



A CHECKLIST OF THE MOLLUSKS FROM THE MIRAFLORES AND PEDRO MIGUEL LOCKS, PANAMA CANAL, PANAMA

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ABSTRACT

The Panama Canal Lock System provides an adequate environment for the settlement and recruitment of marine organisms, being invertebrates which contributes substantially to the local diversity. In July and September of 2019, we sampled inside two of the lock's chambers on the Pacific side of Panama; one at the Miraflores locks and one at Pedro Miguel locks. We illustrate the species found and we made a checklist of the entire molluscan fauna from this and previous studies. A total of 17 species were collected and identified (4 bivalves and 13 gastropods), of which 6 are new reports for the locks. Two bivalves species, *Mytella strigata* and *Brachidontes playasensis*, which are new records for the country, already known from the Tropical Eastern Pacific.

KEYWORDS

Mollusca, Gastropoda, Bivalvia, new records.

RESUMEN

El sistema de esclusas del Canal de Panamá proporciona un ambiente adecuado para el asentamiento y el reclutamiento de organismos marinos, siendo los invertebrados los que aportan una diversidad local sustancial. En julio y septiembre de 2019, muestreamos el interior de dos de las cámaras de esclusas en el lado Pacífico de Panamá; una en las esclusas de Miraflores y otra en las esclusas de Pedro Miguel. Ilustramos las especies encontradas y proporcionamos una lista de especies de toda la fauna de moluscos de este y estudios anteriores. Se recolectaron e identificaron un total de 17 especies (4 bivalvos y 13 gasterópodos) de las cuales 6 son nuevos reportes para

las esclusas. Dos especies, *Mytella strigata* y *Brachidontes playasensis*, son nuevos reportes para el país, ambas especies se conocían del Pacífico Oriental Tropical.

PALABRAS CLAVES

Mollusca, Gastropoda, Bivalvia, nuevos reportes.

INTRODUCTION

Since its opening in 1914, the Panama Canal has served as a freshwater transoceanic passageway connecting the Atlantic and the Pacific Oceans (Bennett & Hammond, 1915). The Panama Water Lock System helps the vessels entering to the canal are lifted to the higher level and later dropped down to the sea level at the other end of the canal- Today, the Canal has 5 sets of locks, two of which were recently inaugurated in 2016. On the Pacific side there are three locks. The original Miraflores and Pedro Miguel locks occurred in sequence while the new Cocoli Lock is in parallel with them (Fig. 1). Miraflores locks has 2 sequential chambers, and Pedro Miguel has one in each direction. On the Atlantic side the Gatun locks has 3 chambers in sequence. Each one of the old chambers is a box made of reinforced concrete measuring 304.8 m (1000 ft) long by 33.5 w (110 ft) with an average depth of 26 meters (40 ft) (ACP, 2020). This mechanism has operated for 100 years without appreciable increases in the salinity of Gatun Lake, and has largely prevented the migration of marine species from one ocean to the other. We focused on the diversity reported in the original locks since the new locks haven't yet been surveyed.

Salinity varies among the chambers thus influencing the diversity found in each one. The first, lower chamber of the Miraflores locks that connects directly to the Pacific Ocean, has a salinity of 26 ‰ (Menziés, 1968). To transit ships in this chamber, it has to be filled with fresh water from the upper chamber which has a salinity of 3 ‰ (Menziés, 1968). To lift ships in the upper chamber, it must be filled with fresh water from Miraflores Lake which has a salinity of 0 – 1 ‰ (Menziés, 1968; Jones & Dawson, 1973). Vessels in the single chamber of the Pedro Miguel Locks meet water salinity which equalizes with the Gatun Lake. The salinity of Pedro Miguel chambers and Gatun Lake is 0 ‰

(Jones & Rützler, 1975). On the Caribbean side, the Gatun Locks also differ in salinity, ranging 0 – 1 ‰, 10 – 16 ‰ and 18 – 20 ‰ in the upper, middle, and lower chambers, respectively (Hildenbrand, 1939).

