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Molluscs (Mollusca: Gastropoda, Bivalvia, Polyplacophora) of Laguna Madre, Tamaulipas, Mexico: Spatial and Temporal Distribution

MARTHA REGUERO AND ANDREA RAZ-GUZMÁN

Molluscs were collected in Laguna Madre from seagrass beds, macroalgae, and bare substrates with a Renfro beam net and an otter trawl. The species list includes 96 species and 48 families. Six species are dominant (*Bittium varium*, *Costoanachis semiplicata*, *Brachidontes exustus*, *Crassostrea virginica*, *Chione cancellata*, and *Mulinia lateralis*) and 25 are commercially important (e.g., *Strombus alatus*, *Busycoarctum coarctatum*, *Triplofusus giganteus*, *Anadara transversa*, *Noetia ponderosa*, *Brachidontes exustus*, *Crassostrea virginica*, *Argopecten irradians*, *Argopecten gibbus*, *Chione cancellata*, *Mercenaria campechiensis*, and *Rangia flexuosa*). Seventeen species were found only in the northern region of the lagoon, 10 in the northern and southern regions, four only in Laguna de Catán, eight only in the south, and five were widely distributed, with the greater numbers of species and the greater density values recorded along “costa mar.” August and December revealed a similar number of species (50 and 53 respectively). Compared with 12 other lagoons along the Mexican Gulf of Mexico, the greater similarity in species composition was recorded for Términos, with 73 shared species, in response to the greater spatial heterogeneity and sampling intensity carried out in these two lagoons. Compared with Laguna Madre–Baffin Bay, Texas, this study recorded 70 more species than one study and 25 more species than another.

INTRODUCTION

Most coastal lagoons are characterized by contrasting habitats that favor the presence of a rich variety of plants, vertebrates, and invertebrates. Among the latter, molluscs are a markedly diverse group with respect to both abundance and species richness. They inhabit terrestrial, freshwater, estuarine, and marine environments and a variety of substrate types and submerged aquatic vegetation (García-Cubas and Reguero, 1994; Reguero, 1994; Pech et al., 2010; Reguero et al., 2010). They are important components of infaunal, semi-infaunal, and epifaunal communities in coastal lagoons where they recycle organic matter (García-Cubas and Reguero, 1994). Some gastropods and bivalves are dominant components, others are rare, and still others are commercially important in local, regional, and national fisheries (García-Cubas, 1988; Yáñez-Arancibia and Aguirre-León, 1988). Molluscs take advantage of seagrass beds that provide nursery areas with ideal conditions for growth, reproduction, and feeding for herbivores, detritivores, carnivores, and filter feeders (García-Cubas, 1988; Reguero, 1994; Hughes et al., 2009).

Laguna Madre provides important nursery and feeding areas that favor the recruitment of estuarine and marine species, wintering migratory birds (Tunnell and Judd, 2002), and species

that support traditional fisheries such as oysters (García-Cubas, 1981), shrimp, swimming crabs, and mullets (Raz-Guzmán and Huidobro, 2002). It also receives pollution runoff from agricultural and urban areas (Rendón-von Osten and García-Guzmán, 1996). The variety of substrates, the submerged aquatic vegetation, and the relative habitat values result in a high heterogeneity of habitats that are available throughout the lagoon for resident and visiting species that form communities with different structures and trophic complexities (Sánchez et al., 1996; Sánchez and Raz-Guzmán, 1997; Raz-Guzmán et al., 2001), among which are invertebrates that have been recorded with high values of abundance (Raz-Guzmán and Barba, 2000; Cid and Raz-Guzmán, 2011). The lagoon has been studied unevenly, with a greater intensity in the central region and a greater emphasis on certain taxonomic groups such as shrimp and fish. Previous studies have included molluscs (Hildebrand, 1958; García-Cubas, 1968; Raz-Guzmán et al., 2001; Reguero, 2002; Luna, 2010), peracarids (Barba and Sánchez, 2005; Ortega, 2013), shrimp (Cid and Raz-Guzmán, 2011), hermit crabs (Raz-Guzmán and Sánchez, 1998; Luna, 2010), fiddler crabs (Thurman, 1987), decapods and fish (Barba, 1999), fish (Raz-Guzmán and Huidobro, 2002), birds and biogeography (Leija-Tristán et al., 2000), an environmental study (García-Gil et al., 1993), a proposal for the

management of risks related to the connection of coastal water bodies (Escofet et al., 1995), and a treatise on the two Laguna Madre systems, in Tamaulipas and Texas (Tunnell and Judd, 2002).

Studies on molluscs of the Mexican Gulf of Mexico coastal lagoons include those of García-Cubas (1981) and Raz-Guzmán et al. (2001) for Términos in the state of Campeche, García-Cubas et al. (1990) for Mecoaacán, García-Cubas and Reguero (1990) for Tupilco-Ostión, and Antolí and García-Cubas (1985) for Carmen-Machona in the state of Tabasco, García-Cubas and Reguero (1995) for Sontecomapan, Reguero and García-Cubas (1989, 1991) and Raz-Guzmán et al. (2001) for Alvarado-Buen País-Camaronera, Reguero and García-Cubas (1993b) for Redonda-Mandinga, Flores-Andolais et al. (1988) for La Mancha, García-Cubas et al. (1992) for Chica-Grande, Reguero et al. (1991) for Tampamachoco, García-Cubas (1969) and Raz-Guzmán et al. (2001) for Tamiahua, Reguero and García-Cubas (1993a) for Pueblo Viejo in the state of Veracruz, and lastly Hildebrand (1958), García-Cubas (1968), Raz-Guzmán et al. (2001), Reguero (2002), and Luna (2010) for Laguna Madre in the state of Tamaulipas. The present study records the spatial and temporal distribution of mollusc species throughout Laguna Madre, together with data on gastropod shells with hermit crabs, species with greatest density, and dominant and commercially important species, and a comparison with 12 Mexican lagoons and one in Texas.

METHODS

Study area.—Laguna Madre is the largest coastal lagoon in Mexico with 200,000 ha. It is 200 km long and is located between 23°48′–25°27′N and 97°23′–97°52′W. It is limited to the north by the delta of the Río Bravo and to the south by the Río Soto la Marina. In 1996 the sand barrier was breached by five inlets: Boca de Mezquital, Boca Ciega, Boca de Catán, Boca de Caballo, and Boca Soto la Marina. The lagoon may be divided into the northern, central, and southern regions, and Laguna de Catán (Fig. 1). It also has two large areas locally called “costa mar” (along the inner margin of the sand barrier) and “costa tierra” (along the western margin of the lagoon). As a result of its location in a semiarid area, its limited interaction with the sea, and the reduced input of freshwater from the Río San Fernando, it is a hypersaline system with salinities of 33 to 62‰,

water temperatures of 25 to 35°C in summer and 19 to 25°C in winter, a maximum depth of 4 m, fine sandy sediment along costa mar and muddy shelly sediment along costa tierra. The submerged aquatic vegetation is characterized by the shoalgrass *Halodule wrightii* Aschers., which forms seagrass beds along costa mar and abundant macroalgae along costa tierra. These last include the green alga *Halimeda incrassata* (Ellis) Lamouroux syn. *H. tridens*, the brown algae *Dictyota dichotoma* (Hudson) Lamouroux and *Rosenvingea intricata* (J. Agardh) Børgensen, and the red algae *Hypnea cervicornis* J. Agardh, *Gracilaria blodgettii* Harvey, *G. cylindrica* Børgensen, *Chondria littoralis* Harvey, and *Digenea simplex* (Wulfen) C. Agardh. The only mangrove species is *Avicennia germinans* (L.) L., which is found only in the extreme south of the lagoon. Two marked climatic seasons, a dry summer and a rainy winter with northers, are characteristic of the region.

Sampling design and data analysis.—Sampling took place in August and December 1996 in order to represent the two main climatic seasons. Sampling took place throughout the lagoon, with 75 localities in August and 32 in December (Fig. 1), considering the spatial heterogeneity in the system determined by depth, islands, input of freshwater and sea water, and submerged aquatic vegetation. In December, only 11 localities in the northern region of the lagoon were sampled for molluscs, as part of a parallel project that focused on the flora and fauna of that region. Note: Figure 1 includes the names of only the localities where molluscs were collected.

Data were recorded at each locality for depth and visibility with a Secchi disk; water temperature was measured with a field thermometer and salinity with a refractometer (Appendix 1). Epifauna and submerged aquatic vegetation were collected with two different nets in order to obtain specimens of different sizes and from different habitats: a Renfro beam net (1-mm mesh size, 50 m² sampling area) and an otter trawl (1-cm mesh size, 1.5–3 min catch per unit effort). Some easily accessible specimens were collected manually and included in the species list, but were not included in the quantitative analyses. All samples were preserved in 10% formalin. The molluscs were placed in 70% alcohol in the lab, and were identified according to the morphological characteristics of the shells established by Abbott (1974), Vokes and Vokes (1983), and García-Cubas and Reguero (2004,

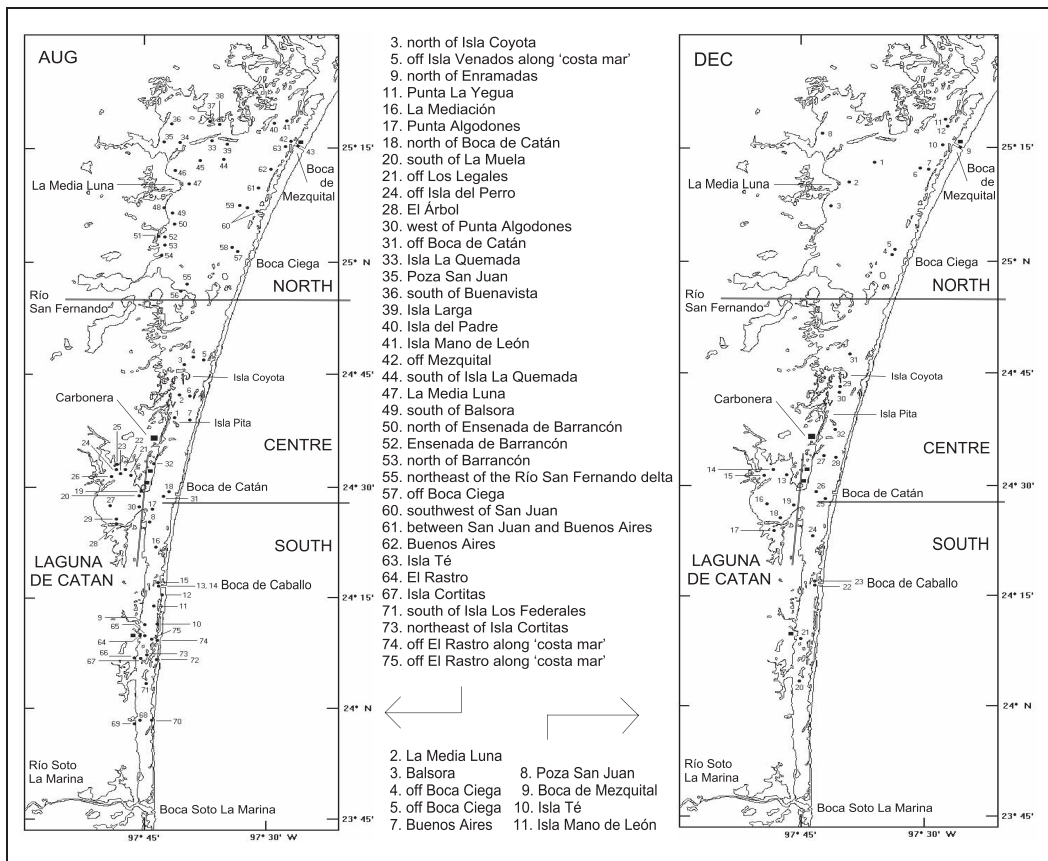


Fig. 1. Laguna Madre toponymy, regions, and sampling stations in August and December 1996.

