Research Article

Bivalves and Gastropods of the Gulf of Tehuantepec, Mexico: A Checklist of Species with Notes on Their Habitat and Local Distribution

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The taxonomic composition of 160 species of bivalves and gastropods recorded in the Gulf of Tehuantepec is presented with information on their habitat and distribution along 10 different localities of the shoreline and 42 stations of the continental shelf. The species were on sandy and rocky beaches, coastal lagoons, estuaries, mangroves, rocky breakwaters of ports, and shallow subtidal areas (14–47 m depth). A total of 78 bivalve species and 82 gastropod species were recorded. Most of these were associated with sandy and rocky beaches and breakwaters of ports. The estuaries host 30 species and the coastal lagoons only two. In the shallow subtidal there were 18 gastropod species and 40 bivalve species representing 36.3% of all. This study adds 24 bivalve species and 29 gastropod species not recorded in previous studies for a total count of 213 species (102 bivalves and 111 gastropods) for Gulf of Tehuantepec.

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1. Introduction

The tropical coastal environments are the most biologically diverse of all marine ecosystems but are being degraded worldwide by human activities potentially leading to numerous extinctions. Conservation efforts targeted toward them could help averting the loss of tropical biodiversity. However, the sustainable use of coastal living resources cannot be properly established without an adequate knowledge of the biodiversity. The molluscs are among the most diverse invertebrates in the coastal tropical environments and the vast majority are found intertidally, in estuaries and coastal lagoons, and in the shallow areas on the continental shelf [1, 2].

The first complete inventory of the subtropical and tropical malacological fauna of the western America is the huge monograph of Keen [3] which comprises approximately 3340 mollusc species, most of them bivalves and gastropods. Other catalogues also include the species of molluscs from

the Mexican Pacific [4–6] and the revisions of the species from the Panamic Province made by Skoglund [7, 8] provide updated information including new species, redefinitions of taxonomic relationships, new records, and their geographic distributions. However, most of the literature on the molluscs from the Mexican Pacific refers to benthic communities of the Gulf of California [2, 9–16].

The molluscan fauna of the southernmost region of the Tropical Mexican Pacific has received little attention. The first inventories of molluscs from the Gulf of Tehuantepec were performed in the 1980s. Most of this research is included in not easily accessible technical reports and theses [17–19] or refers to specific localities and environments of the coast of Oaxaca [20, 21]. More complete lists of species from this region are found in two different catalogues, one for the coast of Oaxaca, mainly from rocky and sandy beaches and from shallow subtidal areas as far as 39 m depth [22], and another one for the coast of Chiapas, collected in 10 different shoreline locations [23].

FIGURE 1: The Gulf of Tehuantepec and sampling localities.

The present study deals with the species of bivalves and gastropods found in the most representative environments of the Gulf of Tehuantepec and includes a checklist of species with information on their habitat and distribution along 10 different localities of the shoreline and 42 stations of the shallow subtidal of the continental shelf. This list is an attempt to both provide a more complete inventory of the mollusc fauna of this region and update the taxonomic names including all synonymies and nomenclatural changes. In addition, the material collected was deposited in two replicate reference collections, one at the Universidad de Guadalajara in Jalisco and the other one at El Colegio de la Frontera Sur (ECOSUR) in Tapachula, Chiapas, Mexico.

2. Methods

The Gulf of Tehuantepec is located in the southeast part of the Mexican Pacific and extends from Puerto Angel, Oaxaca, to the Suchiate River in Chiapas, which is the limit between Mexico and Guatemala (Figure 1). This region has nearly 420 km of shoreline and covers an approximate area of 100 000 km² [24]. The region has a tropical warm subhumid climate with average annual temperature close to 26°C and numerous summer rains (annual rainfall = 2500–3000 mm) making this region one of the wettest of Mexico [25]. Strong seasonal winds, the “Tehuantepec winds,” and hurricanes cause high surf and waves during this period of the year [26]. Long sandy beaches extend to the edge of the continental shelf in a relatively homogeneous geological

and geomorphological region with the sediments of the sand shores and the shelf mostly composed of medium sands, moderately well sorted presenting similar granulometry and mineralogical composition [27]. There is a complex hydrological system along the coastal plains with permanent rivers and temporal streams that form extensive coastal lagoons and estuaries with well-developed mangrove forest communities.

To perform the inventory of the gastropod and bivalve molluscs of the region, samplings and collections were performed from April to December of 2004 in two different types of locations: (a) 10 localities on the shoreline of the Gulf and (b) 55 stations on the continental shelf (Figure 1). In the localities of the shoreline, the field work was performed through direct search during excursions along the different environments and types of habitats of each locality. In the sandy beaches, the shells were collected along the shoreline from the intertidal and the supralittoral areas up to the beach berm and sand dunes where the molluscs frequently concentrate in shell deposits. Similarly, collection of shells was also performed from the sand barriers of the estuaries usually oriented shore-parallel and connected to the ocean by one or more restricted inlets.

In the subtidal area of the continental shelf, the molluscs were obtained on board of the shrimp vessel FIPESCO-63 of the Instituto Nacional de la Pesca of the Mexican Government with a “semi-Portuguese” shrimp trawl net (length = 24.4 m, mesh size = 50.8 mm). Trawls were performed over 55 sampling stations at depths between 14

and 65 m. The average trawling time was of 61.56 min with an average speed of the vessel of 60.80 m/min and an average distance covered during each trawl of 3735.5 m. The total sampled area covered by the vessel was 330 km², from station 19 located in the southeast end to station 35 in the northeast end.

All shells were washed with tap water, labeled, and stored in plastic bags in the laboratory (Laboratorio de Ecología de Manglares of the El Colegio de la Frontera Sur (ECOSUR) in the city of Tapachula, Chiapas). The living molluscs were also washed and the soft parts of the organisms were extracted, leaving only the shells for taxonomic identification; in some cases, the remnants of the adhered epibiota were removed.

