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Benthic foraminifera associated with the invasive ascidian, *Didemnum* sp. A

Mary R. Carman *

Woods Hole Oceanographic Institution, MS#8, WHOI, Woods Hole, MA 02543, USA

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Abstract

The invasive ascidian, *Didemnum* sp. A, first appeared in New England bays and harbors in the early 1990s, and in the waters around Cape Cod in 1993. While ship traffic was the likely vector introducing the species, its origin and precise date and location of its introduction are presently unknown. Colony surfaces of *Didemnum* sp. A appear very clean and not favorable substrates for epibiota settlement, but closer inspection revealed the presence of benthic foraminifera. During 2003 and 2004, 52 samples of *Didemnum* sp. A and other ascidians were collected to determine whether or not the foraminiferal assemblages might also be non-native and thus provide a potential clue to the place of origin of *Didemnum* sp. A. Sample locations included the New England coast from Connecticut to Maine (with a concentration in the Cape Cod area), northern California, Zeeland, The Netherlands, and Shakespeare Bay, New Zealand. From New England samples, 18 species of benthic foraminifera were identified. The most common species represented were *Cornuspira involvens*, *C. planorbis*, *Elphidium galvestonense*, *E. margaritaceum*, *Glabratellina lauriei*, *Miliolinella subrotunda*, *Quinqueloculina bicornis*, and *Rosalina floridana*. Foraminiferal assemblages on *Didemnum* sp. A from other regions sampled were composed of the same cosmopolitan species found in New England, plus other species which were indigenous to each region. Because no exotic foraminifera species were found it is concluded that *Didemnum* sp. A likely did not introduce non-native foraminifera originating from their native habitats into the New England region.

Keywords: Ascidian; Biodiversity; Detritus; Epibiota; Foraminifera; Invasive species

1. Introduction

There has been a rapid increase in the rate of introduced non-indigenous ascidian species to many parts of the world in the past 20–40 years (Lambert, 2001). Changes in seawater temperatures due to global climate change over the last 25 years may be facilitating this spread (Stachowicz et al., 2002). Increasing bacterial and pollution levels (Bak et al., 1996; Valiela et al., 1997) and declining invertebrate biodiversity may also be influencing the spread of nonindigenous species (Stachowicz et al., 1999). Invasive ascidian species commonly occur in New England coastal waters (Whitlatch and Osman, 2000) and most were introduced via shipping vectors (e.g., Carlton and Geller, 1993; Turon et al., 2003). During the past 15 years, a particularly fast growing and quickly spreading species, *Didemnum* sp. A, has proliferated in the nearshore and offshore habitats from Eastport, ME to Niantic, CT (Bullard et al., 2007-this issue). The first documentation of *Didemnum* sp. A in the nearshore of Cape Cod, MA, was in 1993 (Carman and Roscoe, 2003).

Benthic foraminifera have been extensively studied worldwide and can be used as biomarkers or indicators

* Tel.: +1 508 289 2987; fax: +1 508 457 2183.
E-mail address: mcarman@whoi.edu.

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of particular marine or coastal environments (Culver and Buzas, 1980; Alve, 1999). They are usually limited to a geographic location and temperature zone and different species prefer different infaunal or epifaunal positions on the seafloor (Corliss, 1985). Benthic foraminifera have been reported to live on ascidians (Nyholm, 1961; Alexander and DeLaca, 1987), and non-native foraminifera species may have 'piggybacked' on *Didemnum* sp. A when it initially invaded New England. This hypothesis was tested by comparing foraminifera species attached to *Didemnum* sp. A colonies collected from different regions in USA and samples obtained from The Netherlands and New Zealand. Because it was difficult to determine which foraminifera were alive and dead at the time of collection several experiments were conducted to determine which species were associated with, or living on, various ascidian species.