2007). In addition, the papers of Collin (2000), Hülsken et al. (2006), and Reid (2009) were consulted regarding species name changes. Species identification was certified by comparison with the species stored in the Colección Malacológica Dr. Antonio García-Cubas (COMA) of the Instituto de Ciencias del Mar y Limnología (ICML), Universidad Nacional Autónoma de México. The species list was taxonomically updated in accordance with the World Register of Marine Species (WoRMS; 2016a–c), and the families were corroborated in Bouchet and Rocroi (2005, 2010).

Notes on the life habits of the molluscs (substrate preferences and feeding habits) were taken from Purchon (1968), Stanley (1970), Andrews (1971), and the above-stated authors for use in the text where necessary. The specimens of each species were counted in order to obtain density data as individuals (ind)/m² for the Renfro and ind/min for the otter trawl. An

Olmstead–Tükey analysis was applied to the density and spatial frequency data to identify the dominant, frequent, abundant, and rare species. Maps were prepared using a Surfer program (Version 10.1.561. Golden Software, Inc. Golden, CO 80401-1866, USA) to graphically represent the spatial and temporal distribution of the species collected with the two nets. The specimens were deposited in the COMA of the ICML.

The mollusc species of 13 lagoons along the Mexican Gulf of Mexico were compared. These lagoons included Laguna Madre, Laguna Pueblo Viejo, Laguna de Tamiagua, Laguna Tampamachoco, Laguna Chica-Grande, Laguna La Mancha, Laguna Redonda-Mandinga, Laguna Alvarado-Buen País-Camaronera, Laguna Sontecomapan, Laguna Carmen-Machona, Laguna Tupilco-Ostión, Laguna Mecocacán, and Laguna de Términos. A comparison was also carried out

with data recorded by several authors for Laguna Madre–Baffin Bay, Texas.

RESULTS

A total of 10,019 molluscs (90% live) representing 77 species (36 gastropods, 40 bivalves, and one chiton) and 38 families were collected in Laguna Madre. Of these, 6,438 specimens and 50 species (5,731 specimens and 29 species of gastropods, 707 specimens and 21 species of bivalves) were collected in August, and 3,581 specimens and 53 species (1,730 specimens and 19 species of gastropods, 1,850 specimens and 33 species of bivalves, one specimen of the chiton *Ischnochiton papillosus*) were collected in December. Added to these were four species and one family collected by Hildebrand (1958), 14 species and eight families collected by García-Cubas (1968), and one species and one family collected by Luna (2010), for an overall total of 96 species (49 gastropods, 46 bivalves, and one chiton) and 48 families. The list of species includes those recorded by Hildebrand (1958, noted by + in the following list), García-Cubas (1968, ++) and Luna (2010, +++).

Phylum Mollusca
 Class Gastropoda
 Subclass Vetigastropoda
 Order Archaeogastropoda
 Family Turbinidae ++
Lithopoma sp. ++
 Subclass Neritimorpha
 Order Cycloneritimorpha
 Family Neritidae
Neritina usnea Röding, 1798
Neritina virginea (Linnaeus, 1758)
Smaragdia vividis (Linnaeus, 1758)
 Subclass Caenogastropoda
 Order Littorinimorpha
 Family Calyptraeidae
Crepidula convexa Say, 1822
Crepidula depressa Say, 1822
Crepidula formicata (Linnaeus, 1758)
Crepidula maculosa Conrad, 1846
 Family Littorinidae ++
Echinolittorina sp. ++
 Family Elachisnidae
Elachisina floridana (Rehder, 1943)
 Family Cochliopidae ++
Texadina sphinctostoma (Abbott & Ladd, 1951) ++
 Family Naticidae
Tectonatica pusilla (Say, 1822)

Neverita delessertiana (Récluz, 1843)
 Family Tornidae ++
Vitrinella floridana Pilsbry & McGinty, 1946 ++
 Family Caecidae ++
Caecum pulchellum Stimpson, 1851 ++
Meioceras nitidum (Stimpson, 1851) ++
 Family Strombidae +++
Strombus alatus Gmelin, 1791 +++
 Order [unassigned] Caenogastropoda
 Family Modulidae
Modulus modulus (Linnaeus, 1758)
 Family Cerithiidae
Cerithium atratum (Born, 1778)
Cerithium eburneum Bruguière, 1792
Cerithium lutosum Menke, 1828
Bittiolium varium (Pfeiffer, 1840)
 Family Batillariidae
Batillaria minima (Gmelin, 1791)
 Family Potamididae
Cerithideopsis costata (da Costa, 1778) ++
Cerithideopsis pliculosa (Menke, 1829)
 Family Epitoniidae ++
Epitonium sp. ++
 Order Neogastropoda
 Family Columbelloidae
Columbella mercatoria (Linnaeus, 1758)
Costoanachis avara (Say, 1822)
Costoanachis semiplicata (Stearns, 1873)
Parvanachis obesa (C. B. Adams, 1845)
Astyris lunata (Say, 1826)
 Family Busyconidae
Busycoarctum coarctatum (G. B. Sowerby I, 1825)
Busycon contrarium (Conrad, 1840)
Sinistrofulgur perversum (Linnaeus, 1758) +
Fulguroopsis plagosa (Conrad, 1863)
 Family Nassariidae
Nassarius acutus (Say, 1822)
Phrontis vibex (Say, 1822)
 Family Fascioliariidae
Cinctura branhame (Rehder & Abbott, 1951)
Triplofusus giganteus (Kiener, 1840)
 Family Olividae
Oliva scripta Lamarck, 1810
 Family Mangeliidae
Pyrgocythara plicosa (C. B. Adams, 1850)
 Subclass Heterobranchia
 Infraclass [unassigned] Heterobranchia
 Family Pyramidellidae
Eulimastoma canaliculatum (C. B. Adams, 1850) ++
Odostomia bisuturalis (Say, 1822) ++

- Turbonilla interrupta* (Totten, 1835)
 Family Acteonidae
Japonactaeon punctostriatus (C. B. Adams, 1840)
- Infraclass Opisthobranchia
 Order Cephalaspidea
 Family Bullidae
Bulla striata Bruguière, 1792
 Family Haminoeidae
Haminoea succinea (Conrad, 1846)
 Family Acteocinidae
Acteocina canaliculata (Say, 1826)
- Infraclass Pulmonata
 Order [unassigned] Pulmonata
 Family Siphonariidae +
Siphonaria pectinata (Linnaeus, 1758) +
- Class Bivalvia
 Subclass Protobranchia
 Order Nuculanida
 Family Nuculanidae
Nuculana acuta (Conrad, 1831)
- Subclass Pteriomorpha
 Order Arcida
 Family Arcidae
Arca imbricata Bruguière, 1789
Anadara transversa (Say, 1822)
Anadara secticostata (Reeve, 1844)
Lunarca ovalis (Bruguière, 1789)
 Family Noetiidae
Arcopsis adamsi (Dall, 1886)
Noetia ponderosa Say, 1822
- Order Mytilida
 Family Mytilidae
Brachidontes exustus (Linnaeus, 1758)
Ischadium recurvum (Rafinesque, 1820)
Lithophaga nigra (d'Orbigny, 1853)
- Order Pectinida
 Family Anomiidae
Anomia simplex d'Orbigny, 1853
- Order Ostreida
 Family Ostreidae
Ostrea stentina Payraudeau, 1826
Crassostrea virginica (Gmelin, 1791)
 Family Pectinidae
Argopecten irradians (Lamarck, 1819)
Argopecten gibbus (Linnaeus, 1758)
- Subclass Heterodonta
 Order Carditida
 Family Crassatellidae
Crassinella lunulata (Conrad, 1834)
 Family Carditidae ++
Cardites floridanus (Conrad, 1838) ++
- Order Lucinida
 Family Lucinidae
Phacoides pectinatus (Gmelin, 1791)
- Family Montacutidae
Kelliopsis texasiana (Harry, 1969)
- Order Cardiida
 Family Cardiidae
Trachycardium egmontianum (Shuttleworth, 1856)
Trachycardium isocardia (Linnaeus, 1758)
Dallocardia muricata (Linnaeus, 1758)
Laevicardium mortoni (Conrad, 1830)
Dinocardium robustum (Lightfoot, 1786)
- Family Tellinidae
Tellina radiata Linnaeus, 1758
Laciolina laevigata (Linnaeus, 1758)
Euritellina angulosa (Gmelin, 1791)
Tampaella tampaensis (Conrad, 1866)
Ameritella mitchelli (Dall, 1895)
- Family Solecurtidae
Tagelus divisus (Spengler, 1794)
- Family Semelidae
Abra aequalis (Say, 1822)
Semele purpurascens (Gmelin, 1791)
Cumingia tellinoides (Conrad, 1930) ++
- Order Venerida
 Family Veneridae
Macrocallista nimbosa (Lightfoot, 1786)
 +
Cyclinella tenuis (Récluz, 1852)
Chione cancellata (Linnaeus, 1767)
Lirophora obliterata (Dall, 1902) ++
Anomalocardia puella (Pfeiffer in Philippi, 1846)
Mercenaria campechiensis (Gmelin, 1791)
- Family Mactridae
Mactroma fragilis (Gmelin, 1791) +
Mulinia lateralis (Say, 1822)
Rangia flexuosa (Conrad, 1839)
- Order Myida
 Family Corbulidae
Caryocorbula contracta (Say, 1822)
- Family Pholadidae
Cyrtopleura costata (Linnaeus, 1758)
Martesia striata (Linnaeus, 1758)
- Superorder Anomalodesmata
 Order [unassigned] Anomalodesmata
 Family Lyonsiidae ++
Lyonsia floridana Conrad, 1849 ++
- Class Polyplacophora
 Subclass Neoloricata
 Order Chitonida
 Family Ischnochitonidae
Ischnochiton papillosus (C. B. Adams, 1845)
- The mollusc family that presented the most species was Veneridae, with six (including the

TABLE 1. Gastropod species with hermit crabs in Laguna Madre (S, south; CA, Catán; C, central; N, north).

