Biological Invasions **2:** 59–74, 2000.

Detecting invasions of marine organisms: kamptozoan case histories

Kerstin Wasson[1,*], Betsy Von Holle[2], Jason Toft[3] & Gregory Ruiz[4]
[1]*Elkhorn Slough National Estuarine Research Reserve, 1700 Watsonville Road, Watsonville, CA 95076, USA;* [2]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA;* [3]*Wetland Ecosystem Team, School of Fisheries, University of Washington, Box 355020, Seattle, WA 98195, USA;* [4]*Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, USA;* [*]*Author for correspondence (e-mail: wasson@biology.ucsc.edu; fax: +1-831-728-1056)*

Received 12 November 1998; accepted in revised form 5 June 2000

Key words: Chesapeake Bay, Entoprocta, fouling community, introduced species, Kamptozoa

Abstract

Detecting marine invasions can be challenging, especially for lesser-known taxa, and requires (a) thorough field surveys of the region of interest for members of the taxon, (b) systematic analyses to identify all species found, (c) literature searches for the worldwide distribution of these species and for previous records of the taxon in this region, and (d) application of rigorous criteria to assess whether each species found is native or introduced. We carried out these steps in order to detect and document kamptozoan (entoproct) invasions on the American mid-Atlantic coast. We report on the occurrence of two colonial kamptozoans (*Barentsia benedeni, Loxosomatoides laevis*) in Chesapeake Bay (Maryland and Virginia, USA). On the American Atlantic coast, *B. benedeni* had previously only been reported from Massachusetts, although this species has a worldwide distribution in bays and harbors. The genus *Loxosomatoides* had not previously been reported from North America and *L. laevis* was known only from India. Since the genus *Loxosomatoides* was very poorly characterized, we briefly review all four of its species, which differ only slightly from each other. We have also synonymized *L. japonicum* with *L. laevis*. We did not find any of the kamptozoan species previously recorded in surveys of Chesapeake Bay and the American Atlantic coast. This is the first detailed consideration of anthropogenic influences on kamptozoan distributions, and we emphasize that most kamptozoan species are cryptogenic pending further investigation.

Introduction

Detection of recent invasions of new regions by species from elsewhere is straightforward only for taxa for which there are accurate systematic descriptions and extensive and reliable historical records of distributions. Among marine invertebrates, such groups (e.g., large crabs, snails, and sea stars) are in the minority – most species of marine animals are small and inconspicuous, and have been largely overlooked. However, knowledge of the diversity and distribution of this overlooked majority is essential for detecting community changes over time. Moreover, even tiny and obscure organisms may nonetheless be abundant, and have large impacts on their physical environments and biological communities.

How can we detect invasions by lesser-known groups of tiny marine organisms? Collection of these organisms often takes special care and methods. Identification of the species located usually requires thorough taxonomic analyses (with the incidental benefit of increasing our understanding of the systematics of the group). Historical records are limited, and not necessarily reliable. To determine whether the distribution of the species has been affected by anthropogenic influences, knowledge of its ecology (e.g., microhabitat, association with known introductions, salinity tolerances) and life history (especially duration of the larval period and natural dispersal mechanisms) is required, but such information is not usually available in the literature.

Despite these challenges, detection of marine invasions can be readily accomplished. By carefully attending to the ecology and systematics of the species involved, we were able to document the recent invasion of Chesapeake Bay by two species of kamptozoans (entoprocts). The approach we took is applicable to other poorly known taxa of marine organisms.

Kamptozoans constitute a phylum of aquatic, sessile, suspension-feeding invertebrates. Due to their small size (zooids range from less than a millimeter to a few centimeters in height), they are easily overlooked in general surveys. Kamptozoan species are found in all the world's oceans, as well as in estuarine and freshwater habitats, and are sometimes extremely abundant members of the fouling community.

Colonial kamptozoans have only rarely been reported from the Atlantic coast of North America (Table 1). One member of the family Pedicellinidae (*Pedicellina cernua*) and six members of the Barentsiidae (all in the genus *Barentsia*) are known from this coast. In Chesapeake Bay, previous records (Osburn 1944; Wass 1972) document the occurrence of *P. cernua*, *B. discreta*, *B. gracilis*, and *B. laxa*. Based on our survey of the kamptozoan fauna of Chesapeake Bay, we have added a new barentsiid, *Barentsia benedeni*, to this list. Along the American Atlantic coast, this species was previously known only from Massachusetts. We also found a second kamptozoan species, the pedicellinid *Loxosomatoides laevis*, in Chesapeake Bay. The genus *Loxosomatoides* was not previously known to occur in North America.

In the fouling community that included these kamptozoans, the dominant species occupying primary substrate were apparently introduced to this area by anthropogenic means (Von Holle and Ruiz, in prep.). We hypothesize that *B. benedeni* and *L. laevis* are also exotic invaders, and test this hypothesis (vs. the null hypothesis that they are native) using a rigorous set of criteria (Chapman and Carlton 1994). Lindroth

Table 1. Records of colonial kamptozoans on the Atlantic Coast of North America.

Pedicellinidae		
Loxosomatoides laevis	Wasson et al. (this paper)	Chesapeake Bay, MD & VA
Pedicellina cernua	Dublin (1905)	Cold Spring Harbor, Long Island, NY
	Osburn (1912)	Beaufort, NC; Tortugas, FL
	Osburn (1944)	Chesapeake Bay, VA; Chincoteague Bay, VA
	Maturo (1957, 1959)	Beaufort, NC
	Wass (1972)	Chesapeake Bay, VA
	Calder and Maturo (1978)	Various sites, SC
Barentsiidae		
Barentsia benedeni	Jebram and Everitt (1982)	Lagoon Pond, Martha's Vineyard, MA
	Nielsen (1989)	Cape Cod, MA
	Wasson et al. (this paper)	Chesapeake Bay, MD & VA
B. discreta	Osburn (1912)	Woods Hole, MA; Beaufort, NC; Tortugas, FL
	Osburn (1944)	Chesapeake Bay, MD
	Maturo (1957)	Beaufort, NC
	Calder and Maturo (1978)	Charleston Harbor, SC
B. gracilis	Osburn (1944)	Chesapeake Bay, VA
B. laxa[a]	Osburn (1944)	Chesapeake Bay, VA; Chincoteague Bay, MD & VA; Nantucket Island, MA
	Rogick (1948)	Woods Hole, MA
	Maturo (1957, 1959)	Beaufort, NC
	Calder and Maturo (1978)	Various sites, SC
B. major[b]	Osburn (1912)	Woods Hole, MA
B. minuta	Winston and Håkansson (1986)	Capron Shoal, FL

[a]The material identified as *B. laxa* Kirkpatrick, 1890 probably consists of *B. elongata* Jullien & Calvet 1903. *B. laxa* appears to be native to Indopacific, from which it was first described.
[b]The status of *B. major* Hincks, 1888 is very uncertain. Osburn's identification may refer to *B. elongata* Jullien & Calvet 1903.

(1957) was one of the first to propose general criteria for the recognition of introduced species. He focused on terrestrial species, and presented five criteria. Carlton (1979a) expanded these criteria into six sets, divided into 13 categories. Chapman (1988) and Chapman and Carlton (1991, 1994) further developed these criteria, and applied them to some temperate amphipod and isopod crustaceans. To our knowledge, our use of these criteria represents their first application to colonial taxa.

Materials and methods

Field surveys

Our characterization of Chesapeake Bay kamptozoans was part of a larger investigation of the Chesapeake Bay fouling community (G. Ruiz et al., unpublished data). Data from two separate studies were used to identify and quantify the distribution of Chesapeake Bay kamptozoans. The first was a study of the fouling community composition of Chesapeake Bay, designed to identify and track the introduction of fouling organisms (G. Ruiz et al., unpublished data). There were 10 study areas, five clustered in northern Chesapeake Bay around the port of Baltimore, MD and five clustered in southern Chesapeake Bay around the port of Norfolk, VA. Five sites at approximately 2 km intervals were sampled within each area. (The exact location of these sites is available upon request from the authors.) At each site, four settlement plates (10 × 10 cm) were hung about 1 m below mean low water. Plates were set out in March and June 1995, and in June 1996 and 1997. They were collected in July and October–November of 1995, August–September 1996, and October 1997. All foulers that had settled on the plates were identified with light microscopy. Number of individuals (zooids, for colonial species) per species were estimated on the lower surface of one plate from each site.

