

Ascidians at the Pacific and Atlantic entrances to the Panama Canal

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Editor's note:

This paper is a contribution to the proceedings of the 3rd International Invasive Sea Squirt Conference held in Woods Hole, Massachusetts, USA, on 26–28 April 2010. The conference provided a venue for the exchange of information on the biogeography, ecology, genetics, impacts, risk assessment and management of invasive tunicates worldwide.

Abstract

The Panama Canal region is susceptible to non-native species introductions due to the heavy international shipping traffic through the area. Ascidian introductions are occurring worldwide but little is known about introductions at the Panama Canal. Surveys were conducted in 2002, 2008, and 2009 within the Pacific and Atlantic entrances to the canal. We found a high diversity of ascidians on both sides of the canal, dominated by non-native species; six species occurred at both Pacific and Atlantic Panama sites. This is the first report of *Polyandrocarpa anguinea* and *P. sagamiensis* in Atlantic Panama waters and *Ascidia incrassata*, *Ascidia sydneyensis*, *Botrylloides nigrum*, *Botryllus planus*, *Didemnum perlucidum*, *Diplosoma listerianum*, *Microcosmus exasperatus*, *Polyandrocarpa zorritensis*, *Polyclinum constellatum*, *Symplegma brakenhielmi*, *Symplegma rubra*, and *Trididemnum orbiculatum* in Pacific Panama waters. The canal may serve as a major invasion corridor for ascidians and should be monitored over time.

Key words: Panama Canal, tunicates, shipping traffic, species introductions, tropics

Introduction

The narrow isthmus of Central America separates the Pacific and Atlantic Oceans and the Panama Canal has provided intra-oceanic passage for commercial and recreational ships for almost a century. In October 2010, the Panama Canal Authority celebrated the passage of one million ships through the canal since it opened in 1914. Due to the heavy international shipping traffic through the area, the Panama Canal region is susceptible to non-native species

introductions. Shipping (e.g., ship hulls, ballast water, sea chests) provides vectors and dispersal mechanisms for non-indigenous species (Coutts and Dodgshun 2007; Minchin et al. 2009), including ascidians. Cohen (2006) documented the presence of non-native invertebrates at the Panama Canal, including the ascidians *Botryllus schlosseri* (Pallas, 1766) on the Pacific side of the canal and *Botrylloides perspicuum* Herdman, 1886, *Cnemidocarpa irene* (Hartmeyer, 1906), *Diplosoma virens* (Hartmeyer, 1909), and *Polyandrocarpa zorritensis* (Van Name, 1931) on the Atlantic side of the canal.

Transport of exotic species around the world is increasing due to increased activities associated with international trade and movement of people (Cohen 1999), and an increased volume of shipping traffic is concentrated at canal zones (Cohen 2006). Ascidian introductions are occurring worldwide but little is known about introductions at the Panama Canal. Ascidiaceans are highly invasive (Lambert and Lambert 2003; Lambert 2007, 2009) and recent appearances of exotic ascidian species around the world have caused significant ecological and economic damage (Coutts and Sinner 2004; Bullard and Carman 2009; Carman et al. 2010).

The ascidian fauna in Atlantic Panama waters, specifically at Bocas del Toro, has been well documented (Rocha et al. 2005). However, there is no published report of ascidiaceans in the region around the Atlantic entrance to the Panama Canal. Previous ascidian work in the Pacific Panama area is similarly limited. Van Name (1945) documented eight species in Pacific Panama waters and Tokioka (1971, 1972) documented 13 species in neighboring Pacific Costa Rica waters (Table 1). The only analysis of ascidian faunal composition conducted concurrently on both sides of the Panama Canal was a brief rapid assessment survey (RAS) in 2002; the ascidian data are published in full here for the first time. Because the Panama Canal is a critical link to global trade, the canal likely acts as a pathway for ascidian transport. Baseline data on regional ascidian populations provide a foundation for further ecological research of ascidian populations. Therefore, we identified ascidian species on both sides of the canal.

Panama's climate is humid-tropical with marked seasonality, including a dry season (mid December to mid April) and rainy season (mid April to mid December) (Guzman et al. 2004). The Bay of Panama on the Pacific side is an area of seasonal upwelling, large freshwater runoff and high concentrations of inorganic nutrients and plankton (D'Croz et al. 2005). The greater tidal range, wider annual temperature range, and seasonal salinity changes on the Pacific side of the canal may impact subtidal fauna (Cohen 2006). In contrast, the Caribbean coast has more stable oceanographic conditions, small tidal range (<0.5 m), less turbidity and lower concentrations of dissolved nitrate and phosphate (D'Croz and Robertson 1997).

Methods

Surveys were conducted in 2002, 2008, and 2009 at several sites within the Pacific and Atlantic entrances to the Panama Canal (Figure 1). We explored 16 sites (Appendices 1–2) that represented 118 km (74 miles) of Pacific coastline and 109 km (68 miles) of Atlantic coastline and surveyed natural and artificial substrates in shallow waters (<3 m) in different habitats either by walking access or through the use of small coastal research vessels and snorkeling. Each station was surveyed for approximately two hours. All substrates at the surveyed sites were equally searched and when appropriate, small rocks were overturned and examined. Representative ascidian individuals were photographed *in situ*, collected, preserved in formalin, and identified. Voucher specimens are housed at Universidade Federal do Paraná with R. Rocha. Latitude and longitude were recorded for each site with a hand held GPS unit. Salinity was measured at the surface with a refractometer (Atago S–10). The ascidian fauna of the Atlantic Panama Canal is likely more diverse than reflected in our surveys because access to Atlantic sites was limited; due to political instability in the area and upon the advice of our guide, we only surveyed at sites on the Atlantic side of the canal that were deemed safe.