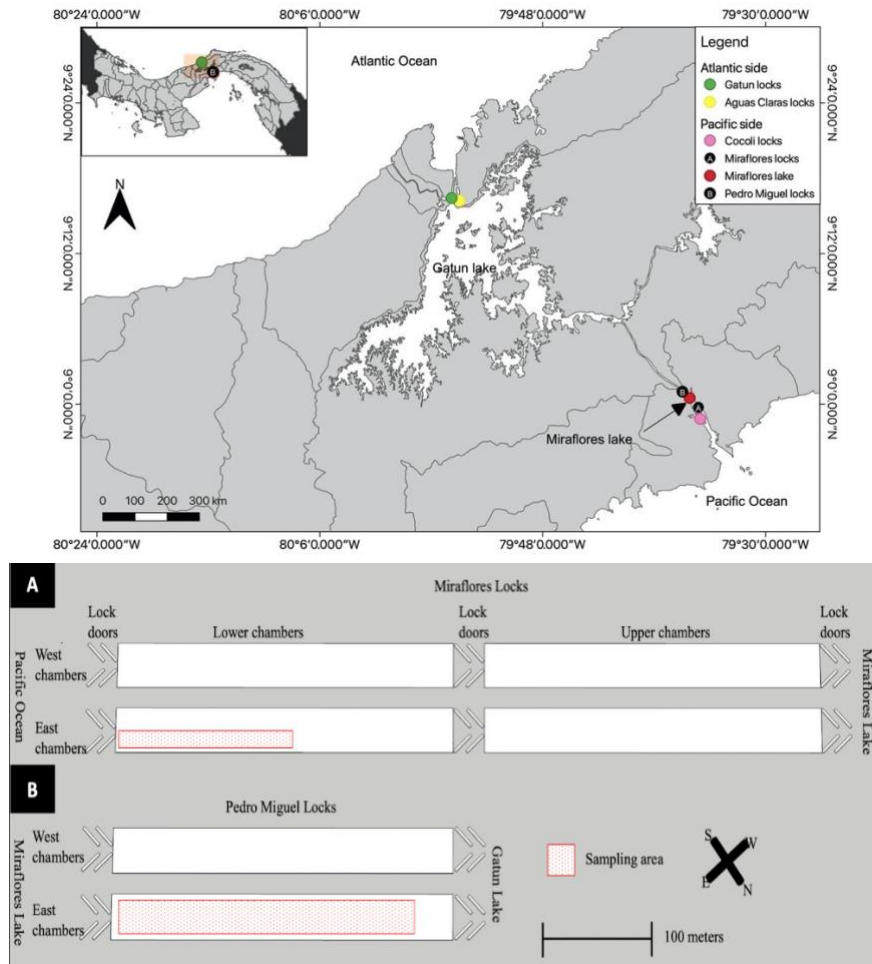
Several authors have made observations about the marine invertebrates found in the Panama Canal Locks and surrounding areas (McCosker & Dawson, 1975; Jones & Rützler, 1975; Abele, & Kim, 1989). Some dated to the early years of the Canal (Hildebrand, 1939), while others focus on the biology of target species (Roche & Torchin, 2007). Several environmental technical reports have documented the benthic mollusks in soft sediments from the Miraflores and Gatun Lake (Toole, 1985; Garcés, & García, 2003a, 2003b, 2004). Hildenbrand (1939) was the first to report 12 species of mollusks occurring inside the lock's chambers. Rosewater (1975a) reported 10 species in Gatun Locks. In the same year, he reported 74 species of mollusks from the entire lock systems (Gatun, Miraflores and Pedro Miguel), collected from 1971 to 1975 (Rosewater, 1975b). Many authors have done additional observations of the mollusks from the lock chambers (McCosker & Dawson, 1975; Jones & Rützler, 1975; Abele, & Kim, 1989). However, in many cases, samples have been collected and vouchered in museums, but the resulting publications provided summary numbers, rather than giving species names.

In this paper, we present a checklist of the diversity of mollusks registered from the Pedro Miguel and Miraflores locks, 44 years after the major mollusk survey made by Rosewater (1975b). We also provide photographs of the mollusk species most recently collected inside these 2 locks.

MATERIALS AND METHODS

Specimens were collected in the Miraflores Locks (8.995114, -79.589696) in July 2019 and in the Pedro Miguel Locks (9.016931, -79.612327) on September 2019 (Fig. 1). Each set of locks is drained every five years for maintenance. During the 2019 maintenance event we sampled the lower east chamber of Miraflores Lock three days after the chamber was totally drained. We collected on the left side of the chamber over the course of three hours. At the Pedro Miguel Locks we collected for 2 hours around the east chamber, a few hours after the chamber was drained.

Fig. 1 Map of the sampling areas in the Miraflores Locks (A) and Pedro Miguel Locks (B).



Samples were handpicked and initially stored in vials with water from the lock chamber until they were processed later the same day. In the laboratory the soft tissue was removed, and shells were gently dried and stored in clear plastic shell cases. The shells were identified with references to the local fauna (Keen 1958; Coan & Valentich-Scott, 2012; Tejera *et al.*, 2016). One representative shell of each species was photographed in standard view with a camera Olympus OM-D EM-5

Mark II with a 60mm f2.8 macro lens, the photos were stacked and arranged in Photoshop CC 2019 (Fig. 2,3). Vouchers were deposited in the Malacology Museum of the University of Panama (MUMAUP). Specimens were collected with the authorization of the Panama Canal Authority (ACP) and with the permission of the Ministry of Environment (Mi Ambiente) under the collection permits SE/AP-26-19.

We compiled literature on the species that have previously been reported in the locks, and records of observations in our curated database of the Marine Biodiversity of Panama (<http://www.invertebase.org/stri/index.php>). The species which contributes to the diversity reports by Rosewater, (1975b) were obtained from the database of the National Museum of Natural History (NMNH), since the original publication did not include the list of species collected, only the total of them. The total list of species was checked for distribution and synonyms by using the World Register of Marine Species (WORMS) database online, then registered as appropriate.

List of museum codes:

FMNH = The Field Museum of Natural History, Invertebrate Zoology Collections (USA)

IZ-YPM = Yale Peabody Museum of Natural History

MCZ = Museum of Comparative Zoology, Harvard University (USA)

NL = Naturalis Biodiversity Center – Mollusca, (Netherlands)

NMNH = National Museum of Natural History, Smithsonian Institution, Invertebrate Zoology Collections (USA)

UF = Florida Museum of Natural History, Invertebrate Zoology (USA)

UMMZ = University of Michigan Museum of Zoology (USA)

RESULTS

A total of 41 gastropods belonging to 13 species from eight families were collected (Table 1, Fig. 2). The two locks had distinct gastropod faunas, with *Clypeolum latissimum* being the only species found at the Pedro Miguel lock, while the other 12 species were found at the Miraflores Lock. Gastropods were located inside crevices in the walls or below the sparse rocky rubble on the lock's floor. Twelve bivalves were collected belonging to two families and four species (Table 1, Fig. 3). *Mytilopsis sallei* was the only bivalve species found at Pedro Miguel

and it was scarcely found inside crevices or holes in the lock walls. Meanwhile the floor from the Miraflores Chamber was carpeted with three species of bivalves: *Brachidontes playasensis*, *Mytella strigata* and *M. guyanensis*.