Species	Region and locality no.															Total
	S							CA	C	N						
	9	11	16	17	64	74	75	30	31	39	40	44	49	50	55	
<i>Neritina usnea</i>		X														1
<i>Neritina virginea</i>			X												X	2
<i>Tectonatica pusilla</i>				X						X		X				3
<i>Neverita delessertiana</i>				X				X	X	X	X	X	X	X		8
<i>Modulus modulus</i>						X										1
<i>Cerithium eburneum</i>			X													1
<i>Cerithium lutosum</i>			X													1
<i>Batillaria minima</i>															X	1
<i>Cerithideopsis pliculosa</i>			X													1
<i>Busycoarctum coarctatum</i>	X		X													2
<i>Fulguroopsis plagosa</i>			X													1
<i>Nassarius acutus</i>			X													1
<i>Cinctura branhami</i>	X						X									2
<i>Triplofusus giganteus</i>					X				X					X		3
Number of species per locality	2	1	7	2	1	1	1	1	2	2	1	2	1	2	2	

dominant *Chione cancellata*), followed by three families with five species each: Columbellidae (including the dominant *Costoanachis semiplicata*), Cardiidae, and Tellinidae. The other families are represented by one to four species each, among which some are dominant and/or commercially important.

Shells of 14 gastropod species distributed mainly in the northern region along costa tierra and the southern region of the lagoon were collected with hermit crabs in August. The most widely distributed of these gastropods was *Neverita delessertiana* (in eight localities throughout the lagoon). The locality with most gastropod shell species (seven) with hermits was La Mediación (loc. 16) in the southern region near Boca de Catán (Table 1).

Density values were calculated for all the species collected. The highest values were recorded for the gastropod *Bittium varium* (Aug.: 105.7 ind/m², Dec.: 32.8 ind/m²) collected with the Renfro, and the bivalves *Brachidontes exustus* (Aug.: 152.6 ind/min, Dec.: 341.7 ind/min), *Chione cancellata* (Aug.: 131.9 ind/min, Dec.: 81 ind/min), *Mulinia lateralis* (Dec.: 68 ind/min), and *Crassostrea virginica* (Dec.: 50 ind/min) collected with the otter trawl (Table 2).

An Olmstead-Tükey analysis provided different species classifications for the samplings of the two months and two nets. In general, the gastropods *Bittium varium* and *Costoanachis semiplicata* and the bivalves *Brachidontes exustus*, *Crassostrea virginica*, *Chione cancellata*, and *Mulinia lateralis* were the dominant species. Most of the

other species were spatially frequent, and species defined as rare were collected only in August with the otter trawl (Table 3).

The mollusc species of Laguna Madre included 25 commercially important species with respect to their use as food or bait or for the fabrication of decorations and arts and crafts (Table 4).

Spatial distribution—Sampling with the Renfro beam net

August: Gastropods were distributed mainly in the northern region of the lagoon, with the greater number of species off Mezquital (loc. 42, 12 species), followed by Ensenada de Barrancón (loc. 52, five species). The greatest densities were recorded for *Bittium varium* in Buenos Aires (loc. 62) with 82.88 ind/m² and off Mezquital (loc. 42) with 18.18 ind/m² (Fig. 2). Bivalves were distributed throughout the lagoon, but only in nine localities, with most species recorded off Mezquital (loc. 42, six species). No species presented high density values (Fig. 3).

December: Gastropods were collected only in the northern region of the lagoon and only along costa mar, with most species in Buenos Aires (loc. 7, nine species), followed by Boca de Mezquital (loc. 9, five species). The greatest density was recorded for *Bittium varium* off Boca Ciega (loc. 5) with 26.6 ind/m² (Fig. 2). Bivalves were distributed as were the gastropods, with most species also in Buenos Aires (loc. 7, nine species), followed by the locality off Boca

TABLE 2. Density of Laguna Madre molluscs (species collected manually not included), in August and December. R, Renfro (individuals/m²); OT, otter trawl (individuals/min).

Species	Aug		Dec	
	R	OT	R	OT
Gastropods				
<i>Neritina usnea</i>	0.02	8.50	0.48	
<i>Neritina virginea</i>	1.74	3.16	0.02	
<i>Smaragdia viridis</i>	0.02		0.02	
<i>Crepidula convexa</i>	0.04			
<i>Crepidula fornicata</i>	0.30			
<i>Crepidula depressa</i>		3.65		
<i>Crepidula maculosa</i>	0.02	0.50	0.02	
<i>Elachisina floridana</i>			0.02	
<i>Tectonatica pusilla</i>		1.72		
<i>Neverita delessertiana</i>		6.19		0.33
<i>Cerithium atratum</i>			0.02	
<i>Cerithium eburneum</i>		0.66		
<i>Cerithium lutosum</i>		0.66		
<i>Bittium varium</i>	105.66	0.66	32.80	
<i>Batillaria minima</i>		0.50		
<i>Cerithideopsis pliculosa</i>		0.66		0.33
<i>Columbella mercatoria</i>	0.02			
<i>Costoanachis avara</i>	0.56	14.00		6.33
<i>Costoanachis semiplicata</i>	1.98	11.48	0.18	1.33
<i>Parvanachis obesa</i>	0.04	0.66		0.66
<i>Astyris lunata</i>	1.42		0.18	
<i>Busycorctum coarctatum</i>		0.99		
<i>Busycon contrarium</i>		1.33		
<i>Fulguropsis plagosa</i>		0.66		
<i>Nassarius acutus</i>		2.66	0.02	1.00
<i>Phrontis vibex</i>	0.16		0.02	1.00
<i>Cinctura branhamae</i>		2.31		
<i>Triplofusus giganteus</i>		1.16		
<i>Pyrgocythara plicosa</i>			0.33	
<i>Turbonilla interrupta</i>			1.66	
<i>Japonactaeon punctostriatus</i>			0.33	
<i>Bulla striata</i>	0.34			
<i>Haminoea succinea</i>	0.08			
<i>Acteocina canaliculata</i>			0.33	
Chiton				
<i>Ischnochiton papillosus</i>				0.33
Bivalves				
<i>Nuculana acuta</i>		0.66		1.33
<i>Arca imbricata</i>	0.02			1.00

TABLE 2. Continued.

Species	Aug		Dec	
	R	OT	R	OT
<i>Anadara transversa</i>	0.24	3.66	0.02	4.66
<i>Anadara secticostata</i>	0.10			0.33
<i>Lunarca ovalis</i>	0.10	8.89	0.04	3.65
<i>Arcopsis adamsi</i>				0.33
<i>Noetia ponderosa</i>		2.32		1.00
<i>Brachidontes exustus</i>	0.14	152.64	1.38	341.70
<i>Ischadium recurvum</i>		0.50		
<i>Lithophaga nigra</i>				1.00
<i>Anomia simplex</i>				1.66
<i>Ostrea stentina</i>				1.00
<i>Crassostrea virginica</i>		11.32		50.02
<i>Argopecten irradians</i>		0.66		0.33
<i>Argopecten gibbus</i>			0.02	1.00
<i>Crassinella lunulata</i>	0.02			7.00
<i>Phacoides pectinatus</i>		1.33		
<i>Kelliopsis texasiana</i>		0.66		0.33
<i>Trachycardium isocardia</i>		0.66		0.33
<i>Dallocardia muricata</i>			0.02	
<i>Laevicardium mortoni</i>			0.04	
<i>Tellina radiata</i>			0.04	
<i>Laciolina laevigata</i>				0.33
<i>Tampaella tampaensis</i>			0.10	
<i>Ameritella mitchelli</i>				0.33
<i>Tagelus divisus</i>				0.33
<i>Abra aequalis</i>				0.33
<i>Semele purpurascens</i>			0.02	
<i>Cyclinella tenuis</i>		0.66		
<i>Chione cancellata</i>	0.12	131.95	0.70	81.02
<i>Anomalocardia puella</i>			0.14	
<i>Mercenaria campechiensis</i>	0.02	2.16		1.32
<i>Mulinia lateralis</i>	0.54	18.82	0.14	68.03
<i>Rangia flexuosa</i>	0.02			2.66
<i>Caryocorbula contracta</i>				0.33
<i>Cyrtopleura costata</i>		0.66		1.33
<i>Martesia striata</i>		0.66		

TABLE 3. Laguna Madre molluscs: dominant (****); spatially frequent (**); high density, low spatial frequency (*); and rare (*) (species collected manually not included), in August and December. R, Renfro; OT, otter trawl.

Species	Aug		Dec	
	R	OT	R	OT
Gastropods				
<i>Neritina usnea</i>	***	**	***	
<i>Neritina virginea</i>	****	***	***	
<i>Smaragdia viridis</i>	***		***	
<i>Crepidula convexa</i>	***			
<i>Crepidula fornicata</i>	***			
<i>Crepidula depressa</i>		***		
<i>Crepidula maculosa</i>	***	*	***	
<i>Elachisina floridana</i>			***	
<i>Tectonatica pusilla</i>		***		
<i>Neverita delessertiana</i>		****		***
<i>Cerithium atratum</i>			***	
<i>Cerithium eburneum</i>		*		
<i>Cerithium lutosum</i>		*		
<i>Bitiohium varium</i>	****	*	****	
<i>Batillaria minima</i>		*		
<i>Cerithideopsis pliculosa</i>		*		***
<i>Columbella mercatoria</i>	***			
<i>Costoanachis avara</i>	***	**		***
<i>Costoanachis semiplicata</i>	****	****	***	***
<i>Parvanachis obesa</i>	***	*		***
<i>Astysis lunata</i>	***		***	
<i>Busycoarctum coarctatum</i>		***		
<i>Busycon contrarium</i>		*		
<i>Fulguroopsis plagosa</i>		*		
<i>Nassarius acutus</i>		***	***	***
<i>Phrontis vibex</i>	***		***	***
<i>Cinctura branhami</i>		***		
<i>Triplofusus giganteus</i>		***		
<i>Pyrgocythara plicosa</i>				***
<i>Turbonilla interrupta</i>				***
<i>Japonactaeon punctostriatus</i>				***
<i>Bulla striata</i>	***			
<i>Haminoea succinea</i>	***			
<i>Acteocina canaliculata</i>				***
Chiton				
<i>Ischnochiton papillosus</i>				***
Bivalves				
<i>Nuculana acuta</i>		*		***
<i>Arca imbricata</i>	***			***
<i>Anadara transversa</i>	***	***	***	***
<i>Anadara sesticostata</i>	***			***
<i>Lunarca ovalis</i>	***	****	***	***
<i>Arcopsis adamsi</i>				***
<i>Noetia ponderosa</i>		***		***
<i>Brachidontes exustus</i>	***	****	****	****
<i>Ischadium recurvum</i>		*		
<i>Lithophaga nigra</i>				***
<i>Anomia simplex</i>				***
<i>Ostrea stentina</i>				***
<i>Crassostrea virginica</i>		****		****

TABLE 3. Continued.