Results

We found ascidiaceans attached to bricks, rocks, corals, bivalves, barnacles, mangrove roots, docks, pilings, mooring lines, and a shipwreck in subtidal shallow waters. No ascidiaceans were observed in intertidal habitats. Salinity measurements at sites where ascidiaceans were present ranged from 28 to 36 psu. At the Pacific entrance to the Panama Canal we found 20 taxa: 17 identified species (3 native, 7 introduced, 7 cryptogenic species), a presumed new species (*Ascidia* sp.), and two taxa identified only to genus (*Botrylloides* sp. and *Didemnum* sp.). At the Atlantic entrance to the Panama Canal we found 19 taxa: 18 identified species (6 native, 2 introduced, 10 cryptogenic species) and an unidentified species (*Didemnum* sp. white with green algae).

Of the 22 species previously found in the Pacific waters of Costa Rica and Panama (Table 1) (some of which were dredged in deeper waters), six were found in our shallow water

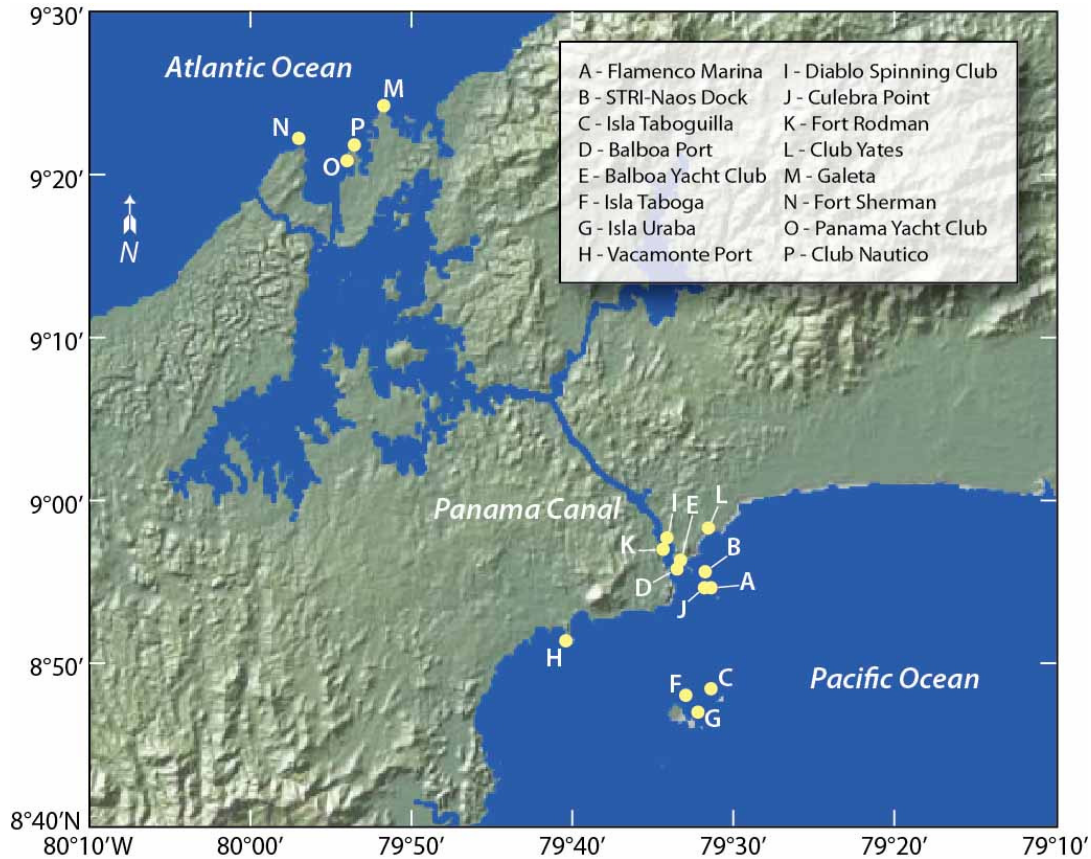


Figure 1. Map of the study area with surveyed sites indicated (for details see Appendix 1).

Pacific surveys (Appendices 1–2). This is the first report of *Polyandrocarpa anguinea* (Sluiter, 1898) and *P. sagamiensis* Tokioka, 1953 in Atlantic Panama waters and *Ascidia incrassata* Heller, 1878, *Ascidia sydneyensis* Stimpson, 1855, *Botrylloides nigrum* Herdman, 1886, *Botryllus planus* (Van Name, 1902), *Didemnum perlucidum* Monniot, 1983, *Diplosoma listerianum* (Milne-Edwards, 1841), *Microcosmus exasperatus* Heller, 1878, *Polyandrocarpa zorritensis* (Van Name, 1931), *Polyclinum constellatum* Savigny, 1816, *Symplegma brakenhielmi* Michaelsen, 1904, *Symplegma rubra* Monniot, 1972, and *Trididemnum orbiculatum* (Van Name, 1902) in Pacific Panama waters.

Both Pacific and Atlantic ascidian faunas at the Panama Canal were dominated by non-native or cryptogenic species. Non-native species were

very abundant; native species were less common or rare (Table 2). Six species occurred on both sides of the canal [*A. sydneyensis*, *B. nigrum*, *D. listerianum*, *M. exasperatus*, *P. constellatum*, and *Styela canopus* (Savigny, 1816)]; all are species common to the fouling communities of ports and marinas of the world. We considered the new species, *Ascidia* sp., as a native species (Table 2) because we found it in Panama waters but it may be a cryptogenic or introduced species.