Fig. 2 Gastropod species from the Miraflores and Pedro Miguel locks in the Panama Canal. A) *Diodora saturnalis* (Carpenter, 1864), B) *Clypeolum latissimum* (Broderip, 1833), C) *Nerita scabricosta* Lamarck, 1822, D) *Bostrycapulus calyptraeiformis* (Deshayes, 1830), E) unidentified sample, F) *Monoplex wiegmanni* (Anton, 1838), G) *Pseudozonaria arabicula* (Lamarck, 1810), H) *Anachis lyrata* (G. B. Sowerby I, 1832), I) *Anachis varia* (G. B. Sowerby I, 1832), J) *Eupleura nitida* (Broderip, 1833), K) *Stramonita biserialis* (Blainville, 1832), L) *Thaisella kiosquiformis* (Duclos, 1832), M) *Triumphis distorta* (Wood, 1828). Scale bars 5 = mm.

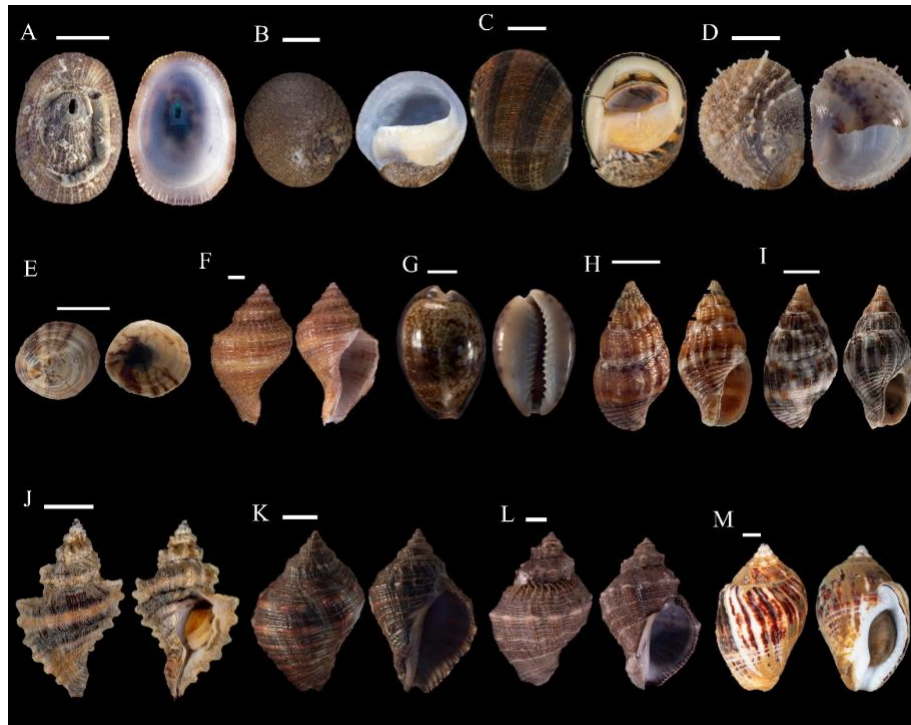


Fig. 3 External and internal views of bivalve species from the Miraflores and Pedro Miguel locks in the Panama Canal. A) *Brachidontes playasensis* B) *Mytella strigata* C) *Mytella guyanensis* D) *Mytilopsis sallei*. Scale bars = 2 mm.

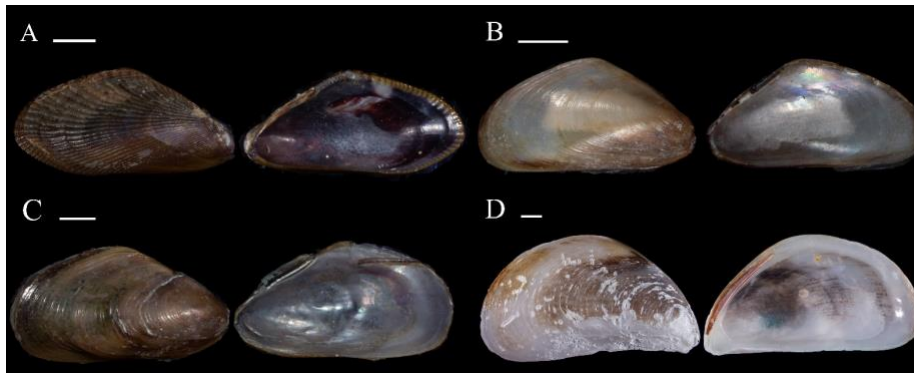
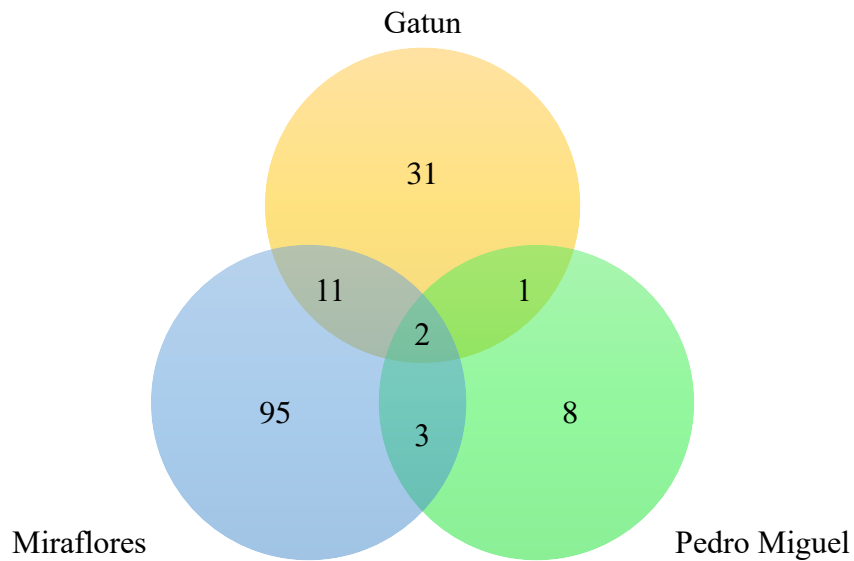