Species	Aug		Dec	
	R	OT	R	OT
<i>Argopecten irradians</i>		*		***
<i>Argopecten gibbus</i>			***	***
<i>Crassinella lunulata</i>	***			***
<i>Phacoides pectinatus</i>		*		
<i>Kelliopsis texasiana</i>		*		***
<i>Trachycardium isocardia</i>		*		***
<i>Dallocardia muricata</i>			***	
<i>Laevicardium mortoni</i>			***	
<i>Tellina radiata</i>			***	
<i>Laciolina laevigata</i>				***
<i>Tampaella tampaensis</i>			***	
<i>Ameritella mitchelli</i>				***
<i>Tagelus divisus</i>				***
<i>Abra aequalis</i>			***	
<i>Semele purpurascens</i>			***	
<i>Cyclinella tenuis</i>		*		
<i>Chione cancellata</i>	***	****	****	****
<i>Anomalocardia puella</i>			***	
<i>Mercenaria campechiensis</i>	***	***		***
<i>Mulinia lateralis</i>	***	****	***	****
<i>Rangia flexuosa</i>	***			***
<i>Caryocorbula contracta</i>				***
<i>Cyrtopleura costata</i>		*		***
<i>Martesia striata</i>		*		

Ciega (loc. 5, five species). No species were recorded with high density values (Fig. 3).

Spatial distribution—Sampling with the otter trawl

August: Gastropods were collected throughout the lagoon, with most species in La Mediación (loc. 16, nine species), followed by a locality to the northeast of the San Fernando River delta (loc. 55, six species) and a locality north of Enramadas (loc. 9, five species). No species had a high density value (Fig. 4). Bivalves were also well represented throughout the lagoon with the greater numbers of species (five species) in six localities: La Mediación (loc. 16), south of La Muela (loc. 20), west of Punta Algodones (loc. 30), north of Ensenada de Barrancón (loc. 50), northeast of the San Fernando River delta (loc. 55), and Isla Té (loc. 63). The greatest densities were recorded for *Brachidontes exustus* (loc. 55) with 140 ind/min, followed by *Chione cancellata* (loc. 16) with 30 ind/min (Fig. 5).

December: Gastropods were collected both along costa mar and costa tierra in the northern region of the lagoon, though only in four localities and with most species off Boca Ciega (loc. 4, nine species). No species had high

TABLE 4. Commercially important Laguna Madre molluscs.

Species	Food	Shells
<i>Crepidula fornicata</i>	food and bait	arts and crafts
<i>Strombus alatus</i>	very high-value food	decoration, arts and crafts
<i>Busycoarctum coarctatum</i>	high-value food	decoration, arts and crafts
<i>Busycon contrarium</i>	high-value food	decoration, arts and crafts
<i>Sinistrofulgur perversum</i>	high-value food	decoration, arts and crafts
<i>Fulguroopsis plagosa</i>	high-value food	decoration, arts and crafts
<i>Cinctura branhami</i>	very high-value food	the big shells: decoration, arts and crafts
<i>Triplofusus giganteus</i>	very high-value food	the big shells: decoration, arts and crafts
<i>Arca imbricata</i>	high-value food	arts and crafts
<i>Anadara transversa</i>	high-value food	arts and crafts
<i>Lunarca ovalis</i>	high-value food	arts and crafts
<i>Noetia ponderosa</i>	very high-value food	arts and crafts
<i>Brachidontes exustus</i>	high-value food	
<i>Ischadium recurvum</i>	high-value food	
<i>Crassostrea virginica</i>	very high-value food	occasionally in arts and crafts
<i>Argopecten irradians</i>	little use	decoration, arts and crafts
<i>Argopecten gibbus</i>	little use	decoration, arts and crafts
<i>Phacoides pectinatus</i>	little use	decoration, arts and crafts
<i>Trachycardium egmontianum</i>	little use	decoration, arts and crafts
<i>Trachycardium isocardia</i>	little use	decoration, arts and crafts
<i>Dinocardium robustum</i>	little use	decoration, arts and crafts
<i>Macrocallista nimbosa</i>	food	decoration
<i>Chione cancellata</i>	very high-value food	decoration, arts and crafts
<i>Mercenaria campechiensis</i>	very high-value food	decoration, arts and crafts
<i>Rangia flexuosa</i>	very high-value food	

density values (Fig. 4). Bivalves presented a wider distribution through the northern region of the lagoon, with high numbers of species in four of the six localities: off Boca Ciega (loc. 4, 20 species), Balsora (loc. 3, nine species), La Media Luna (loc. 2, eight species), and Isla Mano de León (loc. 11, seven species). The greatest densities were recorded for four species, all in locality 4: *Brachidontes exustus* (323.66 ind/min), *Chione cancellata* (68.66 ind/min), *Crassostrea virginica* (48.66 ind/min), and *Mulinia lateralis* (34.66 ind/min) (Fig. 5). Only one specimen of the chiton *Ischnochiton papillosus* was collected with the otter trawl off Boca Ciega (loc. 4) (Fig. 4).

The spatial distribution of the mollusc species presented some interesting patterns for August. December was not included in this analysis as only the northern region was sampled that month (Table 5). *Crepidula depressa*, *Neverita delessertiana*, *Noetia ponderosa*, *Crassostrea virginica*, and *Chione cancellata* (marked 1 in Table 5) were widely distributed throughout the four regions of the lagoon. Ten species (marked 2) were present only in the northern and southern regions. *Costoanachis semiplicata* (marked 3) was present in the northern and central regions and Catán. *Astyris lunata* and *Triplofusus giganteus*

(marked 4) were present only in the northern and central regions. *Lunarca ovalis* (marked 5) was present only in the northern region and Catán. *Cinctura branhami* (marked 6) was present only in Catán and the southern region. Seventeen species (marked 7) were present only in the northern region. *Busycon contrarium*, *Nuculana acuta*, *Kelliopsis texasiana*, and *Cyclinella tenuis* (marked 8) were present only in Catán. Eight species (marked 9) were present only in the southern region. Overall, a greater number of species was recorded in the northern (Renfro and otter trawl) and southern (otter trawl) regions.

Temporal distribution—This analysis was carried out only for the northern region of the lagoon, as in December only this region was sampled.

Sampling with the Renfro beam net: The same pattern was observed, in general, for August and December, with most gastropod (12, Fig. 2) and bivalve (six, Fig. 3) species and most specimens of August recorded along costa mar, and most gastropod (nine, Fig. 2) and bivalve (nine, Fig. 3) species and most specimens of December recorded also along costa mar.

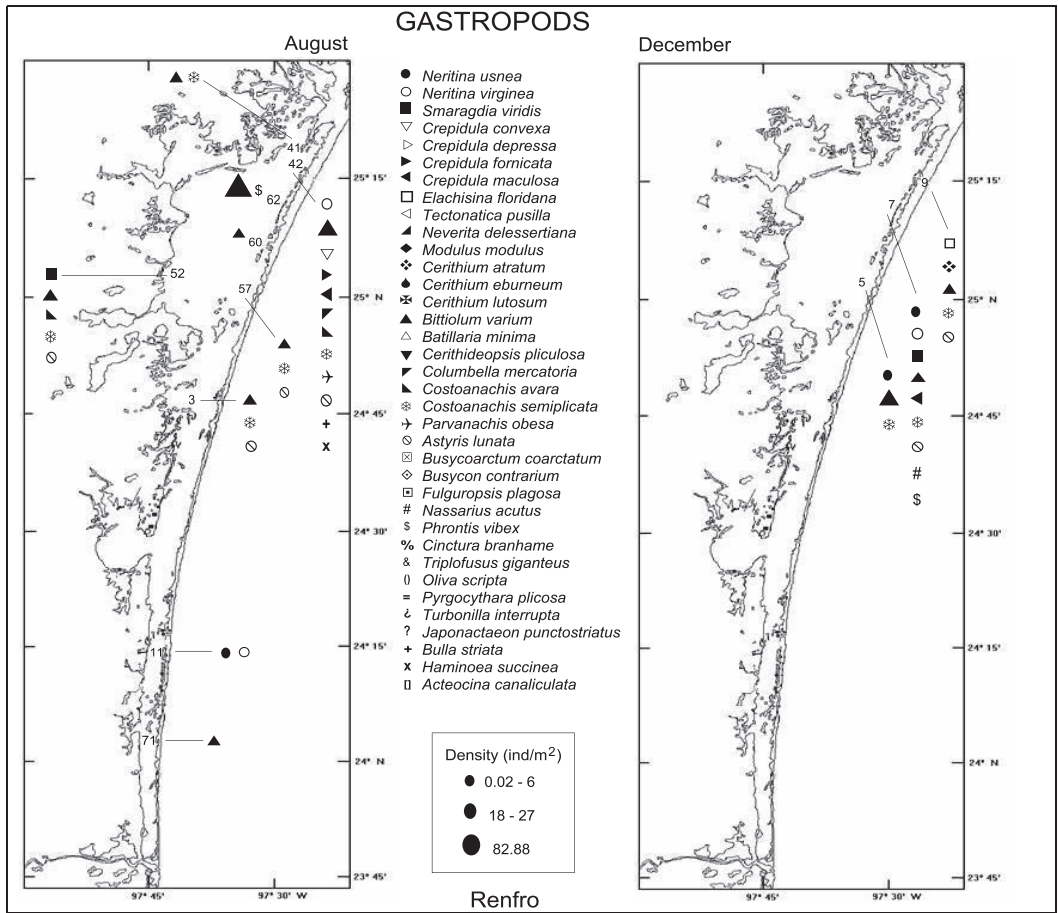


Fig. 2. Spatial distribution of Laguna Madre gastropods (Renfro sampling: August, left; December, right).

Sampling with the otter trawl: Both gastropods and bivalves were distributed throughout the region. However, in general, in August most species and most specimens were collected just above the San Fernando River delta (Figs. 4, 5), while in December most species were found along costa mar: nine gastropod species and the only chiton (loc. 4 off Boca Ciega; Fig. 4) and 20 bivalve species (also loc. 4; Fig. 5).

DISCUSSION

Three considerations are important regarding the sampling dates: 1) that in the other available studies only four species of 12 collected by Hildebrand (1958), 14 species of 36 collected by García-Cubas (1968), and one species of 11 collected by Luna (2010) were not collected in our study; 2) that our study recorded 65 more species than Hildebrand (1958), 41 more species than García-Cubas (1968), and 66 more species

than Luna (2010); and 3) that all the species recorded in these three studies plus ours are presented here, in view of which we consider the species list to be taxonomically updated and valid. The list thus includes our 77 species plus the 19 species recorded by the above-stated authors, for a total of 96 species that represent the malacological fauna of Laguna Madre. The 77 species collected in our study make up 80% of the total species list. The greater number of species recorded in our study reflects the more intensive and widespread sampling carried out, as well as the more varied sampling gear used (Table 6).