Discussion

The ascidian fauna at the Atlantic and Pacific sides of the Panama Canal are very diverse compared to other areas that have been surveyed. We found approximately 20 species of ascidians

Table 1. Ascidian species previously documented in Pacific waters of Panama and Costa Rica. x=present. Author codes: 1. Van Name (1945), 2. Tokioka (1971), 3. Tokioka (1972), 4. Menge et al. (1983), 5. Monniot (1994), 6. Cohen (2006).

Species	Panama	Costa Rica	Authors
<i>Aplidium constellatum</i> (Verrill, 1871)		x	3
<i>Ascidia ceratodes</i> (Huntsman, 1912)		x	3
<i>Botryllocarpa viridis</i> (Pizon, 1908) ¹		x	3
<i>Botryllus schlosseri</i> (Pallas, 1766)	x		6
<i>Chelyosoma inaequale</i> Redikorzev, 1913	x		1
<i>Cnemidocarpa drygalskii</i> (Hartmeyer, 1911)	x		1
<i>Didemnum candidum</i> Savigny, 1813 ²		x	3
<i>Didemnum carnulentum</i> Ritter and Forsyth, 1917	x		1
<i>Didemnum moseleyi</i> (Herdman, 1886)		x	3
<i>Didemnum vanderhorsti</i> Van Name, 1924	x		1
<i>Eudistoma pachecae</i> Van Name, 1945	x		1,4
<i>Eusynstyela</i> sp. cf. <i>tincta</i> (Van Name, 1902)		x	3
<i>Lissoclinum caulleryi</i> (Ritter and Forsyth, 1917)		x	3
<i>Lissoclinum fragile</i> (Van Name, 1902)		x	3
<i>Polyclinum laxum</i> Van Name, 1945		x	3
<i>Pyura lignosa</i> Michaelsen, 1908	x	x	3,5
<i>Pyura vittata</i> (Stimpson, 1852)	x		4
<i>Pyura</i> sp. cf. <i>vittata</i>		x	3
<i>Rhopalaea birkelandi</i> Tokioka, 1971		x	2, 3
<i>Styela milleri</i> Ritter, 1907	x		1
<i>Styela canopus</i> (Savigny, 1816)	x	x	1,3
<i>Trididemnum opacum</i> (Ritter, 1907)	x		1

¹ as *Symplegma pizoni* in Tokioka (1972), but see Kott (1990) for further discussion.

²*D. candidum* is probably an incorrect identification. For many years many white didemnids were identified as *D. candidum* because researchers did not recognize the significance of differences in the larvae, spicules, tunic and other morphological characters.

on each side of the Panama Canal, while Pederson et al. (2005) found 13 species in one RAS along 300 miles of Atlantic coast from Maine to New York City and Cohen et al. (2005) found 26 along 250 miles of Pacific coast in southern California. Cohen (2006) found six ascidian species on the Pacific side of the Panama Canal and 16 ascidian species on the Atlantic side of the canal, but the length of coastline surveyed is unknown. Of the Pacific Panama species observed, only *Ascidia ceratodes* (Huntsman, 1912), *Lissoclinum fragile* (Van Name, 1902), *Pyura lignosa* Michaelsen, 1908, *Rhopalaea birkelandi* Tokioka, 1971, and *S. canopus* have been previously reported in Pacific Panama or Costa Rica waters. Of the Atlantic Panama species observed, all but the two *Polyandrocarpa* species have been previously reported in Atlantic Panama or Caribbean waters (Table 2).

We found more non-native species in the Pacific ascidian fauna (7 species, 35%) than the Atlantic ascidian fauna (2 species, 10%). By comparison, there were seven species (54%) in New England (Pederson et al. 2005) and 14 (54%) in southern California (Cohen et al. 2005). Our figures are conservative because of the high number of species designated as cryptogenic; some if not all of these cryptogenic species may be non-native which would bring the number of Atlantic Panama non-natives to 14 (70%) and Pacific Panama non-natives to 12 (60%). Lambert and Lambert (2003) showed that there is a significant latitudinal increase in non-native ascidian species in estuaries on the Pacific coast from Alaska to southern California.

Ascidian diversity may be related to coastal development patterns and environmental impacts (Carman et al. 2007). Ascidians are common inhabitants of harbors and marinas in temperate

Ascidians at the Panama Canal

Table 2. Ascidian species at the Panama Canal, status and geographic distribution. Abbreviations: C=Cryptogenic; I=Introduced; N=Native.