The second study from which we obtained data on kamptozoans was a quantitative investigation of the effect of an introduced hydrozoan, *Cordylophora caspia*, on the community structure of the Chesapeake Bay fouling community (Von Holle and Ruiz, in prep.). Twenty-four wooden plates (25 × 25 cm) were immersed 2 m below mean low tide at three sites near Baltimore Harbor. The plates were deployed in June 1995 and collected twice, in July and August 1995. All foulers that had settled on the plates were identified with light microscopy. Percent cover by each species was estimated on the lower surface of each plate.

Systematics

Vouchers were taken from settlement plates from both studies described above, and the specimens preserved in 4% buffered formalin solution. We carefully examined and photographed these specimens using light microscopy. For 20 zooids of each species, measurements were taken with an ocular micrometer; the average and standard deviation for each measured parameter was calculated. Colonies from Chesapeake Bay were also cultured in the laboratory; they grew well at 18 °C, salinity approximately 20 parts per thousand, fed twice weekly about 10 cells/μl of a mixture of phytoplankton (*Dunaliella*, *Rhodomonas*, and *Isochrysis*) cultures.

Since the genus *Barentsia* has been fairly well characterized in the literature, identification of one kamptozoan species as *B. benedeni* was straightforward. However, the genus *Loxosomatoides* is poorly known, and identification was more difficult. To correctly identify the *Loxosomatoides* species, we requested type material of all previously described species in the genus.

Criteria for introduced species

To test the hypothesis that the kamptozoans were introduced to Chesapeake Bay rather than native, we assessed how well they met nine criteria presented by Chapman and Carlton (1994): (1) appearance in local regions where not found previously; (2) expansion of local range subsequent to first appearance; (3) access to human mechanism(s) of dispersal; (4) association with known introductions; (5) prevalence in or restriction to artificial or altered environments; (6) discontinuous or restricted regional distribution; (7) disjunct global distribution; (8) insufficient life history adaptations for global dispersal, and (9) exotic evolutionary origin.

Results

The four kamptozoan species reported by Osburn (1944) from the mouth of Chesapeake Bay were not found despite our extensive three-year survey in many regions, including higher salinity sites near the mouth of the Bay. However, two previously unreported kamptozoan species were common on our settlement plates.

Barentsia benedeni *(Foettinger, 1887)*

One of the kamptozoan species collected in Chesapeake Bay was readily identified as *Barentsia benedeni*. The Chesapeake zooids (Figure 1) closely match a recent re-description (Wasson 1997) of *B. benedeni*, in quantitative measurements and qualitative traits, and so a detailed description is not given here. The zooids have a characteristic segmented appearance, consisting of many nodes and rods. The upper nodes are sometimes urn-shaped, tapering basally. The basal nodes are packed with conspicuous storage cells. The rods lack pores, and are often extremely short, such that nodes directly abut each other like beads on a string. There is a thick cuticular septum at the stalk–calyx junction. The calyx is oriented slightly obliquely, tilted towards the oral side. This suite of traits exhibited by the Chesapeake zooids is unique to *B. benedeni*; there is no other species with which the zooids could be confused.

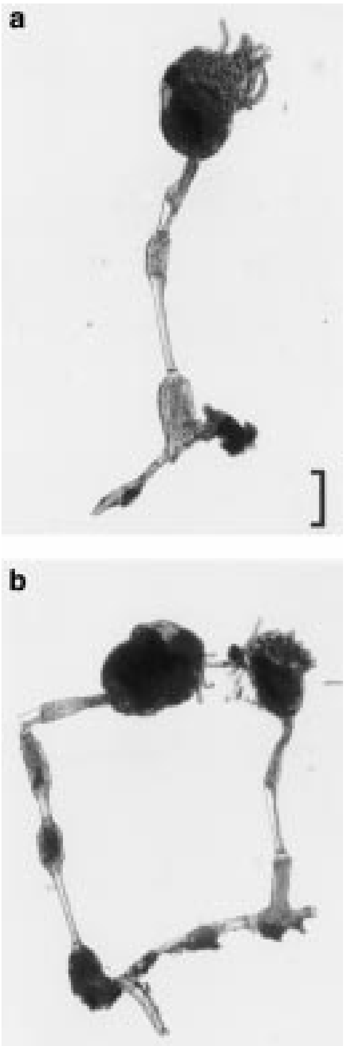


Figure 1. Barentsia benedeni zooids from Chesapeake Bay. Scale bar = 150 μm.

The Chesapeake *B. benedeni* zooids consisted of large, well-developed zooids in lush colonies. No hibernacula were visible in the colonies collected; hibernaculum production may not occur during spring and summer in this population. We have deposited a voucher of this species from Chesapeake Bay in the British Natural History Museum (1998.1.14.1).

B. benedeni was found on settlement plates at six sites and during four collection periods in the first study. In northern Chesapeake Bay, it was collected at one site near the Severn River in summer 1995, and at two sites near Baltimore Harbor in fall 1997. In the southern Bay, it was collected at two sites in Mobjack Bay in spring 1995 and at one site near Norfolk Harbor in summer 1996. *B. benedeni* was not found on any of the 24 plates deployed near Baltimore Harbor during the second study. Salinity ranged from 14 to 21 parts per thousand and temperature ranged 13 °C to 30 °C at these sites when kamptozoans were present. Three of the settlement plates on which *B. benedeni* was found had high (51–100) numbers of zooids, while the fourth had a moderate (11–50) number. *B. benedeni* was found intertwined in the fouling matrix provided by other abundant fouling organisms, including the barnacle *Balanus improvisus*, the bryozoan *Conopeum* sp., the scyphozoan *Chrysaora quinquecirrha*, the polychaetes *Demonax* sp., *Hydroides* sp., *Polydora cornuta*, *Sabella macropthalma* and their associated tubes, and the tunicate *Molgula manhattensis*. The protozoan *Metafolliculina* sp. was found on top of many species listed above as well as on the primary substrate. Common mobile species on the plates included the amphipod *Corophium* sp., various harpacticoid copepods including *Parategastes sphaericus*, and the flatworm *Stylochus ellipticus*.

Loxosomatoides laevis *Annandale, 1915*

The second kamptozoan species collected in Chesapeake Bay was identified as *L. laevis* Annandale,

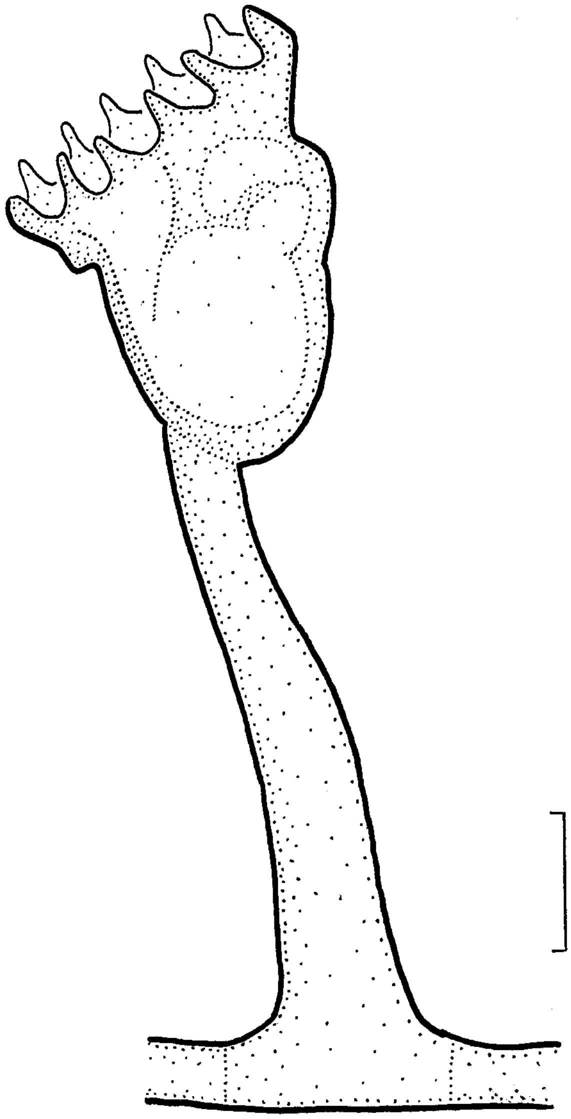


Figure 2. Loxosomatoides laevis. Diagram based on camera lucida drawing of a live, semi-contracted zooid from Chesapeake Bay. Scale bar = 100 µm.