The taxonomic identification of the species was performed using specialized bibliography [3–6, 30–33] and some mollusc catalogues of the region [22, 23, 34]. The taxonomic position of the species was updated according to the revisions of Skoglund [7, 8]. The orders and families of gastropods were arranged according to Bouchet and Rocroi [28]; the orders are equivalent to the higher categories of the clades used by these authors.

3. Results

The bivalves and gastropods were registered in all shoreline localities and in 42 of the 55 subtidal stations of the continental shelf at depths between 14 and 47 m. The bivalves belong to 7 orders, 23 families, and 78 species, and the gastropods belong to 5 orders, 33 families, and 82 species (Table 1). Most of the species (120) were collected in the shoreline localities (68 bivalves and 52 gastropods), and only 58 species (18 bivalves and 40 gastropods) were collected from the continental shelf. The number of species per family varies considerably (1 to 18 species). Seven families of bivalves (30.4%) and 15 families of gastropods (45.5%) are represented by one single species; the most diverse families of bivalves are Veneridae (18 species), Arcidae (8), and Tellinidae (7) and the most diverse families of gastropods are Calyptraeidae (12), Muricidae (9), and Fissurellidae (6).

A large majority of species of the bivalves and gastropods collected from the shoreline locations of the Gulf are associated with sandy (71) and rocky (55) substrata of beaches and breakwaters of ports (Table 2). The estuaries host 30 species and only two are exclusive of the coastal lagoons. Many species of bivalves (18) and gastropods (40) are associated with the sea bottom of the continental shelf, representing the 36.3% of all the species found.

In general, the localities with more than one type of habitat have a larger number of species. More species of bivalves and gastropods were recorded in the estuaries of Suchiate, Cahoacán, and Boca de Cielo (sandy beach and mangrove) than in La Encrucijada, La Joya Buenavista, and Chocohuitl (mangrove). These shallow water bodies contain a distinctive group of species, some living on the roots of the red mangrove *Rizophora mangle* but most of them associated to the sandy and muddy substrata, sometimes forming aggregations of individuals as in the case of the so-called “pata de mula” clams (*Anadara* spp.).

The bivalves found in the Gulf of Tehuantepec are typically associated to soft substrata. In particular the semi-infaunal and infaunal forms were mostly found in the sandy beaches or in the muddy or sandy areas of the mangrove estuaries and lagoons but many of these species were also recorded in the shallow subtidal stations on the continental shelf. Since the shells of most bivalves which live in the shallow subtidal areas are washed onto the shore and become incorporated into sand beach as shell deposits, many species reported here separately in the sandy beaches and in the shallow subtidal coincide in both habitats. These bivalves comprise a prolific assemblage of species living in the tidal and subtidal parts of the sandy shores.

Although the adding of shells washed up on a sandy beach into a sandy beach assemblage not accurately represents the living fauna in the sandy beach habitat, there is a characteristic assemblage that certainly includes many species that extend their distribution through the intertidal zone and may be considered inhabitants of the sandy beaches. In this group the chiones and tivelas, and the species of *Cardites*, *Divalinga*, *Pitar*, *Chione*, *Mulinia*, *Donax*, and *Sanguinolaria* frequently are found in the sandy beaches of the Gulf of Tehuantepec. Among the gastropods, the Naticidae and Nassariidae include species living in the tidal areas of sand beaches and bars; also the olives are common on intertidal or shallow subtidal sandy substratum.

A few epifaunal bivalves live adhered to the mangrove roots of estuaries and coastal lagoons or to the rocky beaches or breakwaters of ports. This group includes the mussels *Choromytilus palliopunctatus*, *Mytella guyanensis*, *M. speciosa*, and *M. strigata*, the oysters *Saccostrea palmula*, *Striostrea prismatica*, *Isognomon janus*, and *I. recognitus*, and the thorny chama *Chama echinata*. Other epifaunal bivalves recorded in the continental shelf are the pearl oyster *Pinctada mazatlanica*, the scallops *Argopecten ventricosus*, and *Leptopecten tumbezensis* and the lime oyster *Spondylus limbatus*. Odd valves, more frequently the unattached valve of mussels, oysters, and scallops, were also found in the sandy beaches.

Gastropods found in the Gulf are mostly associated to the marine environment. Forty species were collected during the shrimp trawls on the continental shelf at depths between 14 and 47 m, or in rocky (33 spp.) and sandy beaches (16 spp.) of the shoreline localities. Only 19 species of gastropods are associated to estuarine habitats, and particularly to the mangrove forest of the estuaries.

Considerable changes in species composition of bivalves and gastropods occur between localities and habitats with many species being exclusive of one type of habitat. Uncommon species (frequency of occurrence less than 25% in the localities with the same type of habitat) comprised 71.16% of all the species found in the Gulf. Approximately 64% occurred in only one type of habitat and were considered habitat-exclusive (Table 3). In the estuaries and coastal lagoons, the habitat-exclusive species formed only 5%, including those associated to mangroves.

The nine species that are exclusive to the mangrove habitat were recorded alive; among these, the painted nerite *Theodoxus luteofasciatus*, the banded periwinkle *Littorina*

TABLE 1: Bivalves and gastropods of the Gulf of Tehuantepec, Mexico. Systematic classification according to Keen [3], modified by Skoglund [7, 8]. The orders (= clades) and families of gastropods according to Bouchet and Rocroi [28]. * : species not recorded in previous studies of the Gulf of Tehuantepec. Numbers between parentheses () indicate the localities where the species were recorded according to the list of Table 2. The depth range in meters is indicated between squared brackets [] for those species collected in the continental shelf. SB: sandy beach; M: mangrove; CL: coastal lagoon; RB: rocky beach, CS: continental shelf.