Species	Pacific	Atlantic	Status	Known distribution	Probable geographical origin	Source
<i>Ascidia ceratodes</i>	x		N	California, USA (Pacific) to N Chile	E Pacific	Van Name (1945), Tokioka (1972), Lambert and Lambert (1998, 2003)
<i>Ascidia curvata</i>		x	N	Bermuda, USA (Florida), Caribbean, Brazil	Tropical W Atlantic	Van Name (1945), Rocha and Kremer (2005)
<i>Ascidia incrassata</i>	x		I	South Africa, Mozambique	SW Indian Ocean	Monniot et al. (2001)
<i>Ascidia interrupta</i>		x	N	Bermuda, USA (North Carolina and Florida), Caribbean, Brazil, Azores, Gulf of Mexico	Tropical W Atlantic	Van Name (1945), Monniot (1983), Monniot and Monniot (1994), Rocha et al. (2005), Lambert et al. (2005)
<i>Ascidia sydneyensis</i>	x	x	I	Caribbean, SE and S Brazil, tropical E Atlantic, South Africa, Philippines, W Pacific, Hawaii, Guam, Palau, Polynesia	W Pacific	Van Name (1945), Kott and Goodbody (1982), Monniot (1983, 1987, 1997), Monniot and Monniot (1987), Abbott et al. (1997), Lambert (2002), Rocha and Kremer (2005)
<i>Ascidia</i> sp.	x		N	Panama (Pacific)	Panama (Pacific)	Bonnet and Rocha unpubl. data
<i>Ascidia panamensis</i>		x	N	Panama (Atlantic)	Panama (Atlantic)	Bonnet and Rocha (2011)
<i>Botrylloides nigrum</i>	x	x	C	Caribbean, Brazil, W and E Africa, Australia, Guam, China, Japan	W Atlantic? W Pacific?	Lambert (2003), Rocha and Kremer (2005), Rocha and Bonnet (2009)
<i>Botrylloides</i> sp.	x					
<i>Botryllus planus</i>	x		I	Bermuda, USA (Florida), Caribbean, Brazil	W Atlantic	Rocha and Kremer (2005), Rocha and Bonnet (2009)
<i>Didemnum psammathodes</i>		x	C	Caribbean, Gulf of Mexico, SE Brazil, E Africa, South Africa, Red Sea, Philippines, tropical W Pacific, Hawaii, Guam	?	Eldredge (1967), Tokioka (1970), Monniot (1983, 1995), Goodbody (1984), C Monniot and F Monniot (1994), F Monniot and C Monniot (1996, 1997, 2001), Rocha and Monniot (1995), Kott (1998), Monniot et al. (2001), Lambert (2002, 2003), Lambert et al. (2005)
<i>Didemnum perucidum</i>	x		I	Caribbean, S and SE Brazil, Senegal, Indo-west Pacific, Zanzibar, Hawaii, Guam, Palau, Florida, Gulf of Mexico	?	Monniot (1983), Rocha and Monniot (1995), Monniot and Monniot (1996), Godwin and Lambert (2000), Paulay et al. (2002), Lambert (2003)
<i>Didemnum</i> sp. white with green algae		x				
<i>Didemnum</i> sp.	x					
<i>Diplosoma listerianum</i>	x	x	C	Wide spread in tropical and temperate waters of all oceans	?	Lambert and Lambert (1998), Lambert (2002), Rocha and Kremer (2005), Rocha and Bonnet (2009)
<i>Herdmania pallida</i>		x	C	USA (Florida) to SE Brazil, Cape Verde, Gabon, South Africa, W Indian Ocean, Indo-west Pacific, Australia, Hawaii, Guam	Indo-west Pacific?	Kott (2002), Monniot (2002), Lambert (2003)
<i>Lissoclinum fragile</i>	x		I	Bermuda, Caribbean, Brazil, Argentina, Azores, Sierra Leone, Arabi Gulf, S Australia, W Pacific, Hawaii, Guam	?	Van Name (1945), Lambert (2003), Rocha and Kremer (2005), Rocha and Bonnet (2009)
<i>Lissoclinum verrilli</i>		x	N	Caribbean, New Caledonia, Brazil, Panama	Caribbean	Van Name (1945), Rocha et al. (2005), Monniot (2007)

Table 2 (continued).