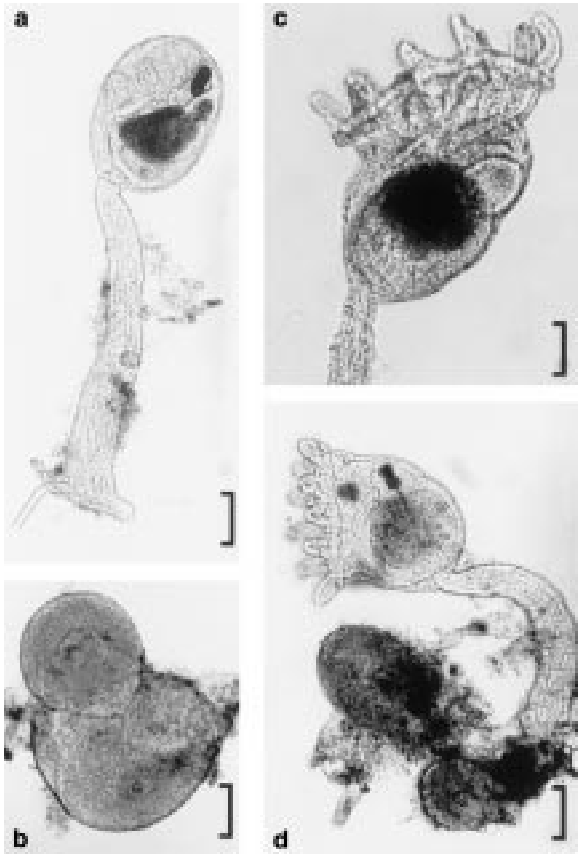


Figure 3. Loxosomatoides laevis from Chesapeake Bay. a: Contracted zooid, scale bar = 100 µm; b: two hibernacula, scale bar = 50 µm; c: semi-contracted calyx, scale bar = 50 µm; d: semi-contracted zooid, scale bar = 100 µm.

1915. Our specimens (Figures 2 and 3) match the original species description, except that our zooids were smaller, and had less pronounced cuticular shields. In order to provide a thorough justification of our identification of this poorly known species, a taxonomic description of material from Chesapeake Bay and a systematic review of the genus is provided in Appendix 1.

L. laevis was detected at 11 different sites, and during all five collection periods in the first study. In northern Chesapeake Bay, it was found at two sites near the Rhode River in spring 1995 and fall 1997, at two sites near the Chester River in spring 1995, and at five sites near Baltimore Harbor in summer 1995, fall 1995, summer 1996, and fall 1997. In the southern Bay, it was found at two sites near Norfolk Harbor in summer 1996 and fall 1997. At sites and times of collection, the salinity ranged from 4.7 to 14.8 parts per thousand, and temperature ranged from 23 °C to 28.1 °C. Zooid numbers ranged from moderate (11–50) to very high (> 1000) on the settlement plates. *L. laevis* occurred on 22 of the 24 plates deployed near Baltimore Harbor in the second study, and increased in abundance in the four weeks between sampling intervals. The average ± standard deviation of percent cover of the species on the plates was 0.03 ± 0.03 in July, but had increased to 2.54 ± 0.25 in August. This species was found in the fouling matrix of primary space occupiers, including the hydroid *Cordylophora caspia*, various bivalves, and the bryozoan *Victorella pavida*. The protozoans *Metafolliculina* sp., *Stentor* sp., *Vorticella* sp., and *Zoothamnium* sp. were found growing on these organisms as well as on the primary substrate. Common mobile species included various flatworms, harpacticoid copepods, and the nudibranch *Tenellia adspersa*.

Discussion

Predicted attributes of anthropogenically introduced species

Both *B. benedeni* and *L. laevis* from Chesapeake Bay display many of the nine predicted attributes (Chapman and Carlton 1991, 1994) of anthropogenically introduced species.

Attribute 1: Appearance in local regions where not found previously. This attribute could be readily assessed because there are reliable historical surveys of the regional fauna; both kamptozoans met this criterion. Osburn (1944) did not find either *B. benedeni* or *L. laevis* in his survey of kamptozoans of Chesapeake Bay (Table 1); he found various kamptozoans near the mouth of the bay, but found none in the upper, more brackish regions. Other surveys of Atlantic coast kamptozoans (Table 1) did not document the presence of these two species, either (Osburn 1912; Maturo 1957, 1959; Calder and Maturo 1978). Jebram and Everitt (1982) and Nielsen (1989) reported the presence of *B. benedeni* in Massachusetts; theirs are the only other report of this species on the Atlantic coast of North America (Table 2). No species in the genus *Loxosomatoides* was reported from this continent before our study (Table 3).

Attribute 2: Expansion of local range subsequent to first appearance. This criterion could not be adequately assessed because ours is the first report of these two species in Chesapeake Bay; we have no information on the exact location at which they first appeared nor any subsequent expansions of their local ranges.

Attribute 3: Access to human mechanism(s) of dispersal. Both of these kamptozoan species have access to human mechanisms of dispersal, locally in Chesapeake Bay and in other parts of their global distributions. We found both species in major ports in Chesapeake Bay. *B. benedeni* is known exclusively from bays and harbors around the world (Carlton 1979a; Emschermann 1994; Wasson 1997). *L. laevis* (and its congeners) is also known only from bays and harbors. Both species thus are found currently and historically in close association with ship traffic, one major human mechanism of dispersal for marine species. Their ability to settle and grow rapidly on panels (Rao et al. 1988; this study) would allow both species to attach to vessels in the short amount of time that the ships are in port. The capacity of both species to form hibernacula would enable them to withstand the stresses of long oceanic voyages. Ship-fouling (externally on the hull or internally in the sea chest and pipes) has been the most ubiquitous human mechanism of transoceanic and intercontinental dispersal of marine organisms during the last several centuries (Scheltema and Carlton 1984; Carlton 1985). Ballast water dumping by large international vessels is another possible vector for these kamptozoans. Fragments of adult colonies could be transported in ballast water from one port to another. Larval transport in ballast tanks is less plausible, since colonial kamptozoans have short-lived larvae. In an intensive sampling of ballast water of ships travelling from Japan to Oregon, Carlton and Geller (1993) did not positively identify any kamptozoan larvae or adults, but larvae may be difficult to recognize, and adults may be transported only occasionally during seasonal peaks in density when fragments are likely to be floating in harbor waters.

Transport and culturing of exotic oysters is another major human dispersal mechanism (Carlton 1992a,b). Both of these kamptozoan species are known to grow in oyster beds. The type colony of *B. benedeni* was collected in 1885 on a Belgian oyster bed (Foettinger 1887) and other *Barentsia* species are often reported on oysters (e.g., Korringa 1951). *L. laevis* was collected growing with oysters in Visakhaptnam harbor, India (Rao et al. 1988).

Attribute 4: Association with known introductions. Both locally in Chesapeake Bay and elsewhere in the world, *B. benedeni* and *L. laevis* grow in a community of introduced fouling organisms. As described above, we found them in Chesapeake Bay with non-native species, especially the bryozoan *V. pavida* and the hydroid *C. caspia*. The first record of *B. benedeni* on the Atlantic coast (Jebram and Everitt 1982) lists this species as part of the community of what we here recognize as introduced victorellids. In Lake

Table 2. The distribution of *Barentsia benedeni*.

Northern Eurasia (North Atlantic and Baltic Coasts)	
Oostende, Belgium	Foettinger (1887)
Osterschelde & Westerschelde, The Netherlands	Emschermann (1994)
Rendsburg (Nord-Ostsee Kanal), Germany	Emschermann (1994)
Western Baltic Sea	Nielsen (1989)
Hull, England	Ritchie (1911)
Port Erin, Isle of Man, Great Britain	Emschermann (1994)
Tynemouth, England	Emschermann (1994)
Southern Eurasia (Black, Caspian, Adriatic, and Mediterranean Seas)	
Sebastopol Bay (Black Sea), Crimean Peninsula, Ukraine	Nasanov (1926); Zernov (1913)
Varna (Black Sea), Bulgaria	Valkanov (1951)
Istanbul Bogazi (off Black Sea), Turkey	Valkanov (1951)
Krasnovodsk Bay (Caspian Sea), Turkmenistan	Zevina and Kuznetsova (1965)
Po River Delta (Adriatic Sea), Italy	Pisano (1980)
Rovinij (Adriatic Sea), Croatia	Emschermann (1994)
Banyuls-sur-Mer (Mediterranean Sea), France	Emschermann (1994)
Western North America (Pacific Coast)	
San Francisco Bay, CA	Craig (1929); Mariscal (1965); Carlton (1979a,b); Cohen and Carlton (1995); Wasson (1997)
Salton Sea, CA	Jebram and Everitt (1982)
Coos Bay, OR	Hewitt (1993); Wasson (1997)
Puget Sound, WA	Mills et al. (2000)
Eastern North America (Atlantic Coast)	
Martha's Vineyard, MA	Jebram and Everitt (1982)
Cape Cod, MA	Nielsen (1989)
Chesapeake Bay, MD & VA	Wasson et al. (this paper)
Japan (Pacific Coast)	
Matsushima Bay, Honshu	Toriumi (1944, 1951)
Australia (Pacific Coast)	
Port Adelaide, South Australia	Wasson and Shepherd (1997)
Port Kembla, New South Wales	

Merritt, Oakland (San Francisco Bay) California, *B. benedeni* was found with introduced bryozoans in the genera *Conopeum* and *Victorella* (Carlton 1979b). *L. laevis* was collected in Visakhaptnam harbor, India, with potentially introduced fouling species including the bryozoan *Bowerbankia gracilis*, the hydroid *Obelia* sp., and the worm-snail *Serpula vermicularis* (Rao et al. 1988).