Fig. 4 Venn diagram summarizing the number of shared species between each one of the systems of lock chambers.



A total of 592 records of mollusks were found in the literature and online databases from museum collections. These records are exclusively from samples collected inside the original lock systems (Gatun, Pedro Miguel and Miraflores). These records represent 150 species, from which 55 are bivalves, 4 cephalopods, 88 gastropods and 3 polyplacophorans. Names of 36 species were updated based on the taxonomy in WORMS. Comparisons with geographic ranges showed that 7 species were away from their natural population distributions (Table 1), suggesting either misidentifications or possible introduction of these species. Miraflores has the greatest number of species (111) followed by Gatun (45) and finally Pedro Miguel (14). Only 13 species of mollusks have been reported to occur in both locks Miraflores and Gatun and two species (*Mytilopsis sallei* and *Melanoides tuberculata*) in all 3 locks (Figure 4). From the 111 species reported for Miraflores Lock's chambers, only 15 were found, but our collecting effort was minimal, and spatially limited to one part of the locks and by the time available for sampling.

Table 1. Mollusca diversity inside the lock chambers of the Panama Canal. G = Gatun locks, M = Miraflores locks, PM = Pedro Miguel locks, + = new reports for the locks (NL), - = new reports for the country (NC), # = species out of their natural distribution range (OD), * = species name updated, bold = samples collected in 2019 and illustrated in **Fig. 2** and **Fig. 3**.

Taxa	Distribution in WORMS	Source of record	M	P M	G	N L	N C	O D
Class Bivalvia								
Family Arcidae								
<i>Anadara emarginata</i> (G. B. Sowerby I, 1833)	Tropical Eastern Pacific	UF 388045	X					
<i>Anadara formosa</i> (G. B. Sowerby I, 1833)	Tropical Eastern Pacific	Rosewater, 1975b	X					

<i>Arca imbricata</i> Bruguière, 1789	Tropical Northwestern Atlantic and Temperate Southern Africa	Rosewater, 1975b			X				
<i>Arca mutabilis</i> (G. B. Sowerby I, 1833)	Tropical Eastern Pacific	Rosewater, 1975b	X		X				
<i>Arca zebra</i> Swainson, 1833	Tropical Northwestern Atlantic	Rosewater, 1975b			X				
Family Carditidae									
<i>Carditamera affinis</i> (G. B. Sowerby I, 1833) *	Tropical Eastern Pacific	Rosewater, 1975b	X						
<i>Carditamera radiata</i> (G. B. Sowerby I, 1833)	Tropical Eastern Pacific	UF 338254	X						
<i>Cardites laticostatus</i> (G. B. Sowerby I, 1833)	Tropical Eastern Pacific	UF 338225	X						
Family Chamidae									
<i>Chama buddiana</i> C. B. Adams, 1852	Tropical Eastern Pacific	Rosewater, 1975b	X						
<i>Chama macerophylla</i> Gmelin, 1791	Tropical Northwestern Atlantic and Temperate Northern Pacific	Rosewater, 1975b			X				
Family Corbulidae									
<i>Caryocorbula biradiata</i> (G. B. Sowerby I, 1833) *	Temperate South America	Rosewater, 1975b	X						
<i>Corbicula leana</i> Prime, 1864	Freshwater United States	Rosewater, 1975b		X	X				
Family Dreissenidae									
<i>Mytilopsis adamsi</i> J. P. E. Morrison, 1946	Indo-Pacific	UF 338297	X						#

<i>Mytilopsis sallei</i> (Récluz, 1849)	Neotropics	Rosewater, 1975b; Jones & Rützler, 1975; Hildebrand, 1939; This study	x	x	x				
Family Gastrochaenidae									
<i>Gastrochaena ovata</i> G. B. Sowerby I, 1834	Tropical Northwestern Atlantic	NMNH 742402			x				
<i>Lamychaena hians</i> (Gmelin, 1791) *	Tropical Northwestern Atlantic	NMNH 759090			x				
<i>Rocellaria dubia</i> (Pennant, 1777)	Northern European Seas, Mediterranean Sea and Temperate Southern Africa	Rosewater, 1975b			x				#
Family Glycymerididae									
<i>Tucetona pectinata</i> (Gmelin, 1791)	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Family Gryphaeidae									
<i>Hyotissa quercina</i> (G. B. Sowerby II, 1871) *	No WORMS distribution	UF 382461	x						
Family Hiatellidae									
<i>Hiatella arctica</i> (Linnaeus, 1767)	Worldwide	Rosewater, 1975b	x						
Family Isognomonidae									