Regarding the gastropod shells recorded with hermit crabs, of the 14 species recorded here, Luna (2010) recorded seven, plus four more for a total of 11 species, and established occupation patterns considering shell species, size, shape, weight, inner volume, ornamentation, and availability, as well as crab size and sex. The greater

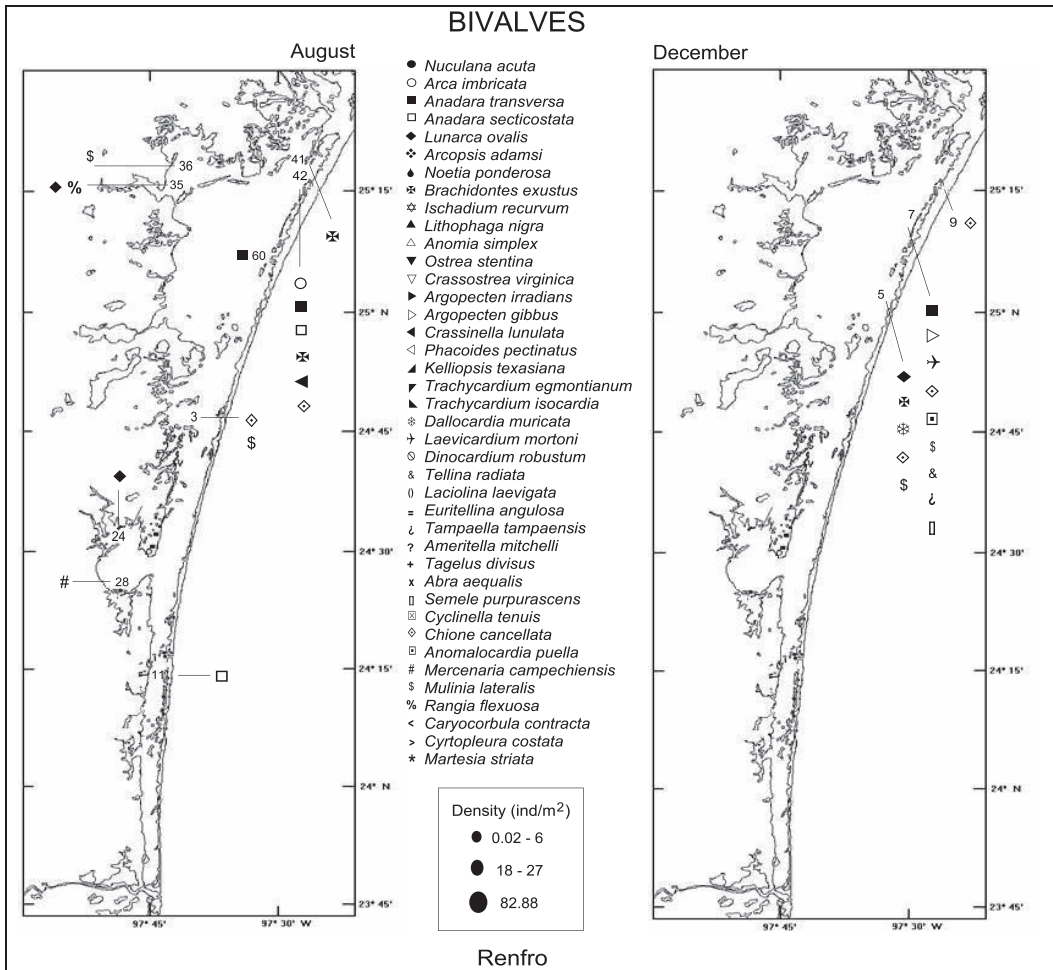


Fig. 3. Spatial distribution of Laguna Madre bivalves (Renfro sampling: August, left; December, right).

part of the gastropod shells obtained with hermit crabs were the larger species *Neverita delessertiana*, *Busycon contrarium*, and *Cinctura branhami*. The hermits included *Clibanarius vittatus* (Bosc, 1802), *Petrochirus diogenes* (Linnaeus, 1758), *Paguristes hummi* Wass, 1955, *Pagurus annulipes* (Stimpson, 1860), *Pagurus maclaughlinae* García-Gómez, 1982, and *Pagurus maclaughlinae pollicaris* Say, 1817. The first, a dominant species, was found in most of the shell species. Most hermit crabs in gastropod shells live in seagrass beds where the physical heterogeneity and complexity favor a greater availability of food and a lower rate of mortality by predation (Tunberg et al., 1994; Raz-Guzmán and Sánchez, 1998; Luna, 2010).

The presence and distribution of dominant species are generally related to salinity and substrate. The dominant mollusc species includ-

ed the bivalves *Brachidontes exustus*, *Chione cancellata*, *Crassostrea virginica*, and *Mulinia lateralis* and the gastropods *Bittiolium varium* and *Costoanachis semiplicata*. *Brachidontes exustus* has no problem finding a hard substrate to settle on, as it uses *Crassostrea* shells to form shoals. *Chione cancellata*, a filter feeder, optimally uses its sandy habitats. *Crassostrea virginica* is a successful species with a larva that quickly settles in high-salinity areas. *Mulinia lateralis* is a small species but very abundant and with a wide distribution. *Costoanachis semiplicata* is a carnivore that lives in seagrass beds where it finds abundant food (Purchon, 1968; Stanley, 1970; Andrews, 1971). In particular, *Bittiolium varium* has been recorded for the Gulf of Mexico as a locally abundant species among submerged aquatic vegetation in shallow areas by García-Cubas (1969, 1981), Andrews (1971), Abbott (1974), and Reguero

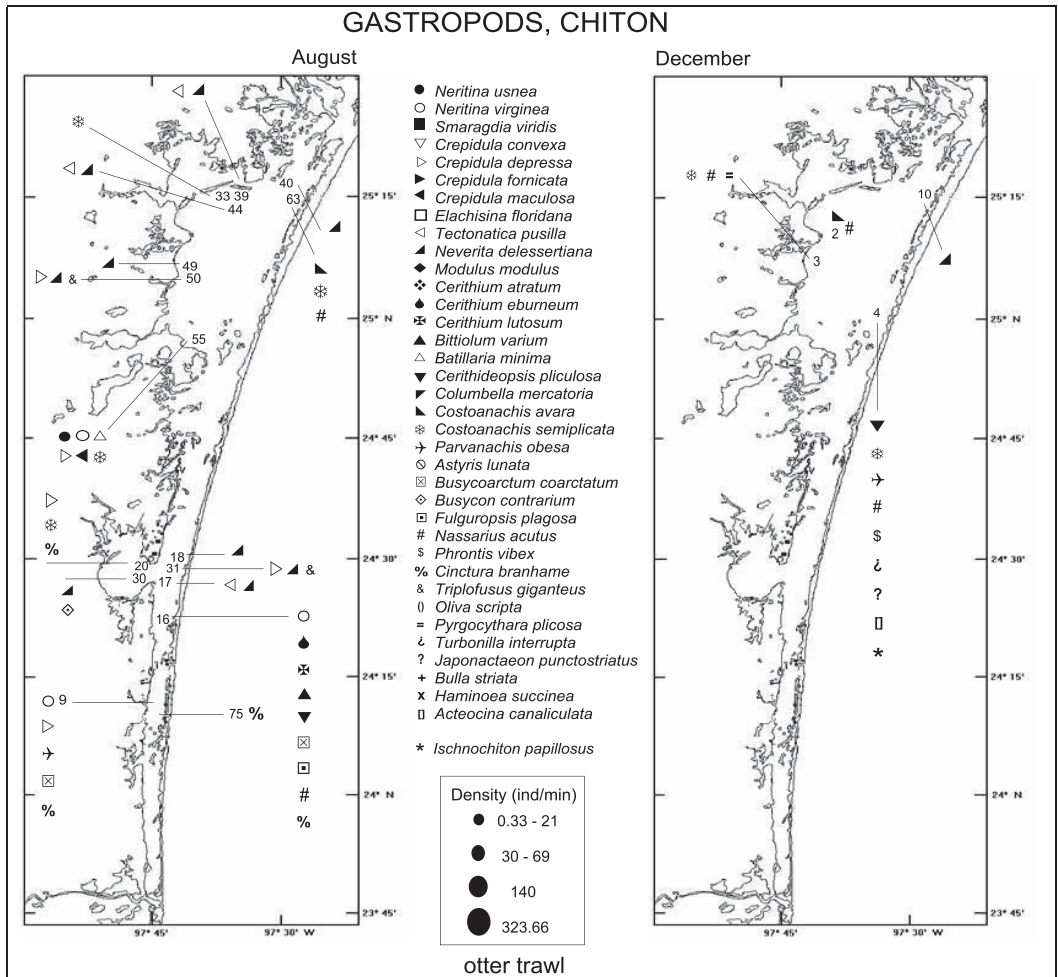


Fig. 4. Spatial distribution of Laguna Madre gastropods and chiton (otter trawl sampling: August, left; December, right).

(1994), and is comparable to the *Bittiolium alternatum* (Say, 1822) cited by Abbott (1974) for Chincoteague, VA.

Among the 25 commercially important species recorded for Laguna Madre, *Strombus alatus*, *Cinctura branhami*, *Triplofusus giganteus*, *Noetia ponderosa*, *Crassostrea virginica*, *Chione cancellata*, *Mercenaria campechiensis*, and *Rangia flexuosa* provide a food source of very high value for human consumption, *Crepidula fornicata* is used as bait in small-scale fishing, and six species have a relatively low value as food. The oyster *Crassostrea virginica* is a common species that sustains an important local fishery, together with its epizoic species *Brachidontes exustus* and *Ischadium recurvum*. These and *Rangia flexuosa* contribute to the diet of the local communities. In addition, *Strombus alatus*, *Busycoarctum coarctatum*,

Triplofusus giganteus, *Anadara transversa*, *Noetia ponderosa*, *Crassostrea virginica*, *Argopecten irradians*, *A. gibbus*, *Chione cancellata*, and *Mercenaria campechiensis* sustain fisheries at the national level and, thus, represent a socioeconomically important resource for the people of the region. With respect to the shells, most of these 25 species are used to make decorations, arts, and crafts that the local population sells to increase their income.