Attribute 5: Prevalence in or restriction to artificial or altered environment(s). Both species were collected in Chesapeake Bay on artificial settlement panels in an otherwise mostly soft-bottom habitat, and both were abundant around the two largest ports in the bay. *B. benedeni* occurs on harbor piers, pilings, and floats around the world (Carlton 1979a; Emschermann 1994; Wasson 1997). Rao et al. (1988) found *L. laevis* on glass panels and harbor structures in India.

Attribute 6: Discontinuous or restricted regional distribution. Too little is known about the regional distribution of either species on the Atlantic coast (Tables 2 and 3) to make a satisfactory assessment. Their known distributions on this coast are disjunct, with known occurrences only in bays associated with ports, but no thorough surveys have been carried out at sites between known occurrences.

Attribute 7: Disjunct global distribution. Both species occur in multiple regions of the world (Tables 2 and 3). It seems unlikely that the distribution of these species is continuous; this would require extension into polar seas or across deep ocean waters. The global distribution of both species is thus considered disjunct.

Attribute 8: Insufficient life history adaptations for global dispersal. Colonial kamptozoans have short-lived larvae that could not traverse oceans by natural mechanisms. The larva of *B. benedeni* is known to settle within hours of release (Mariscal 1965, 1975). The larva of *L. laevis* is not known, but presumably the larval period is extremely short – hours to days – as in other colonial kamptozoans (Nielsen 1989; Emschermann 1994).

These kamptozoan species may settle on drifting algae or wood, and their ability to form hibernacula would allow them to survive long periods of transport. Kamptozoans have never been reported on drifting substrates in intercontinental waters, although careful searches of such substrates might detect them. However, natural movement of drifting substrates from one suitable habitat to another a continent away must be extremely rare, and seems unlikely to account for the global distributions of these species, or their subsequent apparent restriction to bays and estuaries.

Attribute 9: Exotic evolutionary origin. *Barentsia* species are found worldwide. Without a rigorous phylogenetic analysis of all species in the genus, it is impossible to determine where *B. benedeni* originated.

Three of the four *Loxosomatoides* species were described from Asia (the fourth species in the genus, described from South America, probably belongs in the genus *Myosoma*; see Appendix 1). *L. athleticus* and *L. colonialis* are only known from Thailand and India, respectively, while *L. laevis* is known from India, Japan, and now Chesapeake Bay. It therefore seems likely that the genus *Loxosomatoides* in general, and *L. laevis* in particular, originated in Asia, far from Chesapeake Bay.

Table 3. The distribution of *Loxosomatoides* spp.

India (Indian Ocean Coast)		
L. colonialis	Port Canning, Bay of Bengal	Annandale (1908, 1915)
L. laevis	Chilka Lake, Bay of Bengal	Annandale (1915)
	Visakhapatnam Harbor, Bay of Bengal	Rao et al. (1988)
Thailand (Gulf of Thailand)		
L. athleticus	Thale Sap, Malay Peninsula	Annandale (1916)
Japan (Pacific Coast)		
L. laevis	Matsushima Bay, Honshu	Toriumi (1951)
Eastern South America (Atlantic Coast)		
L. evelinae	Bahia de Santos, Brazil	Marcus (1939)
Eastern North America (Atlantic Coast)		
L. laevis	Chesapeake Bay, MD & VA	Wasson et al. (this paper)

Summary of nine attributes. Both *B. benedeni* and *L. laevis* display many of the predicted attributes of invasive species, as summarized in Table 4. To determine whether these two species show more attributes of invaders than do typical kamptozoans, we also show the correspondence of observed to predicted attributes for two other colonial kamptozoan species, *Barentsia hildegardae*, a congener of *B. benedeni*, and *Myosoma spinosa*, a pedicellinid similar to *Loxosomatoides*. Information about these species was taken from Wasson (1997).

B. hildegardae and *M. spinosa* do not have predicted attributes 1, 2, 6, or 7 of invasive species; they are found continuously on the Pacific coast of North America but not elsewhere in the world and have not expanded their ranges. In this regard they differ from the two species in Chesapeake Bay. *M. spinosa* also differs from the Chesapeake Bay species in attributes 3, 4, and 5; it is mostly restricted to natural habitats and therefore does not have access to anthropogenic dispersal

Table 4. Summary of the correspondence of observed attributes of *Barentsia benedeni* and *Loxosomatoides laevis* from Chesapeake Bay and *B. hildegardae* and *Myosoma spinosa* from the northeastern Pacific with predicted attributes of introduced species. See text for description of each attribute.

Species	Attributes								
	1	2	3	4	5	6	7	8	9
B. benedeni	Yes	?	Yes	Yes	Yes	?	Yes	Yes	?
L. laevis	Yes	?	Yes	Yes	Yes	?	Yes	?	Yes
B. hildegardae	No	No	Yes	Yes	Yes	No	No	Yes	?
M. spinosa	No	No	No	No	No	No	No	Yes	?

mechanisms and is not associated with other invaders. *B. hildegardae* is sometimes encountered on floats, and thus tenuously meets the criteria for attributes 3, 4, and 5. The two northeastern Pacific species have short-lived larvae and thus meet the criterion for attribute 8; this attribute is not meaningful for determining whether a particular kamptozoan is invasive, since most kamptozoans have very limited dispersal. The evolutionary origins of the species are unknown, so attribute 9 could not be assessed.

B. benedeni and *L. laevis* in Chesapeake Bay thus display generalized attributes of invasive species, and differ in significant ways, mostly regarding their distribution, from kamptozoans presumed to be native. We therefore conclude that both of these species represent anthropogenic introductions to Chesapeake Bay.

Biogeography of B. benedeni *and* L. laevis

B. benedeni has been reported from selected bays and harbors in Europe, Japan, Australia, and North America (Table 2). Since its colonies are small and inconspicuous, the species has almost certainly been overlooked in many other bays and harbors within its known continental range; it may also be present but as yet unnoticed in other areas, such as South America, Africa, and Asia. Furthermore, it will probably continue to spread to new areas in the future. This species' tolerance of a wide range of salinity and temperature conditions has apparently enabled it to survive in many novel regions to which it has been transported. However, the species seems to be found almost exclusively in disturbed habitats, often in brackish water. Currently we have no evidence whether pre- or post-settlement factors limit its distribution to such habitats.

While *B. benedeni* was probably introduced to most parts of its current distribution by anthropogenic means, namely ship-fouling and oysterculturing (Carlton 1975, 1979a,b; Cohen and Carlton 1995), it must be native somewhere in the world. Where did this species occur naturally, centuries ago? This question cannot be answered given our very limited knowledge about the past and present distribution of this species. It was first reported from northern Europe, then from southern Europe, western North America, Japan, eastern North America, and Australia, in turn (Table 2). Based on this pattern, Carlton (1979a) suggested that the species was native to Europe. However, except for the American Atlantic coast none of the regions in which *B. benedeni* is now known to be present were thoroughly surveyed prior to the first report of the species. Its apparent spread from Europe may simply represent the order in which the kamptozoan fauna of the regions was studied.

We do have evidence that *B. benedeni* was introduced fairly recently to eastern North America, since the kamptozoan fauna of the Atlantic coast, including Chesapeake Bay, had been surveyed by Osburn (1912, 1944) and others (Table 1) and this species was not found until 1982 (Jebram and Everitt, 1982). By far the most common anthropogenic transport mechanism for invertebrates into Chesapeake Bay is international shipping, and the majority of current ship traffic entering Chesapeake Bay is from Europe (Carlton et al. 1995). Therefore, it is likely the Chesapeake populations of *B. benedeni* are derived from European populations transported via ship-fouling. However, other vectors and other source populations cannot be excluded. Ships arrive from other destinations, and oysters have been brought into Chesapeake Bay from the American Pacific coast and from elsewhere (Mann 1979; Mann et al. 1991; Carlton 1992a,b; Lipton et al. 1992). Since *B. benedeni* is known to grow on them, planting of imported oysters is a plausible mechanism of introduction, through a much less frequent event than arrival of ships from distant waters.