<i>Isognomon alatus</i> (Gmelin, 1791)	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
<i>Isognomon recognitus</i> (Mabille, 1895)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Lasaeidae									
<i>Kellia suborbicularis</i> (Montagu, 1803)	Temperate Northern Atlantic	Rosewater, 1975b	x						
Family Lucinidae									
<i>Lucinisca centrifuga</i> (Dall, 1901) *	Tropical Northwestern Atlantic	NMNH 792421			x				
Family Myidae									
<i>Sphenia fragilis</i> (H. Adams & A. Adams, 1854)	Tropical Northwestern Atlantic	Rosewater, 1975b	x		x				
Family Mytilidae									
<i>Brachidontes exustus</i> (Linnaeus, 1758)	Tropical Northwestern Atlantic	Rosewater, 1975b; Hildebrand, 1939	x		x				
<i>Brachidontes playasensis</i> (Pilsbry & Olsson, 1935)	Tropical Eastern Pacific	This study	x			+	-		
<i>Brachidontes puntarenensis</i> (Pilsbry & H. N. Lowe, 1932)	Tropical Eastern Pacific	NMNH 734224			x				
<i>Brachidontes semilaevis</i> (Menke, 1848)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Gregariella coralliophaga</i> (Gmelin, 1791)	Tropical Northwestern Atlantic	Rosewater, 1975b			x				

<i>Leiosolenus attenuatus</i> (Deshayes, 1836) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Leiosolenus bisulcatus</i> (d'Orbigny, 1853) *	Tropical Northwestern Atlantic	Rosewater, 1975b	x		x				
<i>Leiosolenus plumula</i> (Hanley, 1843) *	Central Indo-Pacific	Rosewater, 1975b	x		x				#
<i>Lithophaga (Leiosolenus) spatiosa</i> (Carpenter, 1857)	No WORMS distribution	Rosewater, 1975b	x		x				
<i>Modiolus capax</i> (Conrad, 1837)	Tropical Eastern Pacific	NMNH 828661	x						
<i>Mytella strigata</i> (Hanley, 1843)	United States, Brazil and Singapore	This study	x			+	-		
<i>Mytella guyanensis</i> (Lamarck, 1819)	Tropical Eastern Pacific and Tropical Southwestern Atlantic	Rosewater, 1975b; This study	x						
Family Ostreidae									
<i>Crassostrea columbiensis</i> (Hanley, 1846) *	Tropical Eastern Pacific	Rosewater, 1975b; NMNH 783067	x	x					
<i>Crassostrea corteziensis</i> (Hertlein, 1951) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Ostrea conchaphila</i> Carpenter, 1857	Tropical Eastern Pacific	UF 382486	x						
<i>Saccostrea palmula</i> (Carpenter, 1857) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Striostrea prismatica</i> (Gray, 1825)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Pectinidae									

<i>Argopecten ventricosus</i> (G. B. Sowerby II, 1842)	Tropical Eastern Pacific	UF 382496	x						
<i>Leptopecten bavayi</i> (Dautzenberg, 1900)	Tropical Northwestern Atlantic	NMNH 742403			x				
<i>Leptopecten velero</i> (Hertlein, 1935)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Pholadidae									
<i>Diplothyra curta</i> (G. B. Sowerby I, 1834)	Tropical Northwestern Atlantic and Northwest Atlantic	MCZ 235467	x						
<i>Pholadidea melanura</i> (G. B. Sowerby I, 1834)	No WORMS distribution	MCZ 235295	x						
<i>Pholas chiloensis</i> Molina, 1782	Temperate South America	MCZ 235466	x						
Family Pteriidae									
<i>Pteria sterna</i> (Gould, 1851)	Tropical Eastern Pacific	Rosewater, 1975b; UF 388109	x		x				
Family Semelidae									
<i>Cumingia lamellosa</i> G. B. Sowerby I, 1833	Tropical Northwestern Atlantic	Rosewater, 1975b	x						
Family Teredinidae									
<i>Bankia fimbriatula</i> Moll & Roch, 1931	Tropical Northwestern Atlantic and Mediterranean Sea	Rosewater, 1975b			x				
<i>Nausitora fusticulus</i> (Jeffreys, 1860) *	Tropical Northwestern Atlantic	MCZ 351126	x						
<i>Psiloteredo healdi</i> (Bartsch, 1931)	Tropical Northwestern Atlantic	Harvard 45578		x					

<i>Teredo</i> Linnaeus, 1758	Worldwide	Hildebrand, 1939	x						
Family Ungulinidae									
<i>Phlyctiderma semiasperum</i> (Philippi, 1836) *	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Class Cephalopoda									
Family Loliginidae									
<i>Loligo</i> Lamarck, 1798	Worldwide	Hildebrand, 1939	x						
<i>Lolliguncula (Lolliguncula) panamensis</i> Berry, 1911 *	Tropical Eastern Pacific	NMNH 576936	x						
Family Octopodidae									
<i>Octopus balboai</i> Voss, 1971	Temperate Northeast Pacific	Rosewater, 1975b	x						
Family Sepiidae									
<i>Sepia vermiculata</i> Quoy & Gaimard, 1832	Temperate Southern Africa	Rosewater, 1975b			x				#
Class Gastropoda									
Family Achatinidae									
<i>Leptinaria lamellata</i> (Potiez & Michaud, 1838)	Neotropics	FMNH 63744		x					
Family Amathinidae									
<i>Iselica ovoidea</i> (Gould, 1853)	No WORMS distribution	Rosewater, 1975b	x						
Family Architectonicidae									