Phylum Mollusca	
Class Bivalvia	
Order Nuculanoida	
Family Nuculanidae	
<i>Nuculana polita</i> (G.B. Sowerby I, 1833) (1,2,6) SB	
Order Arcoida	
Family Arcidae	
<i>Anadara aequatorialis</i> (D' Orbigny, 1846) (2,3,6) SB, RB	
<i>Anadara bifrons</i> (Carpenter, 1857)* (1,2,3) SB	
<i>Anadara grandis</i> (Broderip & G. B. Sowerby I, 1829) (2,4,6) SB, M, RB	
<i>Anadara nux</i> (G.B. Sowerby I, 1833)* (1) SB	
<i>Anadara obesa</i> (G.B. Sowerby I, 1833) (1,2,3,6) SB, CS [17–40]	
<i>Anadara perlabiata</i> (Grant & Gale, 1931) (1,3) SB	
<i>Anadara reinhardtii</i> (Lowe, 1935)* (11) CS [46]	
<i>Lunarca brevifrons</i> (G.B. Sowerby I, 1833) (1,2,3) SB	
Family Noetiidae	
<i>Noetia reversa</i> (G.B. Sowerby I, 1833)* (1,2,3,6) SB, CS [17–40]	
Family Glycymerididae	
<i>Glycymeris maculata</i> (Broderip, 1832)* (10,11) RB, CS [18]	
Order Mytiloida	
Family Mytilidae	
<i>Choromytilus palliopunctatus</i> (Carpenter, 1857) (3,7) RB, M	
<i>Mytella guyanensis</i> (Lamarck, 1819) (2,5,6,8,9,10) SB, M, RB	
<i>Mytella speciosa</i> (Reeve, 1857)* (6) M	
<i>Mytella strigata</i> (Hanley, 1843) (4,5,7) M	
Order Pterioidea	
Family Pteridae	
<i>Pinctada mazatlanica</i> (Hanley, 1856) (11) CS [19]	
Family Isognomonidae	
<i>Isognomon janus</i> Carpenter, 1857 (6) SB, M	
<i>Isognomon recognitus</i> (Mabille, 1895) (2,6) SB, M	
Family Ostreidae	
<i>Saccostrea palmula</i> (Carpenter, 1857) (1,2,3,6,8) SB, M, RB	
<i>Striostrea prismatica</i> (Gray, 1825)* (3,6,11) SB, M, RB, CS [17]	
<i>Myrakeena angelica</i> (Rochebrune, 1895)* (3) RB	
Family Pectinidae	
<i>Argopecten ventricosus</i> (G. B. Sowerby II, 1842) (11) CS [14–47]	

TABLE 1: Continued.

Phylum Mollusca	
<i>Leptopecten tumbezensis</i> (D' Orbigny, 1846)* (3) SB	
Family Spondylidae	
<i>Spondylus limbatus</i> G.B. Sowerby II, 1847 (11) CS [28]	
Order Veneroida	
Family Carditidae	
<i>Cardites laticostata</i> (G.B. Sowerby I, 1833) (1,2,3) SB	
Family Corbiculidae	
<i>Polymesoda inflata</i> (Philippi, 1851) (1,4,6) SB, M	
<i>Polymesoda meridionalis</i> (Prime, 1869) (1) SB	
Family Lucinidae	
<i>Ctena mexicana</i> (Dall, 1901)* (10) RB	
<i>Divalinga eburnea</i> (Reeve, 1850) (2) SB	
<i>Luciniscia fenestrata</i> (Hinds, 1845) (1) SB	
<i>Parvilucina approximata</i> (Dall, 1901)* (2,6) SB	
<i>Pegophysema edentuloides</i> (Verrill, 1870) (11) CS [17]	
Family Ungulinidae	
<i>Diplodonta sericata</i> (Reeve, 1850)* (1,2,6,8,9) SB, RB	
Family Chamidae	
<i>Chama echinata</i> Broderip, 1835 (10) RB	
Family Cardiidae	
<i>Americardia biangulata</i> (Broderip & G.B. Sowerby I, 1829)* (10) RB	
<i>Laevicardium clarionense</i> (Hertlein & Strong, 1947)* (10) RB	
<i>Trachycardium consors</i> (G.B. Sowerby I, 1833)* (10) RB	
<i>Trachycardium panamense</i> (G.B. Sowerby I, 1833) (1,2,11) SB, CS [28]	
<i>Trachycardium procerum</i> (G.B. Sowerby I, 1833)* (11) CS [20]	
<i>Trachycardium senticosum</i> (G.B. Sowerby I, 1833) (1,2,3,6) SB	
<i>Trigoniocardia obovalis</i> (G.B. Sowerby I, 1833) (1,2,10) SB, RB	
Family Veneridae	
<i>Chione amathusia</i> (Philippi, 1844) (1,2,10) SB, RB, CS [17]	
<i>Chione pulicaria</i> (Broderip, 1835)* (11) CS [17–43]	
<i>Chione subimbricata</i> (G.B. Sowerby I, 1835)* (10) RB	
<i>Chione subrugosa</i> (Wood, 1828) (6,9,10) SB, RB	
<i>Chione undatella</i> (G.B. Sowerby I, 1835) (2) SB	
<i>Cyclinella saccata</i> (Gould, 1851)* (11) CS [17]	
<i>Dosinia dunkeri</i> (Philippi, 1844) (6, 9) SB, RB	
<i>Dosinia ponderosa</i> (Schumacher, 1817) (11) CS [17–46]	
<i>Periglypta multicostata</i> (G.B. Sowerby I, 1835)* (11) CS [17]	
<i>Pitar concinnus</i> (G.B. Sowerby I, 1835) (1) SB	
<i>Pitar lupanaria</i> (Lesson, 1830) (1,2,6) SB	
<i>Pitar roseus</i> (Broderip & G.B. Sowerby I, 1829) (1,2,3) SB	
<i>Pitar tortuosus</i> (Broderip, 1835)* (2) SB	
<i>Protothaca asperrima</i> (G.B. Sowerby I, 1835) (2,9) SB, CL	
<i>Protothaca macgintyi</i> (Olsson, 1961)* (1,2,3) SB	
<i>Protothaca metodon</i> (Pilsbry & Lowe, 1932) (1) SB	
<i>Tivela byronensis</i> (Gray, 1838) (2,3,6,10) SB, RB	
<i>Tivela delessertii</i> (Sowerby, 1854) (10) RB	

TABLE 1: Continued.