L. laevis is known only from India, Japan, and Chesapeake Bay (Table 3). The closely related species *L. athleticus* and *L. colonialis* are known from Thailand and India, respectively (Table 3). The kamptozoan fauna of Asia (except for Japan) has never been thoroughly surveyed, so it is difficult to determine the nature of the regional distribution of these species. They were collected from brackish bays and harbors, and may be limited by pre- or post-settlement factors to such environments.

Given the current distribution of these *Loxosomatoides* species (Table 3), it seems likely that they are native to Asia, and that *L. laevis* was introduced from somewhere in Asia to Chesapeake Bay sometime after 1944, when Osburn carried out his survey of the region. As discussed in Appendix 1, Chesapeake Bay *Loxosomatoides* zooids are morphologically more similar to Japanese than to Indian material. We therefore suggest that *Loxosomatoides* arrived in Chesapeake Bay on ships travelling from Japan.

If *L. laevis* has been transported from Asia to eastern North America, why has this species not also been introduced to other regions around the world? Of course, it may occur unrecorded in regions that have not been surveyed for kamptozoans. However, the species was not detected in recent surveys of northern Europe (Nielsen 1989; Emschermann 1994), eastern and southern Australia (Wasson and Shepherd 1997), and western North America (Wasson 1997). Members of the genus *Loxosomatoides* are rather distinctive, and not easily confused with other pedicellinids, so the absence of reports probably reflects a real absence from these regions. This absence remains, for now, a mystery, and we will be curious to observe whether *Loxosomatoides* appears in bays and harbors of other regions in coming years. With our current knowledge about its distribution as a baseline, we will be able to document the spread of this species if it invades regions that continue to be regularly surveyed, such as western North America and northern Europe.

Environmental physiology of Chesapeake Bay kamptozoans

B. benedeni and *L. laevis* are the only kamptozoans that we found in the disturbed regions of Chesapeake Bay, and they thrive near the two major ports (Table 1). What enables these species to survive in such disturbed habitats? Both species have wide temperature and salinity tolerances, and both species form hibernacula that enable them to resist extreme environmental fluctuations. *B. benedeni* zooids have been reported to survive temperatures from 5 °C to 30 °C (Wasson 1997; this study) and salinities from 7 to 35 parts per thousand (Emschermann 1994; Wasson 1997; this study). Moreover, new zooids can be regenerated from stalk nodes and hibernacula after months of immersion in pure fresh water (Nasanov 1926). Hibernacula also are resistant to cold temperatures and even freezing, as well as to low oxygen levels and brief periods of desiccation (Emschermann 1994). The multiple stalk nodes of this species may represent an adaptation to sedimentation; new stolons form from upper stalk nodes and allow colony growth to continue when colonies are buried in sediment (Emschermann 1994). *L. laevis* zooids have been found at water temperatures of 23–32 °C (Rao et al. 1988; this study) and salinities of 4.7–28 parts per thousand (Rao et al. 1988; this study). Annandale (1915) collected colonies at salinities of 9–14 parts per thousand, but found colonies could withstand brief immersion in pure fresh water and also survived in very saline (35 parts per thousand) water. Such broad tolerances and the formation of hibernacula are unusual traits for kamptozoans, and are surely related to the brackish water habitats of these species.

Kamptozoans: native, introduced, or cryptogenic?

Many kamptozoans have broad, ‘cosmopolitan’ distributions. For instance, three of the four colonial kamptozoans previously reported from Chesapeake Bay – *Barentsia discreta*, *B. gracilis*, and *Pedicellina cernua* – have been reported from numerous sites around the world (Nielsen 1989; Wasson 1997). Many of these reports may represent misidentifications; non-experts often gave European names to specimens from distant localities without a sufficiently thorough taxonomic investigation to justify doing so. For instance, Wasson (1997) found that all reports of *B. gracilis* and *P. cernua* from the northeastern Pacific were in error, and referred to undescribed endemic species. However, even if literature by non-experts is disregarded, it is clear that some kamptozoan species are currently broadly distributed in bays and harbors around the world.

Are ‘cosmopolitan’ distributions the result of natural processes, or should they be attributed to anthropogenic influences? One way to answer this question is to rigorously compare observed attributes of the species to predicted attributes of introduced species. This method was developed for amphipod and isopod crustaceans (Chapman 1988; Chapman and Carlton 1991, 1994) and was used in this study for kamptozoans, but could be applied to any taxon. Such an analysis can be used to determine whether the hypothesis that a given population of a species is native, or the alternative hypothesis that it has been anthropogenically introduced, is better supported by the available evidence. In the absence of such a test of hypotheses, no assumptions should be made about whether a species is native or introduced. We therefore recognize that most kamptozoan species, especially those with widespread distributions, should be classified as cryptogenic (Carlton 1996). Only further investigations can reveal whether their distributions are the result of natural processes or human influences.

The challenge of detecting marine invasions

We took four steps to detect whether there were any invasive kamptozoans in Chesapeake Bay: (a) thorough field surveys of the region for members of the taxon,

(b) systematic analyses to identify all species found, (c) literature searches for the worldwide distribution of these species and for previous records of the taxon in this region, and (d) application of rigorous criteria to assess whether each species found was native or introduced. These steps are generally applicable to the detection of invasions by any taxon in any region. Based on this study of kamptozoans, we have a few cautionary notes for each of these steps, relevant in particular to other neglected marine organisms.

a) To locate tiny marine organisms, a casual search of substrata will likely not suffice; specialized searching methods may be required. We were able to locate the kamptozoans only through extensive deployment of settlement plates at many sites over multiple seasons.

b) Identification of the species found may not be straightforward for many marine taxa. The taxonomy of tiny organisms, in particular, is often difficult, since described species are not well-characterized in the literature, and many species remain undescribed. Identification therefore often involves far more than simply using an existing key – type specimens must be requested from museums and the original species descriptions obtained. After doing the systematic work necessary for identifying the species, it may be useful to characterize the systematics of the species or genera in question, as we have done here, since this may require little extra effort and provide a critical resource for future investigators.

c) To determine the worldwide distribution of species found in the field, and, for suspected invaders, to investigate their route of spread, it is necessary to search taxonomic papers from around the world. An additional literature search must be carried out for all members of the taxon in the region of interest, to allow for comparison between previous records and the current study. For many marine taxa, there will be few records of the species in question. Those papers that are located often are not straightforward to interpret. The species identifications cannot necessarily be relied upon, since (i) they may have been carried out by non-experts, and (ii) experts may have worked under the assumption that most species have cosmopolitan distributions, and put European names on species found elsewhere despite consistent differences with their name-sakes. If possible, it is best to augment the literature search with an examination of vouchers from the authors of each record.

d) The application of rigorous criteria to determine whether species found in a region are native or introduced requires knowledge of ecological and life history attributes of the species, as well as of their systematics and distribution. This information is often not available in the literature, and must be determined first-hand. We also found it useful to compare closely related species that are presumed to be native to potential invaders (Table 4); this required additional knowledge about the traits of the native species.

Despite these cautionary notes, we strongly advocate taking this type of a thorough approach to the detection of marine invasions. Only through a combination of extensive field surveys, systematic analyses and examination of historical records can we understand the dynamics of invasion for any particular taxon or region, and only by combining knowledge from many taxa and regions can we discover broad-scale patterns of distribution and abundance of invasive species.

Acknowledgements

Field and laboratory work at the Smithsonian Environmental Research Center was fruitfully guided by P. Fofonoff, A. Frese, S. Godwin, L. Hartman, L. McCann, D. Smith, W. Walton, and M. Wonham. The systematic part of this study was carried out at Friday Harbor Laboratories, and we are grateful for the facilities and support provided. B.P. Haldar (Zoological Survey of India) and M. Spencer Jones (Natural History Museum, London) graciously supplied us with type specimens. We are also indebted to librarians A. Haggins (SERC) and V. Silen (University of Washington), who deftly tracked down the necessary references. We are particularly grateful to J.T. Carlton for lively and instructive discussions regarding marine invasions and for his thoughtful, detailed editorial suggestions. This research was supported, in part, by a University of California President's Postdoctoral Fellowship (to KW), and by the Smithsonian Institution and Maryland Sea Grant (to GMR). This is SERC Invasion Biology Program Contribution number 20.

Appendix 1. Systematic review of the genus *Loxosomatoides*

Overview

The genus *Loxosomatoides* was erected in 1908 by Annandale, for *L. colonialis*. He later described *L. laevis* and *Chitaspis athleticus*, both of which were quite similar to *L. colonialis*. Because of this similarity, we hereby synonymize the genus *Chitaspis* Annandale, 1916 with *Loxosomatoides*. In 1939, Marcus described another species in the genus *Loxosomatoides*, *L. evelinae*; this species seems very similar to *Myosoma spinosa* Robertson, 1900. In 1951, Toriumi described *Loxosomatoides japonicum*. This species is here synonymized with *L. laevis* Annandale, 1915.