Species	Pacific	Atlantic	Status	Known distribution	Probable geographical origin	Source
<i>Microcosmus exasperatus</i>	x	x	C	Bermuda, Caribbean, SE USA, Brazil, Mediterranean, South Africa, W Africa, Australia, W Pacific, Hawaii, Guam	?	Van Name (1945), Lambert (2002, 2003), Rocha and Kremer (2005)
<i>Perophora viridis</i>		x	N	Bermuda, Atlantic USA, Caribbean, Brazil, Azores, Sierra Leone, New Caledonia, Easter Island	W Atlantic	Van Name (1945), Millar (1957), Monniot (1974), Goodbody (1994), Rocha and Bonnet (2009)
<i>Phallusia nigra</i>		x	C	Bermuda, USA (Florida), Caribbean, Brazil, Guinea, Angola, Mediterranean, Red Sea, Persian Gulf, Indo-west Pacific, Hawaii, Guam	W Atlantic? Persian Gulf?	Van Name (1945), Millar (1958, 1975), Pères (1958), Abbott et al. (1997), Lambert (2003)
<i>Polyandrocarpa anguinea</i>		x	C	SE USA (Florida), Panama, Martinica, SE Brazil, Sierra Leone, South Africa, Mauricius Island, Indonesia, Phillipines, Australia, New Caledonia	?	Van Name (1918), Millar (1955, 1962), Rodrigues (1977), Monniot and Monniot (1994)
<i>Polyandrocarpa sagamiensis</i>		x	I	Japan, Guam, Hawaii	W Pacific	Tokioka (1953), Abbott et al. (1997), Lambert (2003)
<i>Polyandrocarpa zorritensis</i>	x		C	SW USA (California), Peru, S and SE Brazil, Mediterranean, Japan, Hawaii	?	Van Name (1945), Nishikawa et al. (1993), Abbott et al. (1997), Lambert and Lambert (1998, 2003), Rocha and Kremer (2005)
<i>Polyclinum constellatum</i>	x	x	C	Bermuda, USA (Florida, Gulf of Mexico) to S Brazil, South Africa, W Indian Ocean, W Pacific, Hawaii, S California	?	Van Name (1945), Tokioka (1967), Millar (1975), C Monniot and F Monniot (1987), F Monniot and C Monniot (1997, 2001), Monniot (1987), Abbott et al. (1997), Lambert (2002)
<i>Pyura lignosa</i>	x		N	Caribbean, Costa Rica, Panama (Pacific), Gulf of California, S California, Majuro, Japan, Philippines	Pacific coast Central America	Van Name (1945), Tokioka (1970), C Monniot (1983, 1994), Nishikawa (1984)
<i>Pyura torpida</i>		x	N	Cuba, Guadalupe, Panama, Colombia	Caribbean	Van Name (1945), C Monniot (1983), Rocha et al (2005)
<i>Pyura vittata</i>		x	C	Bermuda, USA (North Carolina and Florida), Caribbean, Brazil, E and W Africa, India, Hong Kong, Indonesia, Palau	W Pacific?	Van Name (1945), Abdal and Sivakumar (2007), Monniot (2009), Rocha and Bonnet (2009)
<i>Rhopalaea birkelandi</i>	x		N	Costa Rica and Panama (Pacific coast)	Pacific coast Central America	Tokioka (1971, 1972)
<i>Styela canopus</i>	x	x	C	E and W Atlantic, Indian Ocean, Australia, W Pacific, Hawaii, Guam, Easter Island, USA (California)	Pacific?	Kott (1985), Lambert and Lambert (1998, 2003), Lambert (2003), Rocha and Bonnet (2009)
<i>Symplegma brakenhielmi</i>	x		C	Caribbean, Brazil, Indian Ocean, W Pacific, Hawaii	?	C Monniot (1983), Kott (1985), C Monniot and F Monniot (1987, 1997), F Monniot and C Monniot (2001), Abbott et al. (1997), Lambert (2002)
<i>Symplegma rubra</i>	x		I	Bermuda, Caribbean, Gulf of Mexico, S and SE Brazil, E Africa, Palau	Caribbean?	F Monniot and C Monniot (1997), Lambert et al. (2005), Rocha and Kremer (2005)
<i>Trididemnum orbiculatum</i>	x		I	Bermuda, USA (Florida), Caribbean, Brazil	W Atlantic	Van Name (1945), F Monniot (1983), Rocha and Bonnet (2009)

and tropical waters (Van Name 1945; Monniot et al. 1991). In particular, because of their ability to be transported by ships and boats, ascidian diversity may be correlated with coastal shipping patterns, especially of non-native species. Thus, the high diversity of ascidians, especially introduced, non-native species, that we found was expected.

It is unclear whether ships introduced the non-native ascidians we found to the Panama Canal area and what role the canal serves as a corridor for these species. The canal is comprised of a series of interconnected freshwater lakes and this barrier probably inhibits some ascidian transfers. However, many ships take only about 11 h to transit the canal and some ascidian species are known to survive long periods with closed siphons (Sims 1984; Katayama and Ikeda 1987; A Coutts unpubl. obs.). In addition, ships are often required to wait several days at the entrance to the canal before they can transit. As a result, ships originating throughout the Pacific and Atlantic cluster together at mooring and anchor sites near the mouths of the canal. These ships could serve as major vectors for intra-oceanic introductions.

Environmental conditions can influence ascidian populations (Lambert 2001, 2005). Rainy season inputs to the study area can be considerable (Ibáñez 2005) but rainfall only temporarily reduces inshore salinity, particularly where tidal fluxes are large. *Ascidia* spp. and *R. birkelandi* must be able to tolerate a wider range of salinity and sediment fluxes than other ascidian species observed in our surveys because we easily found them in waters with salinity measurements of 29 to 36 psu and in shallow waters immediately adjacent to terrestrial sediment sources. High concentrations of nutrients usually coincide with heavy rainfall as well as coastal development; dissolved inorganic nutrients and plankton are at high concentrations in Panama coastal environments (D’Croz et al. 2005). Shallow water ascidians benefit from coastal nutrient input; this may be the reason for high ascidian biomass in Panamanian harbors and marinas on both the Atlantic and Pacific coasts. However, high levels of sediment flushed into systems by rainfall may negatively affect ascidians (Whitlatch and Osman 2000; Petersen 2007).

The ascidian faunas at both entrances to the Panama Canal are probably constantly changing because of frequent species introductions,

disturbances due to coastal development, and seasonal changes in environmental parameters (e.g., rainfall). Two of our sites were surveyed in 2002 (June, beginning of rainy season) and again in December 2008/January 2009 (end of rainy season). We treated the 2002 and 2008/2009 surveys as time-inclusive, though there were changes in the ascidian faunal composition at the two sites that were surveyed in both 2002 and 2008/2009. At the Balboa Yacht Club, three non-native species were recorded in 2002 and only one species (a different non-native species) was observed in 2008/2009. At the dock of the Smithsonian Tropical Research Institute (STRI)-Naos, four species (non-native) were recorded in 2002 and eight species (7 non-native and 1 native) were observed in 2008/2009 (Appendix 2). Increasing anthropogenic development along the Panama coastline may contribute to a change in the ascidian population, as increasing coastal development is associated with the increased presence of non-native species in temperate Pacific waters (Wonham and Carlton 2005). Cohen (2006) documented other non-native taxa at the Panama Canal, including barnacles, sponges, bryozoans, crabs, and fish. The construction of a third lane at the Panama Canal (2008–2014) is expected to double the number of ships going through the canal (Canal de Panamá 2010). To determine how Panamanian ascidian communities change over time, comprehensive baseline data should be collected annually at the same time of year.