2. Materials and methods

2.1. Collection sites

During 2003 and 2004, 47 ascidian colony specimens were collected from 16 natural and 31 artificial substrates at 22 nearshore Massachusetts sites (Fig. 1) and at one site in Maine. *Didemnum* sp. A specimens were also collected

Fig. 1. *Didemnum* sp. A collection sites in Massachusetts.

by colleagues in 2004 (Fig. 2). These included samples from subtidal rocks at Groton, CT; offshore at Georges Bank (41°57.24′N, 67°30.97′W); a submerged peat bank at Zeeland, The Netherlands; rocks in Bodega Bay and Humboldt Bay, CA; and *D. vexillum* Kott, 2002, samples from a wharf in Shakespeare Bay, New Zealand (Table 1). All specimens were placed in glass jars and preserved in 70% isopropyl alcohol.

2.2. Collection and preparation of benthic foraminifera

Ascidians were washed over 63-μm mesh sieves with tap water. Sieves with washed residues were placed in a drying oven (50 °C) for one hour. The washed substrates were then placed in glass beakers containing 6% sodium hypochlorite bleach for 15 min to dissolve the organic matter in the sample residues. The liquid and residues were poured over 63-μm mesh sieves. The procedure was repeated twice for each sample, and the residues were re-dried in the oven and brushed onto a tray. Using a stereomicroscope, foraminifera were sorted and identified (e.g., Todd and Low, 1961, 1981).

In the laboratory, 52 preserved ascidian specimens ranging from 5 to 30 cm diameter were processed. Two of the preserved specimens were rinsed with distilled water and the residues were soaked in Rose Bengal for 24 h and then preserved with alcohol. Rose Bengal staining is a standard procedure used to indicate if a foraminifer was alive at the time of collection, although it may yield inconclusive results (Bernhard, 2000).

Parts of some didemnid colonies attached to rocks at a Sandwich, MA tide pool were exposed during low tide. The duration of exposure to air was timed for one such colony, and a piece of that exposed portion was sampled, preserved, and processed for foraminifera in the laboratory. Dead didemnid colonies were collected from the driftlines on the shore at Sandwich in the winters of 2001 and 2002, and processed for foraminifera. The amount of time that these driftline didemnids were exposed to air is unknown.

3. Results

3.1. Ascidian species

In coastal New England, the ascidians *Aplidium stellatum* (Verrill, 1871), *Ciona intestinalis* (Linnaeus, 1767), and *Molgula manhattensis* (Dekay, 1843) are native residents; *Ascidiella aspera* (D.F. Müller, 1776), *Botrylloides violaceus* Okra, 1927, *Botryllus schlosseri* (Pallas, 1774), *Didemnum* sp. A, *Diplosoma listerianum* (Milne-Edwards, 1841), and *Styela clava* Herdman, 1881, are considered to be introduced species (J. Carlton, personal communication).

3.2. Benthic foraminifera from ascidian substrates

Fifteen species of calcareous benthic foraminifera from 47 ascidian samples were identified from the 21 New England sampling sites (Table 1). The foraminifera