The ample variety of activities that molluscs carry out in their habitats in the lagoon reflects the complexity of their communities (Purchon, 1968; Stanley, 1970; Andrews, 1971), as may be seen in the range of substrate types, with and without submerged aquatic vegetation, and salinities in which they live, and the various feeding habits they present as a group. Most of

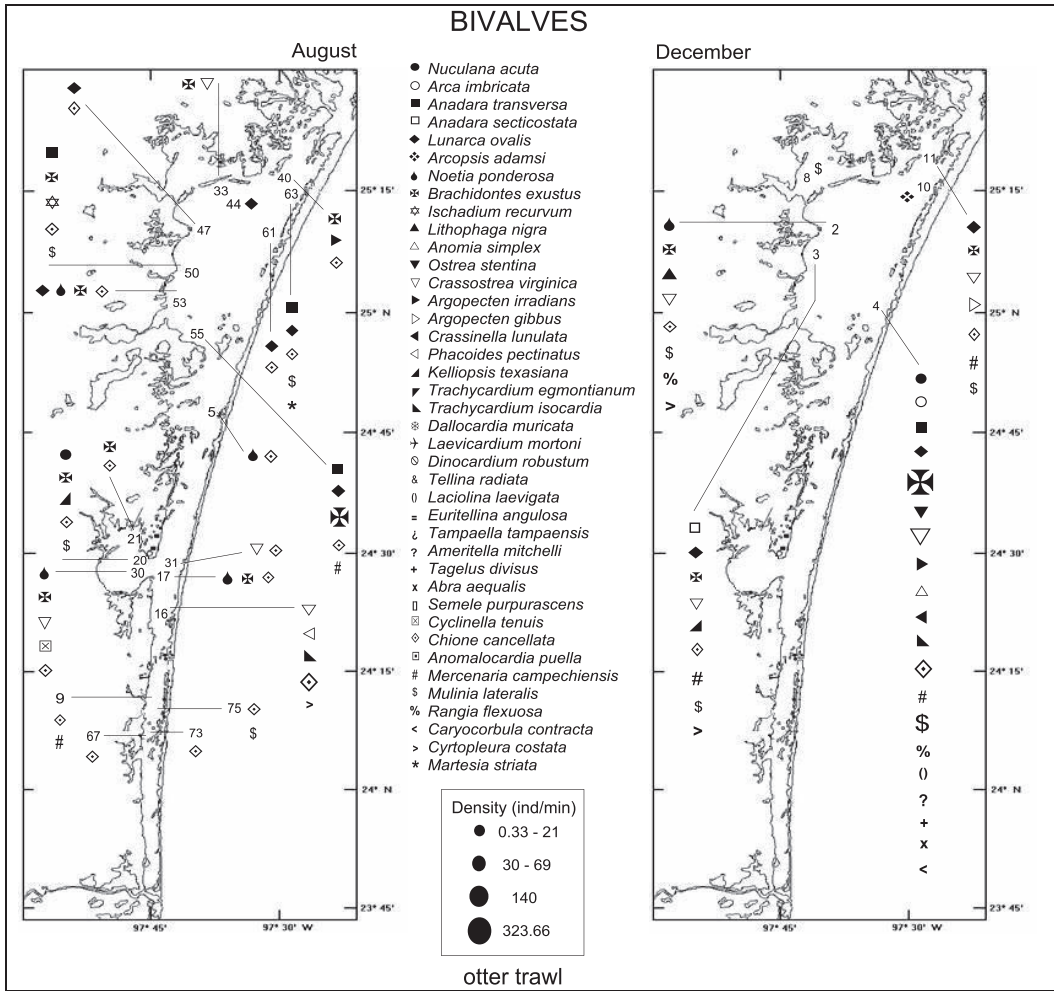


Fig. 5. Spatial distribution of Laguna Madre bivalves (otter trawl sampling: August, left; December, right).

the gastropods of Laguna Madre are epifaunal sand-dwelling carnivores that live among submerged aquatic vegetation in brackish and marine areas, while most bivalves are infaunal sand-dwelling filter feeders found also in brackish and marine areas (Table 7).

Spatial distribution.—The greater species richness and density values recorded for the Renfro beam net were those of the northern region of the lagoon and mostly along costa mar (Boca de Mezquital, off Mezquital, Buenos Aires, off Boca Ciega, Ensenada de Barrancón). This area of the lagoon is characterized by depths of 30 to 120 cm, mostly clear water with temperatures of 21 to 35°C, salinities of 37 to 52‰, *H. wrightii* seagrass beds, some macroalgae, and mostly sandy sediment (Appendix 1). The only species with high

densities in this case was *Bittium varium*, an epifaunal herbivorous gastropod that lives in seagrass beds and macroalgae in brackish and marine environments (van Montfrans et al., 1982; Orth and van Montfrans, 1984; Orth et al., 1984; Reguero, 1994; García-Cubas and Reguero, 2004), such as are found in Laguna Madre. As Reynolds et al. (2014) reported, Cebrian (1999) and Valentine and Duffy (2006) recorded this gastropod as a small dominant mesograzing herbivore in temperate coastal systems, where it may link primary producers with secondary consumers (Duffy and Hay, 2000; Davenport and Anderson, 2007) when feeding on micro- and macroalgae (Valentine and Duffy, 2006).

In turn, the greater species richness and density values obtained with the otter trawl were

TABLE 5. Presence of mollusc species in the four regions of Laguna Madre (N, north; C, central; CA, Catán; S, south), in August. R, Renfro; OT, otter trawl. The numbers indicate the spatial distribution patterns of the species (see text).

Spatial distribution	Species	Net and region							
		R				OT			
		N	C	CA	S	N	C	CA	S
2	<i>Neritina usnea</i>				X	X			
2	<i>Neritina virginea</i>	X			X	X			X
7	<i>Smaragdia viridis</i>	X							
7	<i>Crepidula convexa</i>	X							
7	<i>Crepidula fornicata</i>	X							
1	<i>Crepidula depressa</i>					X	X	X	X
7	<i>Crepidula maculosa</i>	X				X			
2	<i>Tectonatica pusilla</i>					X			X
1	<i>Neverita delessertiana</i>					X	X	X	X
9	<i>Cerithium eburneum</i>								X
9	<i>Cerithium lutosum</i>								X
2	<i>Bittiolium varium</i>	X	X		X				X
7	<i>Batillaria minima</i>					X			
9	<i>Cerithideopsis pliculosa</i>								X
7	<i>Columbella mercatoria</i>	X							
7	<i>Costoanachis avara</i>	X				X			
3	<i>Costoanachis semiplicata</i>	X	X			X		X	
2	<i>Parvanachis obesa</i>	X							X
4	<i>Astyris lunata</i>	X	X						
9	<i>Busycoarctum coarctatum</i>								X
8	<i>Busycon contrarium</i>							X	
9	<i>Fulguroopsis plagosa</i>								X
2	<i>Nassarius acutus</i>					X			X
7	<i>Phrontis vibex</i>	X							
6	<i>Cinctura branhamae</i>							X	X
4	<i>Triplofusus giganteus</i>					X	X		
7	<i>Bulla striata</i>	X							
7	<i>Haminoea succinea</i>	X							
8	<i>Nuculana acuta</i>							X	
7	<i>Arca imbricata</i>	X							
7	<i>Anadara transversa</i>	X				X			
2	<i>Anadara scticostata</i>	X			X				
5	<i>Lunarca ovalis</i>	X		X		X			
1	<i>Noetia ponderosa</i>					X	X	X	X
2	<i>Brachidontes exustus</i>	X				X		X	X
7	<i>Ischadium recurvum</i>					X			
1	<i>Crassostrea virginica</i>					X	X	X	X
7	<i>Argopecten irradians</i>					X			
7	<i>Crassinella lunulata</i>	X							
9	<i>Phacoides pectinatus</i>								X
8	<i>Kelliopsis texasiana</i>							X	
9	<i>Trachycardium isocardia</i>								X
8	<i>Cyclinella tenuis</i>							X	
1	<i>Chione cancellata</i>	X	X			X	X	X	X
2	<i>Mercenaria campechiensis</i>			X		X			X
2	<i>Mulinia lateralis</i>	X	X			X		X	X
7	<i>Rangia flexuosa</i>	X							
9	<i>Cyrtopleura costata</i>								X
7	<i>Martesia striata</i>					X			
	Number of species	23	5	2	4	22	6	13	24

TABLE 6. Sampling effort in the four studies that contributed to the species list.

Study	Lagoon region	Localities	Sampling method	Species
Hildebrand (1958)	north (only Boca Ciega)	4	beach seine, by hand	12
García-Cubas (1968)	north	34	van Veen grab, corer	36
Luna (2010)	center	19	Renfro, otter trawl	11
This study (1996)	north, center, south, Catán	75	Renfro, otter trawl	77

recorded throughout the lagoon, both along costa mar (Isla Mano de León, Isla Té, off Boca Ciega, La Mediación) and costa tierra (La Media Luna, Balsora, north of Ensenada de Barrancón, northeast of the San Fernando River delta, south of La Muela, west of Punta Algodones, north of Enramadas). The environmental characteristics of costa mar are stated above. The localities along costa tierra are different and are characterized by depths of 150 to 270 cm, mostly turbid water with temperatures of 20 to 30°C, salinities of 35 to 56‰, some *H. wrightii*, much macroalgae, and mostly muddy sediment (Appendix 1). The species with the greatest densities collected with this net were *Brachidontes exustus*, *Crassostrea virginica*, *Chione cancellata*, and *Mulinia lateralis*. The first two are epifaunal filter-feeding bivalves that settle on rocks and oysters in shallow brackish environments (the second is a “cementing” species), and the last two are infaunal filter-feeding bivalves that live in sand and mud in shallow habitats (Purchon, 1968; Stanley, 1970; Andrews, 1971; Reguero, 1994; García-Cubas and Reguero, 2007), all common habitats throughout the lagoon.

The gastropods and bivalves collected in Laguna Madre are common inhabitants of sandy substrates and submerged aquatic vegetation. The distribution of seagrasses in the largest coastal lagoons of the Mexican Gulf of Mexico has been observed by Raz-Guzmán and Barba (2000) to be regulated by salinity, turbidity, and type of substrate, indicating that changes in estuarine invertebrate populations may be associated with changes in the environmental conditions. The variety of habitats present in Laguna Madre increases the environmental heterogeneity and complexity that enhances the availability of a great number of microhabitats for soft-bottom and hard-substrate benthic dwellers (Tunnell and Judd, 2002). In agreement with this, previous studies have established the ecological relationship between species and habitat. They have shown that complex habitats harbor a high infaunal and epifaunal biodiversity (Raz-Guzmán and de la Lanza, 1993; Edgar et al., 1994; Heck et al., 1995; Boström and Bonsdorff,

2000), and have recognized the part that submerged aquatic vegetation plays in the recruitment of many invertebrates and fish in coastal lagoons (García-Cubas, 1981; Heck and Crowder, 1991; Reguero, 1994; Barba, 1999; Barba and Sánchez, 2005).

Temporal distribution.—Laguna Madre has two seasons in the year: dry (March to August) and rainy (September to February), with higher temperatures and salinities in spring and summer and lower values in autumn and winter. A similar number of species was recorded in August and December (50 and 53 respectively). However, August had more gastropod species (29) than December (19), and December had more bivalve species (33) than August (21). These differences might be caused by population shifts associated with the physico-chemical conditions in the environment, since during the winter water temperature decreases by $\pm 10^\circ\text{C}$ (Appendix 1), and water agitation induces

TABLE 7. Habitats and feeding habits of the Laguna Madre molluscs, as recorded in the literature (values are percentages [%] for the molluscs collected in this study).