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References

- Abbott DP, Newberry AT, Morris KM (1997) Reef and Shore Fauna of Hawaii. 6B: Ascidians (Urochordata). Special Publications Bernice Pauahi Bishop Museum Press, Honolulu, 64 pp
- Abdul J, Sivakumar V (2007) Occurrence and distribution of ascidians in Vizhinjam Bay (south west coast of India). *Journal of Experimental Marine Biology and Ecology* 342: 189–190, doi:10.1016/j.jembe.2006.10.041

- Bonnet NKY, Rocha RM (2011) The family Ascidiidae Herdman (Tunicata: Ascidiacea) in Bocas del Toro, Panama. Description of six new species. *Zootaxa* 2864: 1–33
- Bullard SG, Carman MR (2009) Current trends in invasive ascidian research. In: Wilcox CP, Turbin RB (eds) (2009) *Invasive Species: Detection, Impact and Control*. Nova Science Publishers, New York, pp 57–79
- Canal de Panamá (2010) <http://www.pancanal.com/eng/index/html> (Accessed 31 October 2010)
- Carman MR, Bullard SG, Donnelly JP (2007) Water quality, nitrogen pollution, and ascidian diversity in coastal waters of southern Massachusetts, USA. *Journal of Experimental Marine Biology and Ecology* 342: 175–178, doi:10.1016/j.jembe.2006.10.037
- Carman MR, Morris JA, Karney RC, Grunden DW (2010) An initial assessment of native and invasive tunicates in shellfish aquaculture of the North American east coast. *Journal of Applied Ichthyology* 26(2): 8–11, doi:10.1111/j.1439-0426.2010.01495.x
- Cohen AN (1999) Exotic organisms. In: Milanes C, Morry D, Parker T, Ricker K (eds) (1999) *Proceedings of California's Emerging Environment Challenges*, California EPA, Office of Environmental Health Hazard Assessment Publishers, June 25–26, 1998. Sacramento, CA, pp 5–9 to 5–13
- Cohen AN (2006) Species introductions and the Panama Canal. In: Gollasch S, Galil B, Cohen A (eds) (2006) *Bridging Divides: Maritime Canals as Invasion Corridors*. Springer, Dordrecht, The Netherlands, pp 127–206
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2005) Rapid Assessment Survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7: 995–1002, doi:10.1007/s10530-004-3121-1
- Coutts ADM, Dodgshun TJ (2007) The nature and extent of organisms in vessel sea-chests: A protected mechanism for marine bioinvasions. *Marine Pollution Bulletin* 54: 875–886, doi:10.1016/j.marpolbul.2007.03.011
- Coutts ADM, Sinner J (2004) An updated benefit-cost analysis of management options for *Didemnum vexillum* in Queen Charlotte Sound. Cawthron Report No. 925, Biosecurity New Zealand, Wellington, New Zealand, 14 pp
- D'Croz L, del Rosario JB, Gondola P (2005) The effect of freshwater runoff on the distribution of dissolved inorganic nutrients and plankton in the Bocas del Toro archipelago, Caribbean Panama. *Caribbean Journal of Science* 41(3): 414–429
- D'Croz L, Robertson DR (1997) Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Proceedings of the 8th International Coral Reef Symposium 2, pp 2053–2058
- Eldredge LG (1967) A taxonomic review of Indo-Pacific didemnid ascidians and descriptions of twenty-three central Pacific species. *Micronesica* 2: 161–261
- Godwin LS, Lambert G (2000) New records of Ascidiacea (Urochordata) in the marine invertebrate fouling community of O'ahu, Hawaii. *Occasional Papers of the Bernice Pauahi Bishop Museum* 64: 59–61
- Goodbody I (1984) Ascidians from Caribbean shallow water localities. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 67(203): 62–76
- Goodbody I (1994) The tropical Western Atlantic Perophoridae (Ascidiacea): I. The genus *Perophora*. *Bulletin of Marine Science* 55(1): 176–192
- Guzman HM, Guevara CA, Breedy O (2004) Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). *Environmental Conservation* 31(2): 1–11, doi:10.1017/S03768929040 01250
- Ibáñez A (2005) Geographical, climatic and geological characteristics of the Bahía Honda region (Veraguas, Panamá). In: Castroviejo S, Ibanez A (eds) (2005) *Studies on the Biodiversity of the Bahía Honda Region (Veraguas, Panamá)*. Consejo Superior de Investigaciones Científicas, Madrid, Spain, pp 627–742
- Katayama K, Ikeda Z (1987) Tolerance of fresh water, hot water and sun-drying by *Didemnum moseleyi*, fouling organisms attached to culture oyster. *Bulletin of the Fisheries Experiment Station, Okayama Prefecture* 2: 104–106
- Kott P (1985) The Australian Ascidiacea, part 1, Phlebobranchia and Stolidobranchia. *Memoirs of the Queensland Museum* 23: 1–440
- Kott P (1990) The Australian Ascidiacea, part 2, Aplousobranchia (1). *Memoirs of the Queensland Museum* 29(1): 1–226
- Kott P (1998) Tunicata. In: Wells A, Houston WWK (eds) (1998) *Zoological Catalogue of Australia*. CSIRO Publishing, Collingwood, Victoria, Australia, pp 51–252, 259–261
- Kott P (2002) The genus *Herdmania* Lahille, 1888 (Tunicata, Ascidiacea) in Australian waters. *Zoological Journal of the Linnean Society* 134: 359–374, doi:10.1046/j.1096-3642.2002.00009.x
- Kott P, Goodbody I (1982) The ascidians of Hong Kong. In: Morton BS, Tseng CK (eds) (1982) *Proceedings of the first International Marine Biological Workshop: the flora and fauna of Hong Kong and Southern China*. Vol.1. Hong Kong University Press, pp 503–504
- Lambert CC, Lambert G (1998) Non-indigenous ascidians in southern California harbors and marinas. *Marine Biology* 130: 675–688, doi:10.1007/s002270050289
- Lambert CC, Lambert G (2003) Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. *Marine Ecology Progress Series* 259: 145–161, doi:10.3354/meps259145
- Lambert G (2001) A global overview of ascidian introductions and their possible impact on the endemic fauna. In: Sawada H, Yokosawa H, Lambert C (eds) (2001) *The Biology of Ascidiacea*, Springer-Verlag, Tokyo, pp 249–257
- Lambert G (2002) Nonindigenous ascidians in tropical waters. *Pacific Science* 56: 291–298, doi:10.1353/psc.2002.0026
- Lambert G (2003) Marine biodiversity of Guam: The Ascidiacea. *Micronesica* 35–36: 588–597
- Lambert G (2005) Ecology and natural history of the protochordates. *Canadian Journal of Zoology* 83: 34–50, doi:10.1139/z04-156
- Lambert G, Faulkes Z, Lambert CC, Scofield VL (2005) Ascidians of South Padre Island, Texas, a key to the species. *Texas Journal of Science* 57(3): 251–262
- Lambert G (2007) Invasive sea squirts: A growing global problem. *Journal of Experimental Marine Biology and Ecology* 342(1): 3–4, doi:10.1016/j.jembe.2006.10.009
- Lambert G (2009) Adventures of a sea squirt sleuth: unraveling the identity of *Didemnum vexillum*, a global ascidian invader. *Aquatic Invasions* 4: 5–28, doi:10.3391/ai.2009.4.1.2
- Menge BA, Ashkenas LR, Matson A (1983) Use of artificial holes in studying community development in cryptic marine habitats in a tropical rocky intertidal region. *Marine Biology* 77: 129–142, doi:10.1007/BF00396310