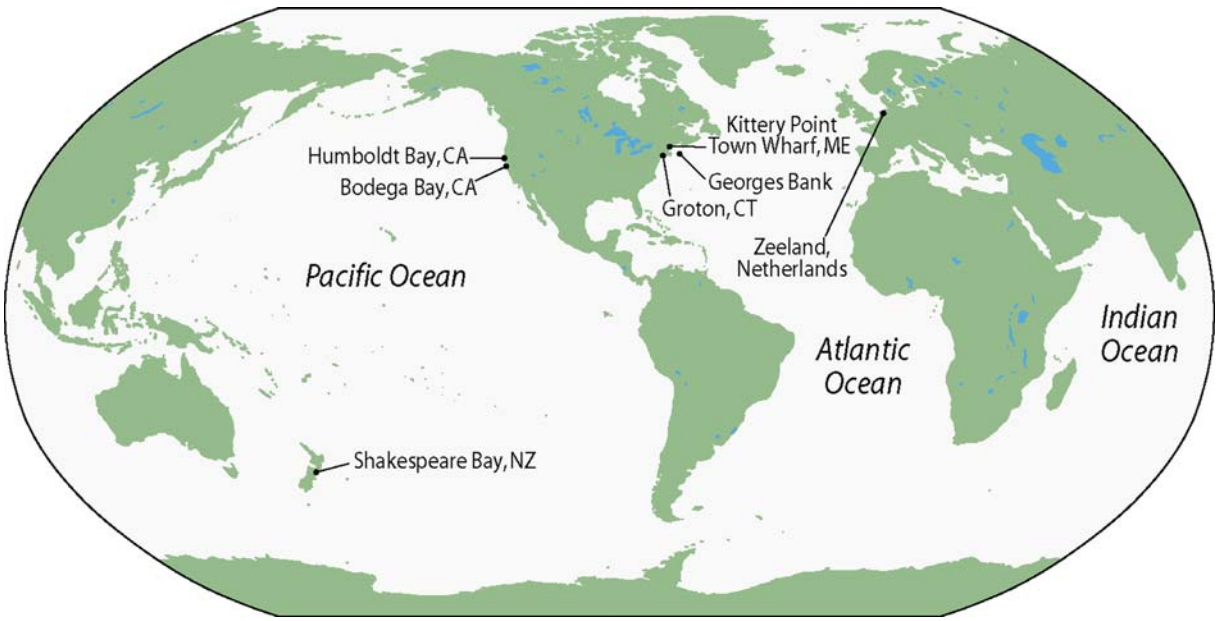

Fig. 2. *Didemnum* sp. A collection sites in New England, California, New Zealand, and The Netherlands.

Table 1
Ascidian specimens and associated benthic foraminifera identified by species

