5	SE 15-20	5R/4ft.
4-23-83	PI	35	27.5	21	5	N-NW 25 knots	3R/2ft.
4-24-83	MI	34	27.5	21.5	5	N-NE 14 knots	2R/2ft.
5-29-83	PI	25	29	26	5	N 14 knots	3R/3ft.
5-30-83	MI	26	29	26	4	SE 10-15	3R/3ft.
6-26-83	PI	25	32	30	4	S-SW 10 knots	3R/2ft.
6-25-83	MI	25	32	30	5	E 12-15 knots	2R/1.5ft.

\*R=Rows of waves

## INFORMATION FOR CONTRIBUTORS

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