- Millar RH (1955) On a collection of ascidians from South Africa. *Proceedings of the Zoological Society of London* 125: 169–221, doi:10.1111/j.1096-3642.1955.tb00597.x
- Millar RH (1957) Further notes on ascidians from Sierra Leone. *Annals and Magazine of Natural History*. 12 ser 10: 369–377
- Millar RH (1958) Some Ascidians from Brazil. *Annals and Magazine of Natural History* 13: 497–514
- Millar RH (1962) Some Ascidians from the Caribbean. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 13(59): 61–77
- Millar RH (1975) Ascidians from the Indo-West-Pacific region in the Zoological Museum, Copenhagen (Tunicata, Ascidiacea). *Steenstrupia* 3(20): 205–336
- Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S (2009) Characterizing vectors of marine invasion. In Rilov G, Crooks JA (eds) (2009) *Biological Invasions in Marine Ecosystems*. Springer, Berlin, pp 109–116
- Monniot C (1974) Ascidiées littorales et bathyales récoltées au cours de la campagne Biaçores: Phlébobranches et Stolidobranches. *Bulletin du Muséum National d'Histoire Naturelle*. 3a ser 173(251): 1327–1352
- Monniot C (1983) Ascidiées littorales de Guadeloupe 2. Phlébobranches. *Bulletin du Muséum National d'Histoire Naturelle* 4 ser. 5(1): 51–71
- Monniot C (1987) Ascides de Nouvelle-Calédonie I. Phlébobranches du lagon. *Bulletin du Muséum d'Histoire Naturelle* Paris 9: 3–31
- Monniot C (1994) *Pyura lignosa* (s. s.), a Pacific ascidian from Central America, with descriptions of species confused under this name. *Zoological Journal of the Linnaean Society* 110: 41–51, doi:10.1111/j.1096-3642.1994.tb01470.x
- Monniot C (1997) Ascides phlébobranches du canal du Mozambique. *Zoosystema* 19(4): 557–571
- Monniot C (2002) Stolidobranch ascidians from the tropical western Indian Ocean. *Zoological Journal of the Linnaean Society* 135: 65–120, doi:10.1046/j.1096-3642.2002.00017.x
- Monniot C, Monniot F (1987) Les ascidiées de Polynésie française. *Mémoires du Muséum d'Histoire Naturelle* ser A. 136: 1–155
- Monniot C, Monniot F (1994) Additions to the inventory of eastern tropical Atlantic ascidians: arrival of cosmopolitan species. *Bulletin of Marine Science* 54: 71–93
- Monniot C, Monniot F (1997) Records of ascidians from Bahrain, Arabian Gulf with three new species. *Journal of Natural History* 31: 1623–1643, doi:10.1080/00222939700770871
- Monniot C, Monniot F, Griffiths CL, Schleyer M (2001) South African Ascidians. *Annals of the South African Museum* 108: 1–141
- Monniot C, Monniot F, Laboute P (1991) Coral Reef Ascidians of New Caledonia. Orstom Editions, Paris, 247 pp
- Monniot F (1983) Ascidiées littorales de Guadeloupe. 1. Didemnidae. *Bulletin du Muséum National d'Histoire Naturelle* 4e ser 5: 5–49
- Monniot F (1995) Ascidiées de Nouvelle-Calédonie XV. Le genre *Didemnum*. *Bulletin Muséum National d'Histoire Naturelle* Paris 16: 3–11
- Monniot F (2007) Some comments on ascidians of New Caledonia. In: Payri CE, Richer de Forges B (eds) *Compendium of marine species of New Caledonia*. Comp. Mar. Tech. 117, 2nd edition, IRD Noumea, pp 349–356
- Monniot F (2009) Some ascidians from Indonesian marine lakes (Raja Ampat Islands, West Papua). *Zootaxa* 2106: 13–40
- Monniot F, Monniot C (1996) New collections of ascidians from the western Pacific and southeastern Asia. *Micronesia* 29: 133–279
- Monniot F, Monniot C (1997) Ascidians collected in Tanzania. *Journal of East African Natural History* 86: 1–35, doi:10.2982/0012-8317(1997)86[1:ACIT]2.0.CO;2
- Monniot F, Monniot C (2001) Ascidians from the tropical western Pacific. *Zoosystema* 23: 201–383
- Nishikawa T (1984) Ascidians from the Truk Islands, Ponape Island and Majuro Atoll (Tunicata, Ascidiacea). *Proceedings of the Japanese Society of Systematic Zoology* 27: 107–140