Sample	Location	SS	Benthic foram species	Ascidian species	Comments
A5	Provincetown Harbor	A	Ms, Rf	Sc, Bv, As	14 Sep. 03
A20	Sandwich Town Beach	N	Bp, Cl, Ci, Gl, Ms, Ph, Qb, Rf	Dsp	2 Nov. 04; 15 °C
B14	Provincetown Harbor	A	Bp, Ci, Cp, Em, Mf, Ms, Qb, Rf	Dsp, Sc	14 Sep. 03
B15	Provincetown Harbor	A	Bp, Ci, Cp, Em, Mf, Ms, Qb, Rf	Dsp	14 Sep. 03; on *Mytilus*
B31	Sandwich Town Beach	?	Cl, Ci, Ee, Em, Ga, Ms, Rf	Dsp	2001 driftline
C10	Groton, CT	N	Bp, Ci, Cp, Ho, Ms, Qb, Rf, Ti	Dsp	15 Jul. 03
C12	Barnstable Harbor	A	Eg, Mf, Ms, Rf	Mm, Bs, Bv	28 Aug. 03
C13	Chatham Harbor	A	Eg, Em, Ms, Rf	Bv	7 Aug. 03
C14	Chatham Harbor	A	Ci, Eg, Ms, Rf	Dsp	7 Aug. 03; on *Mytilus*
C35	Sandwich–CC Canal	N	Ab, Ci, Ms, Rf	Dsp	5 Aug. 03
C37	Sandwich Town Beach	N	Bp, Rf	Bv	28 Sep. 03
C41	Sandwich Town Beach	N	Cl, Ms, Rf	Dsp	5 Aug. 03; 18 °C
C42	Chatham Harbor	A	Ci, Eg, Em, Ms, Rf	Dsp	7 Aug. 03
C81	Eel Pond–Woods Hole	A	Ab, Ci, Cp, Ee, Eg, Gl, Ho, Ms, Rf	Aa, Bs, Mm, Sc	25 Jul. 03
C83	Wood Neck lower estuary	N	Ms, Rf, Ti	Bv	23 Jul. 03
C94	Kittery Point Town Wharf, ME	A	Ci, Ea, Eg, Mf, Ms, Rf	Dsp	18 Aug. 03
C95	Waquoit Bay	A	Eg, Ms, Rf	Mm	6 Aug. 03
C99	Sandwich Town Beach	N	Rf	Dsp	20 Jun. 03; 15 °C
C100	West Falmouth Harbor	A	Em, Ms	Bv	9 Jul. 03
D6	Sandwich Town Beach	?	Em, Ms, Rf	Dsp	2002 driftline
D38	Sandwich Town Beach	N	Cl, Ci, Gl, Ms, Qb, Rf	Dsp	28 Sep. 03; 16 °C
D39	Sandwich Town Beach	N	Bp, Cl, Ci, Ea, Em, Ms, Rf	Bv	17 May. 03
E2	Sandwich Town Beach	N	Cl, Ci, Eg, Em, Gl, Ho, Ms, Rf	Dsp	18 Dec. 03; 5 °C
E3	Sandwich Town Beach	N	Cl, Ci, Em, Ms, Qb, Rf	Dsp	13 Dec. 03; 6 °C
E4	Georges Bank	N	Bp, Cl, Ci, Ea, Eg, Gl, Ms, Qb, Rf	Dsp	1 Nov. 04
E5	Old Silver Beach	N	Em, Gl, Ms, Rf	Bv	7 Aug. 03
E6	Eel Pond–Woods Hole	A	Bp, Ci, Cp, Gl, Ms, Rf	Dsp, Sc	15 Jan. 04; −2 °C
E7	Eel Pond–Woods Hole	A	Bp, Ci, Ee, Eg, Gl, Ms, Qb, Rf	Dsp, Sc	22 Dec. 03; 4 °C
E8	Green Pond	A	Ci, Ee, Gl, Ms, Rf	Bs, Bv, Dsp, Mm, Sc	30 Aug. 03
E9	Vineyard Haven–MV	A	Ci, Cp, Eg, Em, Rf	Bs, Bv, Dsp, Sc	22 Jan. 04
E11	Eel Pond–Woods Hole	A	Bp, Cl, Ci, Cp, Ee, Em, Gl, Rf	Dsp	25 Jul. 03; 25 °C
E12	Sandwich Town Beach	N	Bp, Cl, Ci, Em, Gl, Ms, Qb, Rf	Dsp	3 Feb. 04; 1 °C
E14	West Bay–Osterville	A	Cp	Aa, Bs, Bv, Sc	27 Aug. 03
F1	Sandwich Town Beach	N	Cl, Ci, Em, Ms, Qb, Rf	Dsp	4 Dec. 03; 9 °C
F2	Eel Pond–Woods Hole	A	Cp, Em	Dsp	26 Nov. 03; 8 °C
F3	Eel Pond–Woods Hole	A	Ab, Ci, Cp, Ho, Ms, Qb, Rf	Dsp	20 Aug. 03; 26 °C
F5	Eel Pond–Woods Hole	A	Bp, Ci, Qb, Rf	Dsp, Sc	7 Jan. 04; 2 °C
F6	Eel Pond–Woods Hole	A	Bp	Dsp	15 Nov. 04; on *Mytilus*
F7	Eel Pond–Woods Hole	A	Bp, Ci, Cp, Eg	Dsp	31 Oct. 03; 13 °C
G1	Humboldt Bay, CA	N	Qb, Rg	Dsp	4 Jul. 04
G2	Shakespeare Bay, NZ	N	Bp, Ci, Fsp, Msp, Qb, Rf, Tsp	Dsp	1 Aug. 04
G4	Bodega Bay, CA	N	Qb	Dsp	4 Jul. 04
G5	Zeeland, Netherlands	A	Bp, Ci, Ee, Ef, Ho, Ms, Qa, Qb, Ti, Tm	Dsp	1 Aug. 04
G7	West Falmouth Harbor	A	Ci, Cp, Ga, Ho, Ms, Qb	Dsp	30 Oct. 04
G11	Sandwich Town Beach	N	Bp, Cl, Ci, Em, Gl, Ms, Qb, Rf, Ti	Dsp	17 Nov. 04
G14	Green Pond–Falmouth	A	Em, Gl, Ms, Qb	As, Bs, Bv, Sc	11 Nov. 04
G15	Green Pond–Falmouth	A	Gl, Mf, Qb	Dsp	11 Nov. 04
G16	Wellfleet Harbor	A	Ci, Cp, Gl, Qb	Aa, As, Bs, Bv,	14 Sep. 03

Table 1 (*continued*)