<i>Heliacus infundibuliformis</i> (Gmelin, 1791)	Tropical Northwestern Atlantic and Temperate Southern Africa	NMNH 743203			x				
Family Bulimulidae									
<i>Bulimulus corneus</i> (Sowerby, 1833)	Neotropics	FMNH 63666		x					
Family Bursidae									
<i>Bursa corrugata</i> (Perry, 1811)	Tropical Eastern Pacific, Tropical Northwestern Atlantic and Africa	NMNH 821636	x						
Family Caecidae									
<i>Caecum laeve</i> C.B.Adams, 1852	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Caecum lohri</i> (Strong, A.M. & L.G. Hertlein, 1939)	No WORMS distribution	Rosewater, 1975b	x						
Family Calyptraeidae									
<i>Bostrycapulus calyptraeiformis</i> (Deshayes, 1830) *	Tropical Eastern Pacific, Tropical Northwestern Atlantic and Mediterranean Sea	Hildebrand, 1939; Rosewater, 1975b; UF 353903; This study.	x						
<i>Crepidula excavata</i> (Broderip, 1834)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Crepidula incurva</i> (Broderip, 1834)	Tropical Eastern Pacific and Tropical Northwestern Atlantic	Hildebrand, 1939; UF 353895	x						

<i>Crepidula lessonii</i> (Broderip, 1834)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Crucibulum personatum</i> Keen, 1958	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Crucibulum scutellatum</i> (Wood, 1828)	Tropical Eastern Pacific	UF 338292	x						
<i>Crucibulum spinosum</i> (G. B. Sowerby I, 1824)	Tropical Eastern Pacific and Tropical Northwestern Atlantic	Hildebrand, 1939; UF 354370	x						
Family Cerithiopsidae									
<i>Cerithiopsis greenii</i> (C. B. Adams, 1839)	Temperate Northwest Atlantic and Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Family Cochliopidae									
<i>Cochliopina zeteki</i> J. P. E. Morrison, 1946	Panama	Rosewater, 1975b		x					
<i>Pyrgophorus coronatus</i> (L. Pfeiffer, 1840)	Tropical Northwestern Atlantic	M: UMMZ 117933 PM: UMMZ 67996	x	x					
<i>Pyrgophorus zeteki</i> (J. P. E. Morrison, 1946)	Panama	Rosewater, 1975b		x					
Family Columbellidae									
<i>Anachis fluctuata</i> (G. B. Sowerby I, 1832)	Tropical Eastern Pacific	Rosewater, 1975b			x				
<i>Anachis lyrata</i> (G. B. Sowerby I, 1832)	Tropical Northwestern Atlantic and	This study	x			+			

	Tropical Eastern Pacific								
<i>Anachis pardalis</i> (Hinds, 1843)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Anachis varia</i> (G. B. Sowerby I, 1832)	Tropical Northwestern Atlantic and Tropical Eastern Pacific	G: Rosewater, 1975b M: Rosewater, 1975b; This study	x		x				
<i>Falsuszafraona incerta</i> (Stearns, 1892) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Parvanachis diminuta</i> (C. B. Adams, 1852) *	Tropical Eastern Pacific	NMNH 761011	x						
<i>Parvanachis nigricans</i> (G. B. Sowerby I, 1844) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Cymatiidae									
<i>Monoplex parthenopeus</i> (Salis Marschlin, 1793) *	Worldwide	Rosewater, 1975b	x						
<i>Monoplex pilearis</i> (Linnaeus, 1758) *	Worldwide	Rosewater, 1975b			x				
<i>Monoplex wiegmanni</i> (Anton, 1838)	No WORMS distribution	Hildebrand, 1939; This study	x						
Family Cypraeidae									
<i>Cypraea</i> Linnaeus, 1758	Worldwide	UF 353896	x						
<i>Pseudozonaria arabicula</i> (Lamarck, 1810)	Tropical Eastern Pacific and Indo-Pacific	This study	x			+			
<i>Pseudozonaria robertsi</i> (Hidalgo, 1906) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Dorididae									

<i>Doris pickensi</i> Marcus & Marcus, 1967	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Epitoniidae									
<i>Alexania floridana</i> (Pilsbry, 1945)	Tropical Northwestern Atlantic	Rosewater, 1975b	x		x				
<i>Epitonium acapulcanum</i> Dall, 1917	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Epitonium cumingii</i> (Carpenter, 1856)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Epitonium huffmani</i> DuShane & McLean, 1968	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Epitonium replicatum</i> (G. B. Sowerby II, 1844)	Tropical Eastern Pacific and Temperate Southern Africa	Rosewater, 1975b	x						
<i>Opalia funiculata</i> (Carpenter, 1857)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Euconulidae									
<i>Habroconus zeteki</i> Pilsbry, 1930	Panama	FMNH 63726		x					
Family Fasciolariidae									
<i>Leucozonia rudis</i> (Reeve, 1847) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Polygona concentrica</i> (Reeve, 1847) *	Tropical Eastern Pacific	NMNH 734194	x						
Family Fissurellidae									
<i>Diodora alta</i> (C. B. Adams, 1852)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Diodora saturnalis</i> (Carpenter, 1864)	Tropical Eastern Pacific	This study	x			+			