- Nishikawa T, Kajiwara Y, Kawamura K (1993) Probable introduction of *Polyandrocarpa zorritensis* (Van Name) to Kitakiushu and Koshi, Japan. *Zoological Science*, supplement: 176
- Paulay G, Kirkendale L, Lambert G, Starmer J (2002) The marine invertebrate biodiversity of Apra Harbor: significant areas and introduced species. *Micronesica* 588: 35–36
- Pederson J, Bullock R, Carlton J, Dijkstra J, Dobroski N, Dyrnyda P, Fisher R, Larry H, Hobbs N, Lambert G, Lazo-wasem E, Mathieson A, Miglietta MP, Smith J, Tyrrell M (2005) Marine invaders of the Northeast. Rapid assessment survey of non-native and native marine species of floating dock communities, August 2003. MIT Sea Grant College Program, Cambridge, 40 pp
- Pères JM (1958) Ascidiées récoltées sur les côtes méditerranéennes d'Israël. *Bulletin of the Research Council of Israel* 7B: 143–150
- Petersen JK (2007) Ascidian suspension feeding. *Journal of Experimental Marine Biology and Ecology* 342: 127–137
- Rocha RM, Bonnet NYK (2009) Ascidiées (Tunicata: Ascidiacea) introduzidas no Arquipélago de Alcatrazes, São Paulo, Brasil. *Iheringia Série Zoologia* 99: 27–35
- Rocha RM, Faria SB, Moreno TR (2005) Ascidians from Bocas del Toro, Panama. I. Biodiversity. *Caribbean Journal of Science* 41: 600–612
- Rocha RM, Kremer LP (2005) Introduced ascidians in Paranaguá Bay, Paraná, southern Brazil. *Revista Brasileira de Zoologia* 22: 1170–1184
- Rocha RM, Monniot F (1995) Taxonomic and ecological notes on some *Didemnum* species (Ascidiacea, Didemnidae) from São Sebastião Channel, South-east Brazil. *Revista Brasileira de Biologia* 55: 639–649
- Rodrigues SA (1977) Notes on Brazilian ascidians. II: on the records of *Polyandrocarpa anguinea* (Sluiter) and *P. maxima* (Sluiter). *Revista Brasileira de Biologia* 37: 721–726
- Sims LL (1984) Osmoregulatory capabilities of three macrosympatric stolidobranch ascidians, *Styela clava* Herdman, *S. plicata* (Lesueur) and *S. montereyensis* (Dall). *Journal of Experimental Marine Biology and Ecology* 82: 117–129
- Tokioka T (1953) Ascidians of Sagami Bay. Publications of Iwanami Shoten, Tokyo, 315 pp
- Tokioka T (1967) Pacific Tunicata of the United States National Museum. *U.S. National Museum Bulletin* 251: 1–247
- Tokioka T (1970) Ascidians from Mindoro Island, the Philippines. *Publications of the Seto Marine Biological Laboratory* 18: 75–107
- Tokioka T (1971) A new species of *Rhopalaea* from the Pacific coast of Costa Rica (Tunicata, Ascidiacea). *Publications of the Seto Marine Biological Laboratory* 19: 119–122

- Tokioka T (1972) On a small collection of ascidians from the Pacific coast of Costa Rica. *Publications of the Seto Marine Biological Laboratory* 19: 383-408
- Van Name WG (1918) Ascidians from the Philippines and adjacent waters. *Bulletin of the United States National Museum* 100(1): 49-174
- Van Name WG (1945) The North and South American ascidians. *Bulletin of the American Museum of Natural History* 84: 1-476
- Whitlatch RB, Osman RW (2000) Geographical distribution and organism-habitat associations of shallow-water introduced marine fauna in New England. In: Pederson J (ed) (2000) National Conference on Marine Bioinvasions. MIT Sea Grant Publications, Cambridge, Massachusetts, pp 61-65
- Wonham MJ, Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the northeast Pacific Ocean as a model system. *Biological Invasions* 7: 369-392

Supplementary material

The following supplementary material is available for this article.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2011/AI_2011_6_4_Carman_etal_Supplement.pdf

Appendix 1. Surveyed sites at Pacific and Atlantic entrances to the Panama Canal in 2002, 2008, 2009.

Appendix 2. Ascidian species on natural and artificial substrates at Pacific and Atlantic entrances to the Panama Canal 2002, 2008, 2009.