Loxosomatoides *and related genera*

Loxosomatoides species display all the characteristic traits of the Family Pedicellinidae (*sensu* Emschermann, 1972), to which they belong; they form stolonate colonies of zooids whose stalks are not differentiated into nodes and rods. They differ from *Pedicellina* species in having stronger oral calyx musculature, an obliquely tilted calyx, an aboral shield of thickened cuticle on the calyx, and in general, less laterally compressed calyces (Appendix 2). The genus *Loxosomatoides* differs from *Myosoma* in having somewhat less muscular stalks, in occurring in brackish water, and in sometimes forming hibernacula. Nevertheless, the two genera are rather similar, and could be synonymized.

The four *Loxosomatoides* and two *Myosoma* species can each be differentiated by the attributes presented in the tabular key (Appendix 2). The differences between them may be due to genetic isolation and differentiation; i.e., they actually may represent six distinct biological species. Alternatively, the differences between them may represent environmentally-induced plasticity, or local adaptation; some of these species may turn out to be populations of the same species. All six species are certainly quite similar to each other, and thus are probably very closely related. Their exact status cannot be determined without further material.

We converted the information in Appendix 2 into binary characters, (0 = no, 1 = yes), and analyzed this data matrix of unordered and unpolarized characters using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1.1 (Swofford 1993). An exhaustive search yielded the tree shown in Appendix 3, with length 11, consistency index of 0.82, and retention index of 0.78. A bootstrap analysis with 1000 replicates and a branch-and-bound search with a 50% majority were carried out; the resulting bootstrap values are shown on the nodes in Appendix 3. This tree must be considered a preliminary hypothesis of the relationships between these six species, since it is based on only nine characters and since none of the nodes are very well supported. Nevertheless, this cladogram summarizes our current state of knowledge about the relationship of these taxa, suggesting that (1) *L. colonialis* and *L. laevis* are closely related; (2) the genus *Myosoma* is paraphyletic; (3) *L. evelinae* is not closely allied to the other species in the genus *Loxosomatoides*.

The four *Loxosomatoides* species are briefly discussed below. For a review of *Myosoma*, see Wasson (1997).

Loxosomatoides colonialis *Annandale, 1908*

Synonymy. *L. colonialis* Annandale, 1908: 14–19, Figures 2–7; Annandale, 1915: 129.

Type locality. Brackish ponds at Port Canning, Bay of Bengal, India.

Types. Holotype deposited in the Indian Museum (specimen number unknown); 'cotype' in British museum (BMNH 1908.9.14.3-4).

Material examined. The specimen sent by the Indian Museum consists of two twigs covered by lush growth of a number of different colonies; this specimen bears no number or collection information, but presumably comprises the material deposited by Annandale as the holotype. The British Museum has a 'cotype' (BMNH 1908.9.14.3-4) and two supplementary slides (BMNH 1912.1.1.144, BMNH 1917.1.1.176); we examined the 'cotype' and the former slide.

Brief description and discussion. Zooids of this species are characterized by spines on the aboral side of the calyx, but not on the stalk (Appendix 2). Our examination of the material from India generally matches Annandale's description. Measurements given below (as averages ± standard deviations) are based on our observations. A photomicrograph of this material is available from K. Wasson on request.

The stolon is fairly narrow (63 ± 23 μm), divided regularly into fertile and sterile segments. We observed occasional golden-brown, generally two chambered hibernacula (about 200 μm in diameter) among the stolons; Annandale had not reported hibernacula for this species. The stalk is long (1253 ± 297 μm), tapering slightly from base to apex; it is wider in the middle (183 ± 34 μm) than at the calyx (138 ± 24 μm). The layer of longitudinal muscles in the stalk is somewhat thicker on the oral than the aboral side. There are no stalk spines. The stalk – calyx attachment occurs on the oral side of the calyx, and the calyx is tilted obliquely. The calyx is large (493 ± 72 μm), a bit narrower in lateral view (341 ± 45 μm) than in oral view (365 ± 35 μm); it is not laterally compressed. Within the oral hemisphere of the calyx, there are multiple muscle strands running from the base of the calyx to the esophagus; Annandale did not note this calyx musculature. There are 12–14 tentacles, which are oriented obliquely to the stalk. Calycal spines are invariably present, but differ greatly in length from zooid to zooid; they range from short (5 μm) nubbins to long (20 μm) protuberances. The aboral shield varies from a delicate, pale yellow shell to a thick, dark brown covering, with polygonal cuticular ridges. The whole aboral side of the calyx is generally obscured by adhering debris. The ornamentation pattern we observed on the aboral shield was less conspicuous than Annandale illustrated, perhaps due to the extended period of fixation. Calyces appear to be gonochoric. Female and male calyces seem to occur in separate regions of the substrate, so perhaps the colonies are gonochoric as well.

As the first member of the genus, this species is in no danger of being synonymized with another *Loxosomatoides* species. It does resemble *Myosoma spinosa*, but can be distinguished by its consistent lack of stalk spines and its brackish water habitat.

Loxosomatoides laevis *Annandale, 1915*

Synonymy. *L. laevis* Annandale, 1915: 129–132, Figures 1–3; Rao et al. (1988): 66–67, Figures 12, 13 and 18; *L. japonicum* Toriumi, 1951: 17, Figures 5–8.

Type locality. Chilka Lake, Bay of Bengal, India.

Types. The type (ZEV 6211/7, Indian Museum) is damaged and unavailable for study (12 May 1997, P. Mukhopadhyay, Zoological Survey of India, pers. comm.).

Material examined. Many colonies from Chesapeake Bay.

Description of Chesapeake Bay material. Our specimens (Figures 2 and 3) match the original species description, except that our zooids were smaller, and had less pronounced cuticular shields. A voucher has been deposited in the British Natural History Museum (BMNH 1998.1.14.2). Colonies cultured in the laboratory did not differ from field-collected material. Most of the colonies collected were very small, and contained mostly small zooids close to a growing stolon tip. The measurements given (as averages ± standard deviations) therefore may not encompass the upper limits for many of the parameters.

The stolon is pale and fairly narrow (48 ± 12 μm), divided into fertile (zooid-bearing) and sterile segments, as in most other colonial species. No hibernacula were present in our spring and summer collections, but many hibernacula formed in colonies collected in October and cultured in the laboratory. The hibernacula are dark brown chambers about the size of calyces (192 ± 48 μm), covered with a thick cuticle and filled with granular material. New zooids were observed germinating from hibernacula in lab cultured material in November (one month after collection).

The stalk is fairly wide (73 ± 16 μm in the middle), tapering at the apex just beneath the calyx (46 ± 6 μm at the apex). It is about two times as long (552 ± 153 μm) as the calyx is high. The layer of longitudinal muscles in the stalk is somewhat thicker on the oral than the aboral side. There are no stalk spines. The stalk–calyx attachment occurs on the oral side of the calyx (rather than at the base, as in *Pedicellina*); as a result, the junction is sloped, and the calyx is tilted obliquely. There are about 5–8 star cells bridging the junction.

Most calyces examined were quite small (235 ± 36 μm). They are only slightly wider in side view (166 ± 35 μm) than in aboral or oral view (160 ± 31 μm); calyces are very slightly compressed laterally. There are 12–14 tentacles, which extend obliquely, rather than vertically, due to the orientation of the calyx. Strong muscle fibers prominently run from the base of the calyx to the atrium in the oral half of the calyx. In the smallest calyces, the cuticle of the oral and aboral sides is similar in appearance. In larger calyces, the aboral side of the calyx is covered with debris, apparently adhering to glandular secretions of large, lumpy cells visible in the body wall. In the largest calyces examined, the cuticle on the aboral side was thick and shield-like, and cracked into a reticulated pattern of closely meshed polygons on the calycal surface. No deep depressions or more conspicuous ornamentation was present in any calyces, and spines were always absent.

The larger calyces from all collection dates were sexually mature. They appear to be single-sexed, but calyces of both sexes were sometimes found together in the same clump, suggesting that colonies may be hermaphroditic. The brood chamber is large and thick-walled. Only small embryos were observed in the brood chamber; the larval form is not known. The presence of many tiny colonies on settlement plates during spring and summer suggests that larval recruitment was occurring during this period.