Phylum Mollusca	
Family Mactridae	
<i>Harvella elegans</i> (Sowerby, 1825) (1,2,3,6,7) SB, CS [17]	
<i>Mactrellona exoleta</i> (Gray, 1837) (6,8) SB	
<i>Mulinia pallida</i> (Broderip & G.B. Sowerby I, 1829) (1,2,3,6) SB	
Family Tellinidae	
<i>Macoma lamproleuca</i> (Pilsbry & Lowe, 1932) (6,11) SB, CS [17]	
<i>Strigilla chroma</i> Salisbury, 1934 (1,2,6) SB	
<i>Strigilla dichotoma</i> (Philippi, 1846) (6) SB	
<i>Tellina insculpta</i> Hanley, 1844 (1) SB	
<i>Tellina decumbens</i> Carpenter, 1865 (1,2,6) SB	
<i>Tellina prora</i> (Hanley, 1844)* (2, 6) SB	
<i>Tellina virgo</i> Hanley, 1844 (1) SB	
Family Donacidae	
<i>Donax asper</i> Hanley, 1845 (1) SB	
<i>Donax carinatus</i> Hanley, 1843 (1,2,6) SB	
<i>Donax gracilis</i> Hanley, 1845 (6) SB	
<i>Donax kindermanni</i> (Philippi, 1847) (1,2,3,6) SB	
<i>Donax punctatostriatus</i> Hanley, 1843 (1,2,3,6,8,10) SB, RB	
Family Psammobiidae	
<i>Sanguinolaria bertini</i> (Pilsbry & Lowe, 1932) (1,2,3) SB	
Family Solecurtidae	
<i>Tagelus longisinuatus</i> Pilsbry & Olsson, 1932 (2,9) CL	
<i>Tagelus politus</i> (Carpenter, 1857)* (2,3,6) SB, M	
Order Pholadomyoidea	
Family Periplomatidae	
<i>Periploma planiusculum</i> (Sowerby, 1834) (1,2) SB	
Class Gastropoda	
Order Patellogastropoda	
Family Lottiidae	
<i>Lottia mesoleuca</i> (Menke, 1851)* (3) RB	
<i>Lottia mitella</i> (Menke, 1847)* (3) RB	
<i>Lottia pediculus</i> (Philippi, 1846) (10) RB	
Order Vetigastropoda	
Family Fissurellidae	
<i>Diodora inaequalis</i> G.B. Sowerby I, 1835 (3) SB	
<i>Diodora saturnalis</i> (Carpenter, 1864)* (10) RB	
<i>Fissurella decemcostata</i> McLean, 1970 (10) RB	
<i>Fissurella microtrema</i> G.B. Sowerby I, 1835* (10) RB	
<i>Fissurella rubropicta</i> Pilsbry, 1890 (10) RB	
<i>Fissurella spongiosa</i> Carpenter, 1857* (10) RB	
Order Neritimorpha	
Family Neritidae	
<i>Nerita funiculata</i> Menke, 1851 (6) SB	
<i>Theodoxus luteofasciatus</i> (Miller, 1879) (2,4,7) M	
Order Caenogastropoda	
Family Littorinidae	
<i>Littorina fasciata</i> Gray, 1839* (2,6,7,10) M	
Family Turritellidae	
<i>Turritella banksi</i> Reeve, 1849* (11) CS [28]	
<i>Turritella leucostoma</i> Valenciennes, 1832 (10,11) RB, CS [28]	

TABLE 1: Continued.

Phylum Mollusca	
Family Modulidae	
<i>Modulus catenulatus</i> (Philippi, 1849) (6,9) M, RB	
Family Vermetidae	
<i>Serpulorbis margaritaceus</i> (Chenu, 1844)* (10) RB	
Family Cerithiidae	
<i>Cerithium stercusmuscarum</i> Valenciennes, 1833 (6,9) M, RB	
Family Potamididae	
<i>Cerithidea californica mazatlanica</i> Carpenter, 1857* (5) M	
<i>Cerithidea valida</i> (C.B. Adams, 1852) (6) M	
Family Hipponicidae	
<i>Pilosabia pilosa</i> (Deshayes, 1832) (10) RB	
Family Calyptraeidae	
<i>Calyptraea conica</i> Broderip, 1834 (10) RB	
<i>Calyptraea mamillaris</i> Broderip, 1834 (2,6,11) SB, CS [17]	
<i>Crepidula aculeata</i> (Gmelin, 1791)* (10) RB	
<i>Crepidula excavata</i> (Broderip, 1834) (1,10,11) SB, RB, CS [28–46]	
<i>Crepidula lessoni</i> (Broderip, 1834)* (3, 10) RB	
<i>Crepidula onyx</i> Sowerby, 1824 (9) RB	
<i>Crepidula striolata</i> Menke, 1851 (1,6,9,11) SB, M, RB, CS [41]	
<i>Crucibulum lignarium</i> (Broderip, 1834) (6,11) SB, CS [18–37]	
<i>Crucibulum personatum</i> Keen, 1958* (11) CS [18–44]	
<i>Crucibulum scutellatum</i> (Wood, 1828) (10,11) RB, CS [18]	
<i>Crucibulum spinosum</i> (Sowerby, 1824) (1,2,11) SB, CS [18–40]	
<i>Crucibulum umbrella</i> (Deshayes, 1830) (10) RB	
Family Naticidae	
<i>Natica chemnitzii</i> Pfeiffer, 1840* (6,9) M, RB	
<i>Natica elenae</i> Récluz, 1844* (11) CS [42]	
<i>Sinum cymba</i> (Menke, 1828) (1) SB	
Family Cypraeidae	
<i>Mauritia arabicula</i> (Lamarck, 1811) (10) RB	
Family Tonnidae	
<i>Malea ringens</i> (Swainson, 1822) (11) CS [18–44]	
<i>Tonna sp.</i> (11) CS [25–46]	
Family Ficidae	
<i>Ficus ventricosa</i> (Sowerby, 1825) (10) RB	
Family Ranellidae	
<i>Cymatium wiegmanni</i> (Antón, 1839) (6,11) SB, M, CS [17–41]	
Family Personidae	
<i>Distorsio decussata</i> (Valenciennes, 1832) (11) CS [33–42]	
Family Bursidae	
<i>Bursa corrugata corrugata</i> (Perry, 1811) (11) CS [20]	
<i>Marsupina nana</i> (Broderip & G.B. Sowerby I, 1829)* (11) CS [32]	
Family Muricidae	
<i>Acanthais brevidentata</i> (Wood, 1828)* (10) RB	
<i>Hexaplex brassica</i> (Lamarck, 1822) (11) CS [16–46]	
<i>Murex recurvirostris</i> Broderip, 1833* (11) CS [47]	
<i>Muricanthus nigratus</i> (Philippi, 1845)* (11) CS [18–30]	
<i>Muricanthus radix</i> (Gmelin, 1791) (11) CS [14–20]	
<i>Stramonita biserialis</i> (Blainville, 1832)* (3,6) M, RB	
<i>Stramonita chocolata</i> (Duclos, 1832)* (6) M	