Family Helicinidae								
<i>Lucidella lirata</i> (L. Pfeiffer, 1847)	Neotropics	MCZ 217594		x				
Family Littorinidae								
<i>Littoraria nebulosa</i> (Lamarck, 1822)	Tropical Eastern Pacific and Tropical Northwestern Atlantic	Rosewater, 1975b			x			
<i>Littoraria varia</i> (Sowerby, 1832)	Tropical Eastern Pacific	Rosewater, 1975b	x					
<i>Littoraria zebra</i> (Donovan, 1825)	Tropical Eastern Pacific	Rosewater, 1975b	x					
Family Mitridae								
<i>Mitra</i> Lamarck, 1798	Worldwide	UF 499285	x					
Family Muricidae								
<i>Eupleura nitida</i> (Broderip, 1833)	Tropical Eastern Pacific	Rosewater, 1975b; This study	x					
<i>Hexaplex alatus</i>		Rosewater, 1975b	x					
<i>Hexaplex princeps</i> (Broderip, 1833) *	Tropical Eastern Pacific and Tropical Northwestern Atlantic	Rosewater, 1975b	x					
<i>Hexaplex radix</i> (Gmelin, 1791) *	Tropical Eastern Pacific and Tropical Northwestern Atlantic	Hildebrand, 1939; UF 280404	x					
<i>Nucella</i> Röding, 1798	Worldwide	Rosewater, 1975b	x					
<i>Pteropurpura erinaceoides</i> (Valenciennes, 1832)	Tropical Eastern Pacific	Rosewater, 1975b	x					

<i>Stramonita biserialis</i> (Blainville, 1832) *	Tropical Eastern Pacific	Rosewater, 1975b; UF 361267; This study	x						
<i>Stramonita floridana</i> (Conrad, 1837)	Tropical Northwestern Atlantic	Rosewater, 1975b	x		x				
<i>Stramonita haemastoma</i> (Linnaeus, 1767) *	Atlantic Ocean, Tropical Eastern Pacific	Rosewater, 1975b	x		x				
<i>Thaisella kiosquiformis</i> (Duclos, 1832) *	Tropical Eastern Pacific	Hildebrand, 1939; Rosewater, 1975b; This study	x						
<i>Trachypollia lugubris</i> (C. B. Adams, 1852) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Vitularia salebrosa</i> (P. P. King, 1832)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Nassariidae									
<i>Nassarius nucleolus</i> (Philippi, 1846)	Tropical Eastern Pacific	NL ZMA.MOL L.97462	x						
Family Neritidae									
<i>Clypeolum latissimum</i> (Broderip, 1833) *	Neotropics	Rosewater, 1975b; This study	x	x					
<i>Nerita funiculata</i> Menke, 1850	Tropical Eastern Pacific	NMNH 734400	x						
<i>Nerita scabricosta</i> Lamarck, 1822	Tropical Eastern Pacific	This study	x			+			

<i>Neritina zigzag</i> Lamarck, 1822	Indo-Pacific	NMNH 759045			x				#
<i>Vitta clenchi</i> (Russell, 1940)	Tropical Northwestern Atlantic	NL ZMAMOL L56617			x				
<i>Vitta luteofasciata</i> (Miller, 1879) *	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Vitta meleagris</i> (Lamarck, 1822)	Tropical Northwestern Atlantic	Hildebrand, 1939			x				
<i>Vitta usnea</i> (Röding, 1798) *	Tropical Northwestern Atlantic	Rosewater, 1975b; Jones & Rützler, 1975; NL ZMAMOL L56605, ZMAMOL L56675			x				
Family Ovulidae									
<i>Jenneria pustulata</i> (Lightfoot, 1786)	Tropical Eastern Pacific	Hildebrand, 1939; UF 353643	x						
Family Planaxidae									
<i>Supplanaxis nucleus</i> (Bruguère, 1789) *	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Family Pseudolividae									
<i>Triumphis distorta</i> (Wood, 1828)	Tropical Eastern Pacific	Hildebrand, 1939; Rosewater, 1975b; UF 338241; This study	x						
Family Pseudomelatomidae									

<i>Pyrgospira obeliscus</i> (Reeve, 1845)	No WORMS distribution	Rosewater, 1975b	x						
Family Pyramidellidae									
<i>Asmunda turrita</i> (C. B. Adams, 1852) *	No WORMS distribution	Rosewater, 1975b	x						
<i>Iselica fenestrata</i> (Carpenter, 1864)	Tropical Eastern Pacific	NMNH 759557	x						
<i>Iselica globosa</i> (H. C. Lea, 1843) *	Tropical Northwestern Atlantic	NMNH 759068			x				
<i>Odostomia clathratula</i> (C. B. Adams, 1852)	Tropical Eastern Pacific	Rosewater, 1975b	x						
<i>Phasianema anomala</i>	No WORMS distribution	Rosewater, 1975b			x				
<i>Turbonilla pupoides</i> (d'Orbigny, 1841)	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Family Raphitomidae									
<i>Philbertia doris</i> Dall, 1919	No WORMS distribution	Rosewater, 1975b	x						
Family Thiariidae									
<i>Melanoides tuberculata</i> (O. F. Müller, 1774)	Indo-Pacific, Tropical Northwestern Atlantic and Temperate Southern Africa	Rosewater, 1975b	x	x	x				
Family Triphoridae									
<i>Marshallora nigrocincta</i> (C. B. Adams, 1839) *	Tropical Northwestern Atlantic	NMNH 759071			x				