Discussion. The key trait distinguishing *L. laevis* from *L. colonialis* is the consistent absence of calycal spines in the former (Appendix 2). In *L. colonialis*, spine length can vary greatly; it seems possible that spines might be entirely absent under some environmental conditions, in which case *L. laevis* should be synonymized with *L. colonialis*. However, colonies of *L. laevis* cultured in the laboratory under varying conditions never developed spines.

L. laevis also resembles *Myosoma hancocki* Soule, 1955, but can be distinguished by its lack of oblique stalk musculature, by its brackish water habitat, and by the ability to form hibernacula.

Our material from Chesapeake Bay contained mostly small calyces with thin aboral shields, but the larger calyces we observed had thicker, more ornamented calycal shields. Toriumi (1951) erected *L. japonicum* for a species that resembled *L. laevis* except for the smaller size and less developed aboral shields. The type material for *L. japonicum* does not exist anymore; the jar originally containing the specimen only has a few tiny pieces of an ascidian in it (25 April 1996, P. Emschermann, University of Freiburg, pers. comm.). We find it very likely that Toriumi's material consisted of some young *L. laevis* colonies, and have therefore synonymized *L. japonicum* with *L. laevis*.

Rao et al. (1988) found *L. laevis* in Visakhapatnam harbor, India. Their description matches that of Annandale, so we have confidently included their identification in the synonymy for this species.

Loxosomatoides athleticus *Annandale, 1916*

Synonymy. *Chitaspis athleticus* Annandale, 1916: 17–19, Figure 1 and pl. 1.

Type locality. Thale Sap, Gulf of Thailand.

Types. The type (ZEV 7157/7, Indian Museum) is damaged and unavailable for study (12 May 1997, P. Mukhopadhyay, Zoological Survey of India, pers. comm.).

Material examined. None.

Brief description and discussion. This species strongly resembles *L. laevis*. However, *L. athleticus* has oblique stalk musculature that is apparently absent in the other *Loxosomatoides* species; in this regard, the species resembles *Myosoma*. However, it bears an even greater resemblance to *Loxosomatoides*, especially in terms of the ornamentation of the aboral shield, and its brackish water habitat. Annandale believed that this species differed from *Loxosomatoides* species in having conspicuous calyx muscles; we have found that *L. laevis* and *L. colonialis* have conspicuous calyx musculature as well. The differences between this species and *L. laevis* seem too slight to justify its being in a separate genus, and we therefore have synonymized the genus *Chitaspis* with *Loxosomatoides*.

Loxosomatoides evelinae *Marcus, 1939*

Synonymy. *L. evelinae* Marcus, 1939: 121–122, Pl. 5, Figure 2a–c.

Type locality. Bahia de Santos, Brazil.

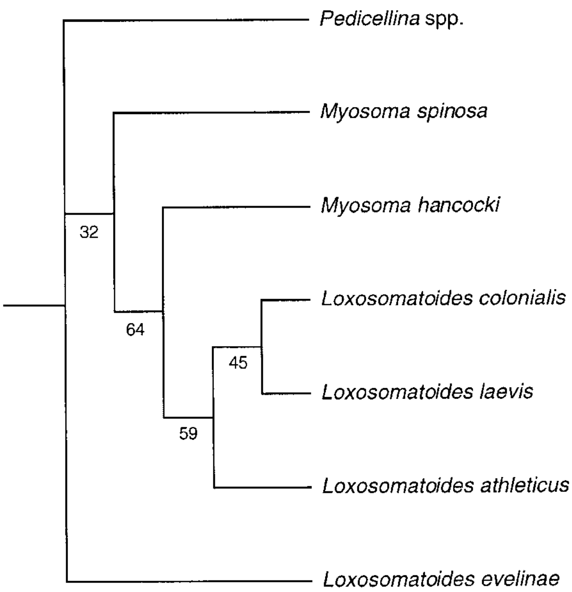
Types. The British Museum has the only known specimen (1948.2.16.77) of this species, but it is currently lost (21 April 1997, M.E. Spencer Jones, British Museum, pers. comm.). There is apparently no type material in the Zoology department of the University of São Paulo, where Marcus worked (4 June 1997, C.E.F. da Rocha, pers. comm.).

Material examined. None.

Brief description and discussion. This species appears to be very similar to *Myosoma spinosa* Robertson, 1900. It differs only in lacking oblique stalk musculature (Appendix 2), but oblique muscles are not always readily visible, even in *Myosoma* (Wasson, pers. obs.). This species differs from the other *Loxosomatoides* species in having a spiny stalk and in lacking ornamentation of the aboral shield.

Appendix 2. Tabular key comparing the four *Loxosomatoides* species, the two *Myosoma* species, and generalized *Pedicellina* species.

Trait	*Loxosomatoides*				*Myosoma*		*Pedicellina* spp.
	colonialis	*laevis*	*athleticus*	*evelinae*	*spinosa*	*hancocki*	
Oblique stalk musculature	No	No	Yes	No	Yes	Yes	No
Stalk spines	No	No	No	Yes	Yes	No	Varies with sp.
Calycal spines	Yes	No	No	Yes	Yes	No	Varies with sp.
Aboral shield present	Yes	Yes	Yes	Yes	Yes	Yes	No
Polygonal ornamentation on aboral region of calyx	Yes	Yes	Yes	No	No	No	No
Calyx oblique; tilted orally	Yes	Yes	Yes	Yes	Yes	Yes	No
Strong calyx musculature	Yes	Yes	Yes	Yes	Yes	Yes	No
Hibernacula	Yes	Yes	?	?	No	?	No
Brackish habitat typical	Yes	Yes	Yes	No?	No	No	No



Appendix 3. Cladogram of the relationships between *Loxosomatoides*, *Myosoma*, and *Pedicellina* species, based on a phylogenetic analysis of the characters shown in Appendix 2. An exhaustive search using PAUP (Swofford, 1993) yielded this single tree, with length 11, consistency index of 0.82, and retention index of 0.78. A bootstrap analysis with 1000 replicates and a branch-and-bound search with a 50% majority were carried out; the resulting bootstrap values are shown on the nodes.

References

Annandale N (1908) The fauna of brackish ponds at Port Canning, Lower Bengal. Part 7: further observations on the polyzoa, with the description of a new genus of Entoprocta. Records of the Indian Museum 2: 11–19

Annandale N (1915) Fauna of the Chilka Lake: Polyzoa. Memoirs of the Indian Museum 5: 119–134

Annandale N (1916) Zoological results of a tour in the Far East. Polyzoa, Entoprocta and Ctenostomata. Memoirs of the Asiatic Society of Bengal 6: 13–37, Plates 1–2

Calder DR and Maturo FJS (1978) Phylum Entoprocta. In: Zingmark RG (ed) An Annotated Checklist of the Biota of the Coastal Zone of South Carolina, pp 230–231. University of South Carolina Press, Columbia, South Carolina

Carlton JT (1975) Introduced intertidal invertebrates. In: Smith RI and Carlton JT (eds) Light's Manual: Intertidal Invertebrates of the Central California Coast, Third Edition, pp 17–25. University of California Press, Berkeley, California

Carlton JT (1979a) History, biogeography and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD Thesis, University of California, Davis

Carlton JT (1979b) Introduced intertidal invertebrates of San Francisco Bay. In: Conomos TJ (ed) San Francisco Bay: The Urbanized Estuary, pp 427–444. American Association for the Advancement of Science, Pacific Division, San Francisco

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology Annual Reviews 23: 313–371

Carlton JT (1992a) The dispersal of living organisms into aquatic ecosystems: the mechanisms of dispersal as mediated by aquaculture and fisheries activities. In: Rosenfield A and Mann R (eds) Dispersal of Living Organisms into Aquatic Ecosystems, pp 13–45. The University of Maryland, College Park, Maryland

Carlton JT (1992b) Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research 11(2): 489–505

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology 77(6): 1653–1655

Carlton JT and Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261: 78–82

Carlton JT, Reid DM and Van Leeuwen H (1995) Shipping study. The role of shipping in the introduction of non-indigenous aquatic organisms to the coastal waters of the United States (other than the Great Lakes) and an analysis of control options. The National Sea Grant College Program, Connecticut Sea Grant Project R/ES-6. Department of Transportation, United States Coast Guard, Washington, DC Report number cg-D-11-95. Government Accession Number AD–A294809

Chapman JW (1988) Invasions of the northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. Journal of Crustacean Biology 8: 364–382

Chapman JW and Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). Journal of Crustacean Biology 11(3): 386–400

Chapman JW and Carlton JT (1994) Predicted discoveries of the introduced isopod *Synidotea laevidorsalis* (Miers, 1881). Journal of Crustacean Biology 14(4): 700–714

Cohen AN and Carlton JT (1995) Biological Study. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. A report for the United States Fish and Wildlife Service, Washington, DC, and The National Sea Grant College Program, Connecticut Sea Grant, NTIS Report Number PB96–166525, 272 pp