Sample	Location	SS	Benthic foram species	Ascidian species	Comments
				Mm	
H1	Sandwich Town Beach	N	Ci, Qb	Dsp	16 Dec. 04; exposed to air
1	Orleans Town Cove	A	No forams	Dsp	26 Oct. 04
2	Hyannis Inner Harbor	A	No forams	Bs, Bv, Mm, Sc	26 Aug. 03
3	Great Pond–Falmouth	A	No forams	Bs, Mm	29 Aug. 03
4	Falmouth Inner Harbor	A	No forams	Bs, Bv, Mm	29 Aug. 03
5	Barlow's Landing–Pocasset	A	No forams	Bs, Bv, Mm, Sc	25. Aug. 03

Location is Massachusetts unless indicated.
Abbreviations: A=artificial; Aa=*Ascidiella aspersa*; As=*Aplidium stellatum*; Ab=*Ammonia beccarii*; Bf=*Buccella frigida*; Bp=*Bolivina pseudoplicata*; Bs=*Botryllus schlosseri*; Bv=*Botrylloides violaceus*; CA=California; CC=Cape Cod; Ci=*Cornuspira involvens*; Cp=*Cornuspira planorbis*; Cl=*Cibicidoides lobatulus*; CT=Connecticut; Dsp=*Didemnum* sp.; Ea=*Elphidium advenum*; Ee=*Elphidium excavatum*; Ef=*Elphidium frigidum*; Eg=*Elphidium galvestonense*; Em=*Elphidium margaritaceum*; Es=*Elphidium subarcticum*; Fsp=*Fursenkoina* sp.; *Gl*=*Glabratellina lauriei*; Ga=*Globotextularia anceps*; Ho=*Haynesina orbiculare*; Hb=*Haplophragmoides bonplandi*; ME=Maine; Mf=*Miliammina fusca*; Mm=*Molgula manhattensis*; Ms=*Miliolinella subrotunda*; Msp=*Miliolinella* sp.; MV=Martha's Vineyard; N=natural; NZ=New Zealand.

assemblages differed on *Didemnum* sp. A specimens collected from the same site and from site to site. Ascidians had a range of abundance (0–141 individuals) of foraminifera.

As it was impossible to determine the abundance of benthic foraminifera per given surface area of the ascidian colonies, total species richness was used as a means of comparison between collection sites. The greatest species richness of benthic foraminifera on individual *Didemnum* sp. A colonies was nine at Sandwich (G11) and Georges Bank (E4), and eight at Provincetown Harbor (B14), Eel Pond (E7), and Groton, CT (C10). The greatest species richness of benthic foraminifera on a cluster of non-didemnid ascidians (*Ascidiella*, *Botryllus*, *Molgula*, and *Styela*) was nine at Eel Pond (C81), and seven on a single colony of *Botrylloides* at Sandwich (D39) (Table 1).

Few agglutinated benthic foraminifera were found on ascidians at most sites (Table 1). Three species (*Globotextularia anceps* Brady, 1884, *Miliammina fusca* (Brady, 1870), and *Trochammina inflata* (Montagu, 1808)) were found from ascidians attached to rocks (C83, C10), floating docks (C12, G7), a lobster trap (C94) and a car tire lying on the seafloor (B14). *Trochammina inflata* and *M. fusca* were retrieved from both didemnids and non-didemnids. *Globotextularia anceps* was rare, and found only on one didemnid colony (Table 1).

All the calcareous and agglutinated benthic foraminifera found on New England *Didemnum* sp. A and other ascidians, were local, previously documented species (Cushman, 1944; Todd and Low, 1961, 1981; Culver and Buzas, 1980; Scott and Leckie, 1990).