TABLE 1: Continued.

Phylum Mollusca	
<i>Thais kiosquiformis</i> (Duclos, 1832) (1,6,11) SB, M, CS [17]	
<i>Thais triangularis</i> (Blainville, 1832) (10) RB	
Family Buccinidae	
<i>Cantharus ringens</i> (Reeve, 1846)* (10) RB	
<i>Cantharus sanguinolentus</i> (Duclos, 1833)* (10) RB	
<i>Engina jugosa</i> (C.B. Adams, 1852)* (10) RB	
<i>Northia northiae</i> (Griffith & Pidgeon, 1834) (11) CS [17–26]	
<i>Phos crassus</i> Hinds, 1843 (11) CS [20]	
Family Columbellidae	
<i>Costoanachis nigricans</i> (Sowerby, 1844)* (6) M	
Family Melongenidae	
<i>Melongena patula</i> (Broderip & G.B. Sowerby I, 1829) (11) CS [16–41]	
Family Nassariidae	
<i>Nassarius bailyi</i> (Pilsbry & Lowe, 1932) (6) SB	
<i>Nassarius luteostoma</i> (Broderip & G.B. Sowerby I, 1829)* (6, 9) SB, M, RB	
<i>Nassarius wilsoni</i> (C.B. Adams, 1852)* (9) RB	
Family Fasciolaridae	
<i>Fusinus dupetitthouarsi</i> (Kiener, 1840) (11) CS [14–47]	
<i>Pleuroploca granosa</i> (Sowerby, 1825)* (11) CS [16–46]	
Family Harpidae	
<i>Harpa crenata</i> Swainson, 1822 (11) CS [26–46]	
Family Olividae	
<i>Agaronia propatula</i> (Conrad, 1849) (6) SB, M	
<i>Oliva incrassata</i> Lightfoot, 1786 (5,11) M, CS [18–29]	
<i>Oliva polpasta</i> Duclos, 1833 (5,11) M, CS [28–42]	
<i>Oliva splendidula</i> Sowerby, 1825* (11) CS [19–42]	
Family Olivellidae	
<i>Olivella volutella</i> (Lamarck, 1811) (308) SB, M, RB	
<i>Olivella zanoeta</i> (Duclos, 1835) (50) SB, M	
Family Vasiidae	
<i>Vasum caestus</i> (Broderip, 1833)* (11) CS [18]	
Family Mitridae	
<i>Mitra swainsoni</i> Broderip, 1836* (11) CS [46]	
Family Cancellaridae	
<i>Cancellaria obesa</i> (Sowerby, 1832)* (11) CS [26]	
<i>Cancellaria solida</i> Sowerby, 1832* (11) CS [18]	
Family Conidae	
<i>Conus archon</i> Broderip, 1833* (11) CS [46]	
<i>Conus patricius</i> Hinds, 1843 (11) CS [14–30]	
<i>Conus poormanii</i> Berry, 1968* (11) CS [47]	
<i>Conus recurvus</i> Broderip, 1833* (11) CS [32]	
<i>Conus tornatus</i> G.B. Sowerby I, 1833* (11) CS [32]	
Family Turridae	
<i>Polystira picta</i> (Reeve, 1843)* (11) CS [41]	
Order Heterobranchia	
Family Ellobiidae	
<i>Melampus carolinianus</i> (Lesson, 1842) (6) SB	

fasciata, and the mussels *Mytella speciosa* and *M. strigata* were relatively abundant and frequent in the roots of the red mangrove *Rizophora mangle*. The razor shell *Tagelus longisinuatus* was found in the muddy bottoms of the coastal lagoons. In the hard substratum of the rocky beaches and the rocky breakwaters of ports, there were 33 exclusive species (20.6%). The bivalves *Americardia biangulata* and *Choromytilus palliopunctatus* and the gastropods *Crepidula lessoni*, *Calyptrea conica*, and *Crucibulum umbrella* were the most abundant species in this habitat.

The largest number (40 spp.) of exclusive species was recorded in the shallow areas of the continental shelf while the sandy beaches included 38 exclusive species (5 bivalves and 33 gastropods) which represent 23.8% of all species. However, since most of the species recorded in the sandy beaches were collected as shells of dead molluscs that once lived in the adjacent shallow subtidal areas of the shores, only the species collected alive in the intertidal zone may be considered as truly exclusive inhabitants of the sandy beaches.