Craig ME (1929) The Bryozoa of Lake Merritt. Zoology 112 student report, University of California, Berkeley (available from the library of Bodega Marine Laboratory, Bodega Bay, CA 94923, USA)

Dublin LI (1905) The history of the germ cells in *Pedicellina americana*. Annals of the New York Academy of Science 16(1): 1–64

Emschermann P (1972) *Loxokalypus socialis* gen. et sp. nov. (Kamptozoa, Loxokalypodidae fam. nov.), ein neuer Kamptozoentyp aus dem nördlichen Pazifischen Ozean. Ein Vorschlag zur Neufassung der Kamptozoensystematik. Marine Biology 12(3): 237–254

Emschermann P (1994) Kamptozoa. In: Schwoerbel J and Zwick P (eds) Süßwasserfauna von Mitteleuropa, Vol. I, Part 3, pp 113–141. Gustav Fischer Verlag, Stuttgart

Foettinger A (1887) Sur l'anatomie des Pédicellines de la côte d'Ostende. Archives de Biologie 7: 299–329

Hewitt CL (1993) Marine biological invasions: the distributional ecology and interactions between native and introduced encrusting organisms. PhD Thesis, University of Oregon, Eugene

Hincks T (1988) The Polyzoa of St. Lawrence: a study of arctic forms. Part II. Annals and Magazine of Natural History 6(1): 214–227

Jebram DS and Everitt B (1982) New victorellids (Bryozoa, Ctenostomata) from North America: the use of parallel cultures in bryozoan taxonomy. Biological Bulletin 163: 172–187

Jullien J and Calvet L (1903) Bryozoaires provenant des campagnes de *l'Hirondelle* (1856–1888). Résultats des campagnes scientifiques accomplies sur son Yacht par Albert 1er (Monaco) 23: 1–188

Kirkpatrick R (1890) Reports on the zoological collection made in Torres Straits by A.C. Haddon. Hydroida and Polyzoa. Proceedings of the Royal Dublin Society (NS) 6: 603–626

Korringa P (1951) The shell of *Ostrea edulis* as a habitat. Archives Neerlandaises de Zoologie 10: 32–152.

Lindroth CH (1957) The Faunal Connections between Europe and North America. John Wiley & Sons, New York, 232 pp

Lipton DW, Lavan EF and Strand IE (1992) Economics of molluscan introductions and transfers: the Chesapeake Bay dilemma. Journal of Shellfish Research 11(2): 511–519

Mann R (ed) (1979) Exotic Species in Mariculture. MIT Press, Cambridge, Massachusetts, 363 pp

Mann R, Burreson EM and Baker PK (1991) The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non-native species, *Crassostrea gigas* (Thunberg, 1793). Journal of Shellfish Research 10(2): 379–388

Mariscal RN (1965) The adult and larval morphology and life history of the entoproct *Barentsia gracilis* (M. Sars, 1835). Journal of Morphology 116(3): 311–338

Mariscal RN (1975) Entoprocts and lesser coelomates. In: Giese AC and Pearse JS (eds) Reproduction of Marine Invertebrates, Vol. II, pp 1–41. Academic Press, New York

Marcus E (1939) Briozoários Marinhos Brasileiros III. Boletins da Faculdade de Filosofia, Ciencias e Letras Universidade de São Paulo 13 Zoologia 3: 111–353

Maturo FJS (1957) A study of the Bryozoa of Beaufort, North Carolina, and vicinity. Journal of the Elisha Mitchell Scientific Society 73: 11–68

Maturo FJS (1959) Seasonal distribution and settling rates of estuarine Bryozoa. Ecology 40: 116–127

Mills CE, Cohen AN, Berry HK, Wonham MJ, Bingham B, Bookheim B, Carlton JT, Chapman JW, Cordell J, Harris LH, Klinger T, Kohn AJ, Lambert C, Lambert G, Li K, Secord DL and Toft J (2000) The 1998 Puget Sound Expedition: a shallow water rapid assessment survey for nonindigenous species, with comparisons to San Francisco Bay. Proceedings of the National Conference on Marine Bioinvasions, Cambridge, Massachusetts, January 1999 (in press)

Nasanov NV (1926) *Arthropodaria kovalevskii* n. sp. (Entoprocta) und die Regeneration ihrer Organe. Wissenschaftliche Arbeite des zoologischen Laboratoriums der biologischen Station der Akademie der Wissenschaften von der SSSR in Sebastopol (Ser. II) 5: 1–38

Nielsen C (1989) Entoprocts: Keys and Notes for the Identification of the Species. E. J. Brill, Leiden, 131 pp

Osburn RC (1912) The Bryozoa of the Woods Hole region. Bulletin of the U.S. Bureau of Fisheries 30: 201–266

Osburn RC (1944) A survey of the Bryozoa of Chesapeake Bay. Chesapeake Biological Laboratory Publication 63: 1–55

Pisano E (1980) Alcune osservazioni sui Biozoi della Sacca de Canaria (Delta del Po, Italia). Memorie di Biologia Marina e di Oceanografia (Suppl) 10: 433–434

Rao KS, Saraswathi M and Bhavanarayana PV (1988) Entoprocta in the fouling communities at Visakhapatnam Harbor, Bay of Bengal. In: Thompson M-F, Sarojini R and Nagabhushanam R (eds) Marine Biodeterioration: Advanced Techniques Applicable to the Indian Ocean, Chapter 5, pp 57–79. Oxford & IBH Publishing, New Delhi

Ritchie J (1911) On an entoproctan polyzoan (*Barentsia benedeni*) new to the British fauna with remarks on related species. Transactions of the Royal Society of Edinburgh 47: 835–848

Robertson A (1900) Studies on Pacific coast Entoprocta. Proceedings of the California Academy of Sciences 2: 323–348

Rogick MD (1948) Studies on marine Bryozoa. II. *Barentsia laxa* Kirkpatrick 1890. Biological Bulletin 94: 128–142

Scheltema RS and JT Carlton (1984) Methods of dispersal among fouling organisms and possible consequences for range extension and geographical variation. In: Costlow JD and Tipper RC (eds) Proceedings of the Symposium on Marine Biodeterioration (Uniformed Services University of Health Sciences, 20–23 April 1981), pp 127–133. United States Naval Institute, Annapolis, Maryland

Soule JD (1955) A new species of *Myosoma* from the Pacific (Entoprocta). In: Essays in the Natural Sciences in Honor of Captain Allan Hancock, pp 173–177. University of Southern California Press, Los Angeles

Swofford DL (1993) Phylogenetic analysis using parsimony (PAUP) version 3.1.1. Illinois Natural History Survey, Champaign, Illinois

Toriumi M (1944) Brackish water Bryozoa. Zoological Magazine Tokyo 56: 20–25

Toriumi M (1951) Some entoprocts found in Matsushima Bay. Science Reports of the Tohoku University 4th Ser. (Biology) 19(1): 17–22

Valkanov A (1951) Eigentümlichkeiten in dem Bau und der Organisation von *Arthropodaria kovalevskii* Nasonov im Zusammenhang mit ihrer Überwinterung. Arbeiten aus der Biologischen Meeresstation am Schwarzen Meer in Varna, Bulgarien 16: 47–62

Von Holle B and Ruiz GM (in prep.) The effect of the introduced hydroid, *Cordylophora caspia* (Pallas, 1771; *lacustrus* = Allman) on the fouling community structure of the Chesapeake Bay

Wass ML (1972) A checklist of the biota of lower Chesapeake Bay. Virginia Institute of Marine Science Special Scientific Report 65

Wasson K (1997) Systematic revision of colonial kamptozoans (entoprocts) of the Pacific coast of North America. Zoological Journal of the Linnean Society 121: 1–63

Wasson K and Shepherd SA (1997) Nodding heads (Phylum Kamptozoa or Entoprocta). In: Shepherd SA and Davies M (eds) Marine Invertebrates of Southern Australia, Chapter 17, Part 3, pp 975–992. South Australia Fauna and Flora Handbooks Committee, Adelaide

Winston JE and Håkansson E (1986) The interstitial bryozoan fauna from Capron Shoal, Florida. American Museum Novitates 2865: 1–50

Zernov SA (1913) Zur Frage der Beschreibung der Fauna des Schwarzen Meeres. Mémoires de l'Académie Impériale des Sciences de St. Petersbourg; Classe de Sciences physiques et mathématiques Series 8 32(1): 226

Zevina GB and Kuznetsova IA (1965) The part played by navigation in modifying the Caspian Fauna. Oceanology 5: 101–108 [English] (Okeanologiya 5: 518–527 [Russian])