The benthic foraminifera on single specimens of *Didemnum* sp. A collected from California and The Netherlands and a single New Zealand specimen of *D. vexillum* included the same cosmopolitan species found on specimens of *Didemnum* sp. A collected in New England, plus species indigenous to their respective regions. The Netherlands specimen of *Didemnum* sp. A (G5) included species native to the region: *Elphidium frigidum* (Cushman, 1933), *Quinqueloculina auberiana* d'Orbigny, 1839, and *Trochammina macrescens* Brady, 1870. The New Zealand specimen of *D. vexillum* (G2) yielded native species: *Fursenkoina* sp., *Miliolinella* sp., and *Trochammina* sp. The California samples from Humboldt Bay (G1) and Bodega Bay (G4) contained specimens of a species native to the region, *Rosalina globularis* d'Orbigny, 1826 (Table 1).

Didemnum sp. A attached to a group of blue mussels (*Mytilus edulis*) at Chatham Harbor (C14) contained specimens of four species of benthic foraminifera; specimens of two species on *Didemnum* sp. A on *M. edulis* at Eel Pond docks (F6); and specimens of eight species on *Didemnum* sp. A on *M. edulis* at Provincetown Harbor (B15).

Two residues that were exposed to Rose Bengal and picked wet, contained foraminifera that appeared to be dead at the time of collection. The residue from *Didemnum* sp. A, sample G11, contained 14 benthic foraminiferal specimens that were not stained (11 *R. floridana*, 2 *M. subrotunda*, and 1 *B. pseudoplicata*). The residue from *Didemnum* sp. A, sample A20, contained 18 foraminiferal specimens that were not stained (15 *R. floridana*, 2 *C. lobatulus*, and 1 *B. pseudoplicata*). Thus, of the foraminifera exposed to Rose Bengal, 100% were dead.

3.3. Benthic foraminifera from seasonally collected *Didemnum* substrates

A seasonal study revealed that *R. floridana* was the most commonly found benthic foraminifera on didemnid

specimens throughout the year (Table 1). The greatest diversity of benthic foraminifera on didemnids tended to occur during the fall and winter at Sandwich and during the summer and winter at Eel Pond. A lower diversity of benthic foraminifera occurred in the spring (one species represented) when didemnid colonies were small, and in summer (up to three species represented). In the fall, in Eel Pond, didemnid colony samples contained a moderate diversity (up to four species of benthic foraminifera represented). Analysis of thin, winter colonies showed that empty tests of benthic foraminifera, quartz grains, pieces of seaweed, diatoms, bits of bivalve shells, and other detritus were scattered throughout ascidian tunics and spicules.

3.4. Benthic foraminifera from air-dried Didemnum substrates

A sample from the part of a didemnid colony naturally exposed to air for two hours during low tide (H1) contained specimens of two species of benthic foraminifera, *C. involvens* and *Q. bicornis*. Two dead didemnid colonies found in driftlines that were dried from having been exposed to air for an unknown amount of time; these colonies contained specimens of benthic foraminifera. The dried 2001 colony of *Didemnum* sp. A (B31) had specimens of *C. lobatulus*, *C. involvens*, *E. excavatum*, *E. margaritaceum*, *G. anceps*, *M. subrotunda*, and *R. floridana.* The dried 2002 colony of *Didemnum* sp. A (D6) had specimens of *E. margaritaceum*, *M. subrotunda*, and *R. floridana* (Table 1).

4. Discussion

Tunic surfaces of *Didemnum* sp. A were generally devoid of foraminifera and other organisms. Several foraminifera specimens were released after exposing the ascidian to bleach, suggesting some species may burrow into or erode the tunic as part of the attachment process, or that some foraminiferids may have been overgrown by the ascidian's tunic. Tunic surfaces may be clean because of anti-predator chemical defenses (Pisut and Pawlik, 2002).

Didemnum sp. A has been increasing in abundance and spreading in nearshore and offshore invertebrate habitats over the last fifteen years throughout New England (Bullard et al., 2007-this issue). Specimens of *Didemnum* sp. A from The Netherlands and California and a specimen of *D. vexillum* from New Zealand had the same cosmopolitan species of benthic foraminifera as the New England didemnid specimens, in addition to species endemic to their respective regions. Results suggest that benthic foraminifera found on the surface (and within the tissue) of *Didemnum* sp. A are not living; and that colonies of *Didemnum* sp. A have not transported or introduced non-native foraminifera to new locations from their native habitats.

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