Notably, when both habitats are considered as one continuous environment (e.g., the intertidal and subtidal parts of the sandy shores), the number of species increases to 115 (48.8% are exclusive of this environment). The few species collected alive in the intertidal of the sandy shores were burrowed to avoid being washed away by waves and currents as in the case of the gastropods *Agaronia propatula*, *Olivella volutella*, and *O. zanoeta* and the bivalve *Donax carinatus*.

4. Discussion

Marine molluscs are among the most diverse group of shelf macrobenthos [35]. Recent studies on the diversity gradients of the molluscan fauna of the Northern Hemisphere, both in the Western and Eastern Pacific, indicate that species richness increases toward the tropics [35, 36]. This increase has a stepwise form, with the steps corresponding to provincial boundaries that form at the boundaries between major water masses or water types [37, 38]; this diversity gradient has been documented for many marine taxonomic groups [39].

In the Northeastern Pacific, the number of species of bivalves increases notably between latitudes 5°N (Peru) and 23°N (Sinaloa, Mexico) but reaches maximal values between 9 and 14°N (Panama-Chiapas) [35]. This diversity gradient is very similar for gastropods of the same region [35, 36]. Results of the present study coincide with this general pattern, with the Gulf of Tehuantepec (14–16°N) being within a region of high richness of molluscs.

This high diversity is well documented in the monograph of Keen [3] which is the most complete compendium of molluscs from the Mexican Pacific. This publication records approximately 800 species of bivalves and 2440 species of gastropods with almost 50% found in Mexican waters. The more recent reviews of Skoglund [7, 8] revealed an additional 478 species of bivalves and gastropods. However, although Keen's monograph includes the geographical distribution of the species, in most cases it does not give details of the

TABLE 2: Distribution of the species of bivalves and gastropods in the localities and habitats of the Gulf of Tehuantepec.

Locality	Bivalves	Gastropods	Total
(1) Estero Suchiate (sandy beach, estuary + mangrove)	37	5	42
(2) Estero Cahoacán (sandy beach, estuary + mangrove)	39	5	44
(3) Puerto Chiapas (sandy beach, rocky breakwater)	22	8	30
(4) La Encrucijada (estuary + mangrove)	3	1	4
(5) La Joya Buenavista (estuary + mangrove)	2	4	6
(6) Estero Boca de Cielo (sandy beach, estuary + mangrove)	32	20	52
(7) Estero Chocohtital (estuary + mangrove)	4	2	6
(8) Puerto Arista (sandy beach)	4	1	5
(9) Laguna Mar Muerto (coastal lagoon + mangrove)	7	8	15
(10) Bahía Tangolunda (sandy and rocky beach)	14	21	35
(11) Continental shelf (sandy bottom)	18	40	58
<i>Habitat</i>			
Estuary + mangrove	11	19	30
Coastal lagoon + mangrove	2	0	2
Rocky beach and rocky breakwater	22	33	55
Sandy beach	55	16	71
Sandy bottom of the continental shelf	18	40	58

localities and it cannot be used to know the specific richness of a particular region. Other catalogues of molluscs from the Mexican Pacific also lack this information [4–6, 30].

With a total of 160 species, 56 families, and 10 orders of bivalves and gastropods, the present study compiles the largest biodiversity of molluscs recorded for the Gulf of Tehuantepec. Previous studies report different species composition compared to the present study (Table 4): González-Bulnes [17] with only 8 species in common (3.0%); Gómez-Farías [18] with 12 species (5.0%); Holguín Quiñones and González-Pedraza [22] with 54 species (33.12%); Sevilla-Hernández [23] with 74 species (30.7%); De León-Herrera [20] with 5 species (2.6%); and Ramírez-González and Barrientos-Luján [29] with 18 species (7.7%). Differences in species composition are mostly related to the sampling effort and the method used to collect the molluscs. For example, González-Bulnes [17] and Gómez-Farías [18] report very different species mostly because they used a geological grab to collect the organisms. The geological grabs are very efficient in collecting the infaunal forms from the soft sediments in subtidal areas, including the smaller shells and the juveniles; these forms comprise most of the species of bivalves and many small gastropods not collected with trawling nets. Therefore, different sampling methods performed in the different localities and habitats complement each other to have a better compilation of the diversity of molluscs from the Gulf.

The present study adds 24 species of bivalves and 29 species of gastropods not reported in previous studies—but certainly included in Keen's [3] monography and in other catalogues for this region—for a total count of 213 species (102 bivalves and 111 gastropods) recorded in the Gulf of Tehuantepec. These figures, however, still underestimate the diversity of molluscs of this region due to lack of sampling,

especially in the shallower and deeper zones of the shelf. Below 50 m depth the appropriate equipment and expertise is particularly required; also the areas less than 10 m depth along the open shoreline regions are difficult to access because of the surf and strong currents except for some locations where sampling may be performed during SCUBA diving. There is certainly a different group of species living in the deeper parts of the shelf but their composition in the Gulf of Tehuantepec is still not well documented. Indeed, studies on the bathymetric distribution of molluscs in other regions of the Mexican Pacific have shown that the highest diversity is found in the coastal fringe (<20 m depth) and the number of species remains relatively high across the shelf as far as the 100 m depth (e.g., [2, 9, 15, 40, 41]).

Recently, because of the ongoing mass extinction of species due to human activities, the question of how many species occur in certain areas or habitats has grown more important [42]. Most of these species are being lost in the tropics [43]. Therefore, it is important to have a reasonable estimate of how many species are present in a particular environment in order to have a base against which to measure the losses.

The Gulf of Tehuantepec has been identified by the CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) as a region of high priority for the conservation of biodiversity [44]. However, there are no complete inventories for most of the marine animal groups. The region holds some of the tallest mangroves in Mexico, with trees reaching heights of 25 m [45], in an almost continuous hydrological system with swamps, estuaries, lagoons, and mangrove forests running northwest to southwest along the coastal plain of the Gulf. These environments serve as a nursery to fish and invertebrates, and provide refuge for many endangered animals [46].