<i>Triphora alternata</i> C. B. Adams, 1852	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Truncatellidae									
<i>Truncatella caribaeensis</i> Reeve, 1842	Tropical Northwestern Atlantic	NMNH 759055			x				
<i>Truncatella pulchella</i> Pfeiffer, 1839	Tropical Northwestern Atlantic	Rosewater, 1975b			x				
Family Valloniidae									
<i>Pupisoma dioscoricola</i> (C. B. Adams, 1845)	Indo-Pacific and Temperate Southern Africa	FMNH 63722		x					#
Family Vermetidae									
<i>Eualetes tulipa</i> (Rousseau in Chenu, 1843)	Tropical Northwestern Atlantic	NMNH 734179	x						
<i>Petalococonchus</i> H. C. Lea, 1843	Worldwide	UF 353902	x						
<i>Thylacodes arenarius</i> (Linnaeus, 1758)	Mediterranean Sea, Temperate Southern Africa and Central Indo-Pacific	UF 353902	x						#
Gastropoda Unidentified sample		This study							
Class Polyplacophora									
Family Callistoplacidae									
<i>Callistochiton elenensis</i> (G. B. Sowerby I, 1832)	Tropical Eastern Pacific	Rosewater, 1975b	x						

<i>Chaetopleura lurida</i> (G. B. Sowerby I, 1832)	Tropical Eastern Pacific	Rosewater, 1975b	x						
Family Chitonidae	Worldwide	Rosewater, 1975b	x						

DISCUSSION

The diversity of Mollusca in the Gulf of Panama was entirely reviewed recently by Keen (1958). Most recently efforts have been made to document additional biodiversity in localized sites (Córdoba *et al*, 2010; Tejera *et al*, 2016) and samples from Panama are often included in taxon-specific revisions (e.g., Collin, 2005; Reid *et al*, 2010; deMaintenon, 2014; Raines, 2020). With each biodiversity study, new species and/or new reports are added to the Mollusca fauna in Panama. In this review of the fauna of the Panama Canal locks, we recorded two new species for the country: *Mytella strigata* and *Brachidontes playasensis*. These two species are native to the Eastern Pacific Ocean (Keen, 1958; Coan & Valentich-Scott, 2012) and they have been reported for Colombia (Puyana *et al*, 2012), and Mexico (Lopez-Rojas *et al*, 2017), so its presence in Panama should be expected.

The salinity of each one of the locks's chambers shapes the diversity of species in that chamber (Figure 4). There is very little overlap of the fauna in each set of locks; and very few species occur in multiple locks. In the lower chambers of the Miraflores Locks, the high salinity and frequent water exchange promotes the arrival of larvae and survival of settlers from the diverse mollusk's fauna of the Bay of Panama (Keen, 1958; Menzies, 1968).

After 40 years, since the last two major mollusk censuses in the locks (Hildenbrand, 1939; Rosewater, 1975b), we observed lower diversity and some new records for the locks. According to Rosewater (1975b), *Mytilopsis sallei* was a bivalve commonly found in all the lock chambers. We only found this species at the Pedro Miguel Locks, but they were not entirely covering the lock walls as stated by Hildebrand

(1939). Instead, were scarcely found inside of crevices in the lock's walls. Historically, *M. sallei* has been one of the two species of mollusk that was found in the three locks systems. Due to its high tolerance to changes in salinity, temperature and its fast growth and reproductive rate (Morton, 1981) *M. sallei* has invaded many sites in Australia (William *et al*, 2000), Malaysia and Singapore (Tan & Morton, 2006). Outside the lock's chambers, this species can be found covering hard substrates around the Gatun Lake (M.M. pers. Obs.). It is likely that *M. sallei* was found at the upper chambers in Miraflores Locks, where the salinity is 3 ‰ (Menzies, 1968), and where we did not collect samples. In the upper chambers *M. sallei* would not be released from competition for space with species of *Brachidontes* that were commonly found at the lower chamber and which are less tolerant to low salinities (Sara *et al*, 2008). Rosewater (1975b) found the freshwater snail *Melanoides tuberculata*, an invasive species capable of surviving at salinities up to 21.56‰ (Farani *et al*, 2015), in the three sets of locks, but we did not find this species.

Overall, each set of locks chambers has different communities of mollusks reflecting the differences in salinity generated by the constant exchange of ocean water from the lower chambers of the Miraflores and Gatun locks. If the salinity changes it is likely that the distribution of the more euryhaline species may expand to include more locks.

CONCLUSION

We provide an annotated checklist of 150 species of mollusks found at the Miraflores, Pedro Miguel and Gatun Locks compiled over 80 years of observations in the Panama Canal. We added six new records (*Brachidontes playasensis*, *Mytella strigata*, *Anachis lyrata*, *Pseudozonaria arabicula*, *Diodora saturnalis*, *Nerita scabricosta*, and an unidentified Patellogastropoda) from our observations of the Miraflores Locks. We hope that this compilation will facilitate the detection of new or introduced species in the future.

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