	Gastropods	Bivalves	Chiton
Habitat			
Epifaunal	64	20	1
Infaunal	8	78	
Semi-infaunal	23		
Seagrass and macroalgae	32	9	
Sand	47	54	
Mud	32	26	
Rocks, shells	21	22	1
Wood		4	
Brackish	64	24	1
Marine	59	26	
Feeding			
Herbivore	19		1
Detritivore	19	9	
Filter feeder	8	91	
Carnivore	47		
Ectoparasite on molluscs	4		

TABLE 8. Presence of mollusc species in the lagoons of Términos (TE), Mecoaacán (ME), Tupilco-Ostión (TO), Carmen-Machona (CM), Sontecomapan (S), Alvarado-Buen País-Camaronera (ABC), Redonda-Mandinga (RM), La Mancha (LM), Chica-Grande (CG), Tampamachoco (TP), Tamiahua (TA), Pueblo Viejo (PV) and Madre (MA). Symbols: species with ° are present only in Laguna Madre; species with °° are present in the 13 Mexican lagoons; species present in Laguna Madre, Tamps. and Laguna Madre-Baffin Bay, TX, are those with + (for Montagna and Kalke, 1995) and = (for Tunnell and Alvarado, 1996). References: 1, Hildebrand (1958); 2, García-Cubas (1968); 3, García-Cubas (1969); 4, García-Cubas (1981); 5, Antolí and García-Cubas (1985); 6, Flores-Andolais et al. (1988); 7, Reguero and García-Cubas (1989); 8, García-Cubas et al. (1990); 9, García-Cubas and Reguero (1990); 10, Reguero and García-Cubas (1991); 11, Reguero et al. (1991); 12, García-Cubas et al. (1992); 13, Reguero and García-Cubas (1993a); 14, Reguero and García-Cubas (1993b); 15, García-Cubas and Reguero (1995); 16, Raz-Guzmán et al. (2001); 17, Luna (2010); 18, this study.

Species	Lagoons												
	TE	ME	TO	CM	S	ABC	RM	LM	CG	TP	TA	PV	MA
Gastropods													
<i>Lithopoma</i> sp.°													2
<i>Neritina usnea</i>	4,16	8			15	7,10,16	14	6	12	11		13	16,18
= <i>Neritina virginea</i> °°	4,16	8	9	5	15	7,10,16	14	6	12	11	3,16	13	16,18
<i>Smaragdia viridis</i>	4,16						14						16,18
= <i>Crepidula convexa</i>	4,16										16		16,18
= <i>Crepidula fornicata</i> +	4,16												16,18
= <i>Crepidula depressa</i>	4,16	8	9	5	15	10,16		6		11	3,16	13	16,18
= <i>Crepidula maculosa</i>	4,16												16,18
<i>Echinolittorina</i> sp.°													2
<i>Elachisina floridana</i>	4,16			5		7,16	14	6	12		3,16		16,18
<i>Texadina sphinctostoma</i>	4,16					7,10,16					3,16		2
<i>Tectonatica pusilla</i>				5									16,18
<i>Neverita delessertiana</i>	4,16				15							13	16,18
<i>Vitrinella floridana</i>											3,16		2
= <i>Caecum pulchellum</i> +	4,16										3,16		2
<i>Meioceras nitidum</i>	4,16										3,16		2
<i>Strombus alatus</i> °													17
<i>Modulus modulus</i>	4,16										3,16		16,18
<i>Cerithium atratum</i>	4,16												16,18
<i>Cerithium eburneum</i>	4,16												16,18
= <i>Cerithium lutosum</i> +	4,16							6			3,16		16,18
= <i>Bittolum varium</i> +	4,16	8		5	15	10,16	14	6	12	11		13	16,18
<i>Batillaria minima</i>	4,16												16,18
<i>Cerithideopsis costata</i>											3,16		2
= <i>Cerithideopsis pliculosa</i> °°	4,16	8	9	5	15	7,10,16	14	6	12	11	16	13	16,18
<i>Epitonium</i> sp.°													2
<i>Columbella mercatoria</i>	4,16												16,18
= <i>Costoanachis avara</i>	4,16		9		15					11			16,18
<i>Costoanachis semiplicata</i> +	4,16	8		5						11			16,18
= <i>Parvanachis obesa</i>	4,16									11	3,16		16,18
= <i>Astyris lunata</i>	4,16			5	15					11	3,16		16,18
<i>Busycoarctum coarctatum</i> °													16,18
<i>Busycon contrarium</i>	4,16												16,18
<i>Sinistrofulgur perversum</i>	4,16												1
<i>Fulguroopsis plagosa</i>	4,16			5									16,18
<i>Nassarius acutus</i> +	4,16	8	9	5	15	7,16	14			11	3,16		16,18
= <i>Phrontis vivex</i> +	4,16		9	5	15			6		11		13	16,18
<i>Cinctura branhami</i>	4,16												16,18
<i>Triplofusus giganteus</i>	4,16												16,18
<i>Oliva scripta</i> °													16,18
= <i>Pyrgocythara plicosa</i>	4,16			5		10,16		6		11		13	16,18
<i>Eulimastoma canaliculatum</i>											3,16		2
= <i>Odostomia bisuturalis</i> °													2
= <i>Turbonilla interrupta</i>	4,16	8	9	5		10,16				11	3,16		16,18

TABLE 8. Continued.

Species	Lagoons												
	TE	ME	TO	CM	S	ABC	RM	LM	CG	TP	TA	PV	MA
<i>Japonactaeon punctostriatus</i> +	4,16		9	5						11	3,16	13	16,18
= <i>Bulla striata</i>	4,16		9	5	15								16,18
= <i>Haminoea succinea</i>	4,16			5	15					11	3,16		16,18
= <i>Acteocina canaliculata</i> °	4,16	8	9	5	15	7,10,16	14	6	12	11	3,16	13	16,18
<i>Siphonaria pectinata</i>	4,16												1
Total	38	9	10	17	13	11	8	10	6	16	20	10	49
Bivalves													
= <i>Nuculana acuta</i>	4,16			5	15						3,16		16,18
<i>Arca imbricata</i>	4,16												16,18
= <i>Anadara transversa</i>	4,16	8			15	10,16		6	12	11	3,16	13	16,18
<i>Anadara scticostata</i>	4,16				15								16,18
<i>Lunarca ovalis</i>	4,16	8	9	5	15								16,18
<i>Arcopsis adamsi</i>				5				6					16,18
= <i>Noetia ponderosa</i>				5								13	16,18
= <i>Brachidontes exustus</i> +	4,16	8	9	5	15	7,16	14		12	11		13	16,18
= <i>Ischadium recurvum</i>	4,16	8	9	5		7,10,16	14	6	12	11	3,16	13	16,18
<i>Lithophaga nigra</i> °													16,18
= <i>Anomia simplex</i>	4,16			5	15	10,16					3,16		16,18
<i>Ostrea stentina</i>	4,16			5									16,18
<i>Crassostrea virginica</i>	4,16	8	9	5		7,10,16		6			3,16	13	16,18
= <i>Argopecten irradians</i> °													16,18
<i>Argopecten gibbus</i>				5									16,18
<i>Crassinella lunulata</i>	4,16		9	5						11	3,16		16,18
= <i>Cardites floridanus</i>	4,16												2
= <i>Phacoides pectinatus</i>	4,16	8	9	5	15	10,16		6	12	11			16,18
= <i>Kelliopsis texasiana</i>	16									11			16,18
<i>Trachycardium egmontianum</i> °													16,18
<i>Trachycardium isocardia</i>	4,16		9	5									16,18
<i>Dallocardia muricata</i>	4,16			5	15		14				3,16		16,18
= <i>Laevicardium mortoni</i> +	4,16	8	9	5							3,16		16,18
<i>Dinocardium robustum</i>	4,16	8	9	5									16,18
<i>Tellina radiata</i> °													16,18
<i>Laciolina laevigata</i>	4,16						14						16,18
<i>Euritellina angulosa</i>	4,16												16,18
= <i>Tampaella tampaensis</i> °+													16,18
<i>Ameritella mitchelli</i>	4,16	8							12	11		13	16,18
= <i>Tagelus divisus</i>	4,16		9	5	15		14			11	3,16		16,18
= <i>Abra aequalis</i>	4,16				15			6	12	11	3,16		16,18
= <i>Semele purpurascens</i>	4,16												16,18
= <i>Cumingia tellinoides</i>	4,16												2
<i>Macrocallista nimbosa</i> °													1
<i>Cyclinella tenuis</i>	4,16	8	9	5	15						3,16		16,18
= <i>Chione cancellata</i> +	4,16	8	9	5	15			6	12	11	3,16	13	16,18
<i>Lirophora obliterated</i>											3,16		2
<i>Anomalocardia puella</i> +	4,16		9	5		10,16			12	11			16,18
= <i>Mercenaria campechiensis</i>	4,16		9	5	15					11			16,18
= <i>Mactroma fragilis</i> °+													1
= <i>Mulinia lateralis</i> °°+	4,16	8	9	5	15	7,10,16	14	6	12	11	3,16	13	16,18
<i>Rangia flexuosa</i> °°	4,16	8	9	5	15	7,10,16	14	6	12	11	3,16	13	16,18
<i>Caryocorbula contracta</i>	4,16		9	5	15	10,16				11			16,18
= <i>Cyrtopleura costata</i>	4,16		9								3,16		16,18
<i>Martesia striata</i>	4,16		9		15			6					16,18
= <i>Lyonsia floridana</i> °													2
Total	34	13	19	24	17	10	7	10	10	15	16	9	46

TABLE 8. Continued.

Species	Lagoons												
	TE	ME	TO	CM	S	ABC	RM	LM	CG	TP	TA	PV	MA
Chiton													
= <i>Ichnochiton papillosus</i>	4,16												16,18
Total	1	0	0	0	0	0	0	0	0	0	0	0	1
Sum of species	73	22	29	41	30	21	15	20	16	31	36	19	96

suspension of sediment particles and turbidity increases.

Water temperature plays an important role in the workings of ecosystems through the regulation of other abiotic factors such as salinity, viscosity, gas and nutrient solubility, pH, Eh and surface tension. All these interactions in turn affect the physiological processes of the species, including metabolism, nutrition, growth, maturity, and reproduction, and thus the composition of the communities and the distribution of species in ecosystems (Fuentes and Massol-Deyá, 2002). Regarding molluscs, studies have proved that water temperature may affect how they obtain oxygen in three ways: 1) it increases metabolism and thus oxygen requirements, 2) it decreases oxygen solubility forcing the animals to pump more water through their gills to obtain the same amount of oxygen, and 3) it negatively affects the affinity between hemocyanin and oxygen (Brix et al., 2005). However, mollusc communities tend to remain stable, and this is the case of the species in Laguna Madre, most of which are eurythermal and euryhaline and, thus, eurytopic.