Type of habitat

Mangroves of estuaries and coastal lagoons	Rocky beaches and rocky breakwaters of ports	Sandy beaches	Shallow subtidal areas of the continental shelf (14–47 m)
Bivalves (1) <i>Mytella speciosa</i> (2) <i>Mytella strigata</i> (3) <i>Togelus longisinuatus</i> Gastropods (1) <i>Theodoxus luteofasciatus</i> (2) <i>Littorina fasciata</i> (3) <i>Cerithiidea mazatlanica</i> (4) <i>Cerithiidea valida</i> (5) <i>Stramonita chocolata</i> (6) <i>Costoanachis nigricans</i>	Bivalves (1) <i>Americardia biangulata</i> (2) <i>Choromytilus palliopunctatus</i> (3) <i>Chama echinata</i> (4) <i>Ctena mexicana</i> (5) <i>Myrakeena angelica</i> (6) <i>Laevicardium clarionense</i> (7) <i>Trachycardium consors</i> (8) <i>Chione subimbricata</i> (9) <i>Tivela delessertii</i> Gastropods (1) <i>Crepidula lessoni</i> (2) <i>Calyptrea conica</i> (3) <i>Crucibulum umbrella</i> (4) <i>Diodora saturnalis</i> (5) <i>Fissurella decemcostata</i> (6) <i>Fissurella microtrema</i> (7) <i>Fissurella rubropicta</i> (8) <i>Fissurella spongiosa</i> (9) <i>Lottia mesoleuca</i> (10) <i>Lottia mitella</i> (11) <i>Lottia pediculus</i> (12) <i>Serpulorbis margaritaceus</i> (13) <i>Pilosabia pilosa</i> (14) <i>Crepidula aculeata</i> (15) <i>Crepidula onyx</i> (16) <i>Mauritia arabicula</i> (17) <i>Ficus ventricosa</i> (18) <i>Distorsio decussata</i> (19) <i>Acanthais brevidanta</i> (20) <i>Thais triangularis</i> (21) <i>Cantharus ringens</i> (22) <i>Cantharus sanguinolentus</i> (23) <i>Engina jugosa</i> (24) <i>Nassarius wilsoni</i>	Bivalves (1) <i>Donax kindermanni</i> (2) <i>Lunarca brevifrons</i> (3) <i>Mulinia pallida</i> (4) <i>Nuculana polita</i> (5) <i>Anadara bifrons</i> (6) <i>Anadara nux</i> (7) <i>Anadara perlabiata</i> (8) <i>Leptopecten tumbezensis</i> (9) <i>Cardites laticostata</i> (10) <i>Polymesoda meridionalis</i> (11) <i>Divalinga eburnea</i> (12) <i>Luciniscia fenestrata</i> (13) <i>Parvilucina approximate</i> (14) <i>Trachycardium senticosum</i> (15) <i>Chione undatella</i> (16) <i>Pitar concinnus</i> (17) <i>Pitar lupanaria</i> (18) <i>Pitar roseus</i> (19) <i>Pitar tortuosus</i> (20) <i>Protothaca magintyi</i> (21) <i>Protothaca metodon</i> (22) <i>Macrellona exoleta</i> (23) <i>Strigilla chroma</i> (24) <i>Strigilla dichotoma</i> (25) <i>Tellina insculpta</i> (26) <i>Tellina decumbens</i> (27) <i>Tellina prora</i> (28) <i>Tellina virgo</i> (29) <i>Donax asper</i> (30) <i>Donax carinatus</i> (31) <i>Donax gracilis</i> (32) <i>Sanguinolaria bertini</i> (33) <i>Periploma planiusculum</i>	Bivalves (1) <i>Anadara reinhardtii</i> (2) <i>Pinctada mazatlanica</i> (3) <i>Argopecten ventricosus</i> (4) <i>Spondylus limbatus</i> (5) <i>Pegophysema edentuloides</i> (6) <i>Trachycardium procerum</i> (7) <i>Chione pulicaria</i> (8) <i>Cyclinella saccata</i> (9) <i>Dosinia ponderosa</i> (10) <i>Periglypta multicosata</i> Gastropods (1) <i>Turritella banksi</i> (2) <i>Crucibulum personatum</i> (3) <i>Natica elenae</i> (4) <i>Malea ringens</i> (5) <i>Tonna</i> sp. (6) <i>Distorsio decussata</i> (7) <i>Bursa corrugata corrugata</i> (8) <i>Marsupina nana</i> (9) <i>Hexaplex brassica</i> (10) <i>Murex recurvirostris</i> (11) <i>Muricanthus nigrinus</i> (12) <i>Muricanthus radix</i> (13) <i>Northia northiae</i> (14) <i>Phos crassus</i> (15) <i>Melongena patula</i> (16) <i>Fusinus dupetitthouarsi</i> (17) <i>Pleuroploca granosa</i> (18) <i>Harpa crenata</i> (19) <i>Oliva splendida</i> (20) <i>Vasum caestus</i> (21) <i>Mitra swainsoni</i> (22) <i>Cancellaria obesa</i>

TABLE 4: Studies on the molluscan fauna from the Gulf of Tehuantepec. The habitats and the sampling method of each study are detailed for comparisons. The shared species are those reported in other studies and in the present checklist.