The temporal distribution of the Laguna Madre molluscs was analyzed only for the northern region of the lagoon. Gastropods were distributed throughout this region both in August and December, but with more species and greater densities along costa mar (Figs. 2, 4), similarly to the bivalves (Figs. 3, 5). The greater presence of species and specimens in this area reflects the close relationship that exists between the molluscs and the marine water that enters the lagoon through Boca de Mezquital and Boca Ciega (see Fig. 1), and emphasizes the marine origin of all mollusc species (Reguero, 1994). Another clear relationship is that between the molluscs and the *H. wrightii* seagrass beds, characteristic of this area, that provide an ideal habitat as nursery, feeding, and protection areas (Heck and Crowder, 1991; Boström and Bonsdorff, 2000).

Comparison of lagoons.—The mollusc species of 13 lagoons along the Mexican Gulf of Mexico were compared. Of the 96 species recorded here for Laguna Madre, 73 have been reported for Laguna de Términos. Fewer species are shared with Carmen-Machona (41), Tamiahua (36), Tampamachoco (31), Sontecomapan (30), Tupilco-Ostión (29), Mecoacán (22), Alvarado-Buen País-Camaronera (21), La Mancha (20), and Pueblo Viejo (19). The lagoons least similar to Laguna Madre regarding species composition are Chica-Grande (16) and Redonda-Mandinga (15) (Table 8).

The greater similarity between Laguna Madre and Laguna de Términos may respond to the intensity of sampling carried out in these two systems. Also, the spatial heterogeneity in both systems provides seagrass and macroalgae habitats, as well as hard substrates, where species may find nursery and feeding areas (Sánchez and Raz-Guzmán, 1997; Raz-Guzmán et al., 2001; Tunnell and Judd, 2002), and infaunal and epifaunal biodiversity may increase (Edgar et al., 1994; Heck et al., 1995; Boström and Bonsdorff, 2000).

On the other hand, it is surprising that Laguna Madre shares only 36 species with Laguna de Tamiahua, considering that they are environmentally very similar, with *H. wrightii* seagrass beds along costa mar and macroalgae along costa tierra, and that Cabo Rojo (the island barrier of Tamiahua) presents a boundary for the northern dispersal of tropical shallow water fauna (Thurman, 1987). This should lead one to expect a similar mollusc species composition in these two systems, as in fact occurs in the case of crustaceans (Raz-Guzmán and Sánchez, 1998; Raz-Guzmán et al., 2001; Cid and Raz-Guzmán, 2011).

Regarding the species, seven gastropods and eight bivalves (15 species, marked in Table 8 with °) have been recorded only for Laguna Madre (*Lithopoma* sp., *Echinolittorina* sp., *Strombus alatus*, *Epitonium* sp., *Busycoarctum coarctatum*, *Oliva scripta*, *Odostomia bisuturalis*, *Lithophaga nigra*,

Argopecten irradians, *Trachycardium egmontianum*, *Tellina radiata*, *Tampaella tampaensis*, *Macrocallista nimbosa*, *Mactroma fragilis*, *Lyonsia floridana*). This may be due to most of these species having a high affinity for low-temperature, highsalinity environments, typical in this lagoon, as well as the lagoon's location in a transition area between the Transatlantic and Caribbean provinces, which favors the presence in the system of malacological fauna of these two provinces. In contrast, only three gastropods and two bivalves (five species, marked in Table 8 with °) have been recorded for the 13 lagoons (*Neritina virginea*, *Cerithideopsis pliculosa*, *Acteocina canaliculata*, *Mulinia lateralis*, *Rangia flexuosa*), and this may correspond to the fact that these species tolerate the wide ranges of temperature and salinity values that are common in estuarine systems.

A comparison was also carried out between Laguna Madre in Tamaulipas and Laguna Madre–Baffin Bay in Texas, for which several publications were consulted and two were selected considering that sampling took place around the same time.

Montagna and Kalke (1995) identified 26 mollusc species, of which 16 were gastropods and 10 were bivalves. They recorded the greater number of species in Laguna Madre, TX, in high-salinity areas and seagrass beds, and fewer species in the open bay habitats of Baffin Bay. Comparing the 96 species recorded for Laguna Madre, Tamaulipas, with the 26 species recorded for Laguna Madre–Baffin Bay, TX; 15 species (eight gastropods and seven bivalves, marked in Table 8 with +) are present in the two coastal systems. This low number of shared species may be the result of the Texas molluscs including only infaunal species, the lack of seagrass habitats in Baffin Bay and sampling during a brown tide event. In contrast, Laguna Madre, Tamps. receives little runoff from the San Fernando River, which generates a euhaline–hypersaline environment that favors the recruitment of the mostly marine mollusc species. The other notable difference between these two systems has to do with in the dominant species, as *Bittium varium*, *Costoanachis semiplicata*, *Brachidontes exustus*, *Crassostrea virginica*, *Chione cancellata*, and *Mulinia lateralis* were dominant in Laguna Madre, Tamps. and *Haminoea antillarum* (Orbigny, 1841) and *Mulinia lateralis* were dominant in Laguna Madre–Baffin Bay, TX.

In contrast with the previous case, Tunnell and Alvarado (1996) recorded 70 species (35 gastro-

pod and 35 bivalve), most of which were collected from seagrass beds, followed by bay bottoms and lastly tidal flats, confirming the advantages that seagrass beds provide benthic species. When the 95 species (49 gastropod and 46 bivalve) recorded for Laguna Madre, Tamps. were compared with the 70 species recorded by these authors for Laguna Madre–Baffin Bay, TX, 41 species were seen to be present in both areas (19 gastropods and 22 bivalves, marked in Table 8 with =). The chiton *Ischnochiton papillosus* was also recorded in both areas, bringing the total of shared species to 42. This higher number of shared species compared with those of the previous case reflects a more natural situation for the Texas coastal systems as the element of the brown tide was not present, together with the great number of publications from which the species list was compiled.

Systematic studies and inventories of living resources contribute to the knowledge of the natural capital of a country, particularly in developing countries where economic and social needs impinge on the integrity of natural ecosystems. They also support basic research that makes possible a solid perception of probable modifications to an ecosystem, as well as the design of holistic ecological models for the planning of sustainable management strategies that include the rational use and preservation of natural systems, among which estuaries are particularly rich as they play the part of bridges between watersheds and the sea. Considering that the sampling on which this study was based took place 20 yr ago, it becomes possible to establish a baseline from which future studies may compare the biodiversity in the lagoon and its state of conservation, identify changes in hydrologic conditions, and judge potential socioeconomic effects in the area. Of note is that, at the time of the study, the hydrologic and biotic integrity of the system was threatened by a proposal to construct an intracoastal canal which, fortunately, did not take place. For molluscs, thus, it is considered important that a management plan be implemented for the conservation of their habitats, taking into account their ecological relevance in trophic chains and their potential use in aquaculture.

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APPENDIX. Locality number (Loc no.), depth (cm), visibility (Visib, cm), water temperature (Temp, °C), salinity (Sal, ‰), submerged aquatic vegetation (SAV: Hal, *Halodule wrightii*; MA, macroalgae), sampling net (R, Renfro; OT, otter trawl) and manual for the Laguna Madre localities sampled in August and December 1996, where molluscs were collected (—, no data).

Locality and date	Loc no.	Depth	Visib	Temp	Sal	SAV	Net
August 2							
North of Isla Coyota	3	—	—	32	41	Hal	manual
Off Isla Venados along costa mar	5	110	—	31	37	Hal, MA	OT
August 3							
North of Enramadas	9	150	—	29	44	Hal, MA	OT
Punta La Yegua	11	100	—	30	42	MA	R
La Mediación	16	150	20	28	35	Hal, MA	OT
Punta Algodones	17	150	15	30	37	MA	OT
August 4							
North of Boca de Catán	18	150	20	30	40	MA	OT
South of La Muela	20	—	30	29	45	Hal, MA	OT
Off Los Legales	21	150	35	28	50	MA	OT
Off Isla del Perro	24	40	20	32	55	MA	R
El Árbol	28	—	15	—	—	Hal	manual
West of Punta Algodones	30	150	20	30	45	Hal	OT
Off Boca de Catán	31	150	—	28	33	MA	OT
August 6							
Isla La Quemada	33	30	10	29	53	Hal, MA	R
Isla La Quemada	33	120	10	29	53	Hal, MA	OT
Poza San Juan	35	120	20	29	50	Hal, MA	R
Poza San Juan	35	175	26	29	51	—	OT
South of Buenavista	36	30	5	30	51	—	R
South of Buenavista	36	90	15	29	53	—	OT
Isla Larga	39	175	30	31	40	MA	OT
Isla del Padre	40	130	30	31	51	MA	OT
Isla Mano de León	41	30	30	35	47	MA	R
Off Mezquital	42	30	15	31	39	Hal, MA	R
August 7							
South of Isla La Quemada	44	300	—	28	—	—	OT
La Media Luna	47	270	—	29	45	MA	OT
South of Balsora	49	270	25	30	41	—	OT
North of Ensenada de Barrancón	50	210	35	30	45	MA	OT
Ensenada de Barrancón	52	40	10	32	46	Hal	R
North of Barrancón	53	180	40	30	44	MA	OT
Northeast of the Río San Fernando delta	55	210	50	30	56	MA	OT
Off Boca Ciega	57	90	90	34	52	MA	R
Southwest of San Juan	60	70	70	33	46	Hal, MA	R
Between San Juan and Buenos Aires	61	280	30	30	47	Hal	OT
Buenos Aires	62	40	40	32	47	MA	R
August 9							
Isla Té	63	200	25	30	46	MA	OT
El Rastro	64	—	—	—	—	—	manual
Isla Cortitas	67	100	25	28	42	MA	OT
South of Isla Los Federales	71	80	30	28	54	—	R
Northeast of Isla Cortitas	73	100	35	29	48	MA	OT
Off El Rastro along costa mar	74	—	—	—	—	—	manual
Off El Rastro along costa mar	75	100	30	30	34	—	OT
December 6							
La Media Luna	2	170	60	20	40	Hal, MA	OT
Balsora	3	235	60	20	39	Hal, MA	OT
Off Boca Ciega	4	200	50	20	39	Hal, MA	OT
Off Boca Ciega	5	70	70	22	37	Hal, MA	R
Buenos Aires	7	120	120	21	39	Hal, MA	R

APPENDIX. Continued.

Locality and date	Loc no.	Depth	Visib	Temp	Sal	SAV	Net
Poza San Juan	8	120	15	23	34	Hal, MA	OT
Boca de Mezquital	9	100	15	22	38	Hal, MA	R
Isla Té	10	200	10	21	40	Hal, MA	OT
Isla Mano de León	11	150	10	22	36	Hal, MA	OT