Locality	Habitat (sampling method)	Total species	Shared species	Reference
Gulf of Tehuantepec	continental shelf (geological grab)	39 bivalves	5	González-Bulnes [17]
		68 gastropods	3	
Salina Cruz, Oax.	continental shelf (geological grab)	42 bivalves	9	Gómez-Farías [18]
		46 gastropods	3	
Coast of Oaxaca	rocky and sandy beach, continental shelf (direct search)	55 bivalves	25	Holguín-Quiñones & González-Pedraza [22]
		98 gastropods	29	
Coast of Chiapas	estuary, coastal lagoon, rocky and sandy beach (direct search)	78 bivalves	42	Sevilla-Hernández [23]
		73 gastropods	32	
Central coast of Oaxaca	rocky beach (direct search)	5 bivalves	1	De León-Herrera, [20]
		26 gastropods	4	
Bahías de Calacuta (Huatulco), Oax.	rocky and sandy beach (direct search)	30 bivalves	7	Ramírez-González & Barrientos-Luján [29]
		59 gastropods	11	
Gulf of Tehuantepec	estuary, coastal lagoon, rocky and sandy shores, continental shelf (direct search, trawling net)	78 bivalves	54	Present study
		82 gastropods	53	
Total species registered in the Gulf of Tehuantepec		Bivalvia	102	
		Gastropoda	111	
		Total	213	

A good example of fieldwork conducted specifically to document molluscan richness for all size classes in a complex tropical coastal environment is the study by Bouchet et al. [47]. This massive collecting effort involving 400 day-persons at 42 discrete stations on a 295 km² site on the west coast of New Caledonia, south-west Pacific, revealed 2738 species of marine molluscs. This is several times the number of species recorded from any area of comparable extension anywhere in the world. Schlacher et al. [48] suggest that three main factors had, separately or together, contributed to the underestimation of actual richness in many studies on tropical marine molluscs: (1) inadequate or insufficient coverage of spatial heterogeneity over the area of study (a high number of species may be found at only one station), (2) inadequate sampling of the very specialized species (those living in a very specific habitat), and (3) overemphasis on macromolluscs. On a total of 42 stations sampled in the continental shelf of the Gulf of Tehuantepec, 58.6% of the species were collected at single stations and 72.4% at three or less stations with a total of 1-8 individuals. A similarly high incidence of “ecological endemism” was found by Schlacher et al. [48] in the lagoon of Great Astrolabe Reef (Fiji) and Bouchet et al. [47] at the New Caledonia site. That

their studies and the present study reach similar results despite very different sampling approaches and habitats (Schlacher et al. [48] sampled the soft bottom macrofauna of a lagoon, and Bouchet et al. [47] the molluscs from a coral reef) confirms the classical statement that many rare species are important in determining the structure of a marine benthic community and these rare species increase the richness component of the biological diversity. In addition, a large number of species of gastropods and bivalves are micromolluscs (Bouchet et al. [47] found that 33.5% of the species have an adult size smaller than 4.1 mm including at least five of the eight most speciose families and many species in the remaining three families) which require particular collecting/sorting attention and specific taxonomic expertise. This is why much of the literature focuses on macromolluscs (seashells) and tends to ignore or grossly underestimate the smaller species. Indeed, faunal surveys and inventories have a tendency to focus on the large species of “seashells” and neglect the smaller species. However, as Bouchet et al. [47] point out, the emphasis on macromolluscs is a perfectly valid approach when limited collecting and sorting resources are available in the field.

In the present study, species represented only by empty shells are included because it is highly likely that they are part of the ecosystem at the spatial scale of the study site. Although some shells may be transported for several kilometers, they still will be found within the extensive area of this study. Those species represented only by empty shells may not have been collected alive for a number of possible reasons: they live in a habitat that is difficult to sample (e.g., narrow fissures or cavities in rocks, deep burrowing bivalves), they have a very specialized habitat (e.g., eulimids associated with echinoderms), they are exceedingly rare; they live at a season different from the study period, or several of these factors operate together. Also, some organisms have very seasonal or sporadic occurrences and no survey, whatever its intensity, can approach a complete coverage of such species if restricted to a single period of the year. The seasonality of molluscs is well documented in temperate waters, and there is also evidence that the occurrence of many tropical species is locally unpredictable [49–51].

Recent work has suggested that molluscan death assemblages in marine intertidal habitats are sufficiently representative of regional biodiversity to be used in rapid, comparative biodiversity assessments. The evaluation of beach-washed death assemblages [52–54] suggested that aggregations of dead shells may be useful indicators of biodiversity over regional scales. Most of these studies have found that death assemblages strongly represent the species richness of living fauna with from 60%–100% of species found alive also occurring as dead shells [55, 56]; poor live-dead agreement is restricted to shelves that are both narrow and anthropogenically eutrophied [57]. In general, a very strong agreement has been documented between the live community and death-assemblage estimates of species composition, richness, and abundance in benthic mollusc communities [56, 58–62]. Several findings have emerged from this work, including the recognition that out-of-habitat shell transportation affects relatively few individuals [54, 56, 59]. These studies suggest that death-assemblage data can be used as an accurate proxy for species rank abundance in the live molluscan community.

The coastal ecosystems of the Gulf of Tehuantepec have great economic value. The main economic activity is the agriculture in the coastal plains but the artisan fishery and some tourism are also important. Dumping of organic and inorganic waste threatens the survival of many species. Development both residential and commercial is threatening these ecosystems due to the human population growth as well as tourism, which could displace mangrove communities. Economic and social problems have forced rural human communities to overexploit animal species through over hunting and fishing for the wildlife trade including several marine species, mammals, and reptiles such as turtles and iguanas. As a result, these species have acquired endangered status.

Immediate management and planning of conservation strategies are required for nearly the entire region. Agricultural expansion, shrimp farming, logging, and road construction activities continue to threaten the diversity of this region [46].

We did not recorded endemic species for this region; however, there are species that merit special attention, such as the pearl oyster *Pteria sterna*, which is mentioned in the NOM-059-ECOL-2001 (a Mexican standard for the wild terrestrial and aquatic flora and fauna species in danger of extinction, threatened, rare, and the subject ones to special protection).

Although many species are of commercial interest, there is no formal fishery or aquaculture of molluscs in the Gulf of Tehuantepec. Despite their relative abundance, variety, and nutritional value the current production of molluscs in the region is based on the exploitation of natural banks. Some species are collected from the estuaries and coastal lagoons for self-consumption or sell by local artisan fishermen to the restaurants and markets of small to medium communities along the coast. Many species are incidentally caught during shrimp fishing activities but only a few are usually delivered to the ports and consumed by men. Additionally, some shells are used as jewelry or used in handcrafts.

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