

Contribution to the biology and ecology of the spongivorous snail *Cerithiopsis greenii* (Gastropoda: Cerithiopsidae) in New England, USA

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ABSTRACT

Cerithiopsis greenii (C. B. Adams, 1839) is a common intertidal snail on rocky shores in southern New England in the summer and fall, and is also found in estuarine fouling communities. It feeds on the sponge *Halichondria bowerbanki* and in the laboratory also fed upon the sponge *Clathria prolifera*. *Halichondria bowerbanki* has expanded north of Cape Cod, Massachusetts, since the 1950s; we predict that, in concert with both warming trends and with prey expansion, *Cerithiopsis* has already moved, or will move, into northern New England.

Additional keywords: *Cerithiopsis*, spongivory, *Halichondria*, *Haliclona*, *Chalinula*, *Clathria*, climate change

INTRODUCTION

Many marine organisms, including invertebrates, fishes, and turtles, eat sponges either as specialized predators or opportunistic grazers (McClintock et al., 2005; Peters et al., 2009; Todt et al., 2009). Marine snails, ranging from limpets and pleurotomariids to opisthobranchs, are especially well-known sponge predators (Strong and Harasweych, 1999; Beeerro et al., 2003; McDonald, 2007). Among shelled marine snails, species in the globally-occurring hypsogastropod family Cerithiopsidae are widely-recognized as spongivores (for example, Fretter, 1951, and Marshall, 1978, who reviews anecdotal records from England, Alaska, California, Australia, and New Zealand), although actual observations of predation have been made for only a few species in the family.

Two species of *Cerithiopsis* occur along the New England coast of the United States (Emerson and Jacobson, 1976; Rosenberg, 2009). The most common of these is *Cerithiopsis greenii* (occasionally misspelled

greenii and often misspelled *greeni*), described in *Cerithium* by C. B. Adams in 1839 from Dartmouth harbor, Massachusetts, in Buzzards Bay, in southern New England. Adams (1839) noted that it was “found clinging to marine plants, a few feet below low water mark, in company with *Cerithium reticulatum*, Totten, and *Cerithium nigrocinctum*, Nob.” The latter two species are now known as *Bittium alternatum* (Say, 1822) and *Marshallora nigrocincta* (C. B. Adams, 1839). Although Emerson and Jacobson (1976) stated that this species was named after Jacob Green, an American naturalist, this is in error; it was named for Thomas A. Greene of New Bedford, MA (Adams, 1839: 288), author of an often-overlooked early checklist of the marine shells of the state (Greene, 1833).

Cerithiopsis greenii is a small snail, the height of adult shells reported between 3 and 5 mm (Moore, 1961; Emerson and Jacobson, 1976; Andrews, 1981), although Pollock (1998) gave a size of 6 mm without noting a source. The shell of *Cerithiopsis greenii* is glossy-brown (amber glass) in color, with each post-nuclear whorl bearing three beaded spiral cords. The uppermost cord of each whorl, consisting of the smallest beads, may also form a black spiral band.

The published range of *C. greenii* is large, from the Gulf of St. Lawrence in Canada to Argentina (Bousfield, 1960; Farinati, 1994). However, as is typical of a number of marine invertebrates (Whiteaves, 1901), the Gulf of St. Lawrence populations (Winkley, 1888; Bousfield, 1960) are disjunct from the main populations of *C. greenii*, which are reported from southern Cape Cod and south (Table 1). Although historically recorded from the Gulf of Maine (Stimpson, 1851: Boston Harbor), it is not reported in modern times from northern New England (Wagner, 1979; Bromley, 1979; Trott, 2004, the latter summarizing historical records rather than recent surveys), leading us to suspect that the mid-nineteenth century Boston record may have been based upon specimens transported north, as discussed below. We comment below on its potential range north of Cape Cod.

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Table 1. Reported habitats of the spongivorous snail *Cerithiopsis greenii*, arranged geographically from north to south.

Location	Habitat	Reference
Canada: Gulf of St. Lawrence	in oyster beds, shallow water	Bousfield, 1960
Massachusetts: Boston Harbor	3 fathoms [5.5 meters]	Stimpson, 1851
Massachusetts: Dartmouth Harbor	“clinging to marine plants, a few feet below low-water mark”, along with the snails <i>Bittium alternatum</i> and <i>Marshallora nigrocincta</i> [we interpret this as 3 to 4 feet, and thus 0.9 to 1.2 meters]	Adams, 1839
Massachusetts: Vineyard Sound	3 to 10 fathoms [5.5 to 18.3 meters] rocky shores; wharf piles; rocky bottoms of bays and sounds; in algae “on these bottoms” “gravelly and shelly bottoms”	Verrill and Smith, 1873
New York: Long Island	low water to 2 fathoms [4 meters]	Smith, 1859
New York: Long Island	dredged on oyster beds, along with the snails <i>Seila adamsii</i> and <i>Triphora</i> sp.	Balch, 1899
New York: Long Island	in eelgrass <i>Zostera marina</i> community, brackish water, 1-3 meters, “on silty sand bottoms, with low, slow tides”	Conrad, 1935
New York: New York City	in mud, sand, under stones and shells	Jacobson and Emerson, 1961
Delaware: Delaware Bay	mud-fine sand; estuarine in 28 – 32 ‰	Leathem and Maurer, 1975
North Carolina: Newport River	on oyster beds	Wells, 1961
Florida: Indian River Lagoon	sea grass, mud, oyster beds, and sand	Mikkelsen et al., 1995
Mississippi: Ship Island	under side of rocks, on encrusting yellow sponge	Moore, 1961
Texas	bays, inlets, shelly sand; on marine plants	Andrews, 1981
Cuba	to 40 meters depth	Rolán and Espinosa, 1995
Mexico: Yucatan Peninsula	sand, marshes, rocky areas, and offshore reef	Vokes and Vokes, 1984
Mexico: central Gulf coast: Lobos Island and surrounding reef	among shell debris in sands near grass beds	Britton and Morton, 1989
Mexico: Tabasco	“epifaunal de aguas costeras y lagunares”	García-Cubas and Reguero, 1990
Costa Rica: Limón	under stones in seagrass <i>Thalassia</i> beds	Houbriek, 1968
Colombia	algae, gravel, and sand, in shallow estuarine water	Díaz-Merlano and Hegedus, 1994

Records of “*Cerithiopsis greenii*” in the southeastern United States and the Gulf of Mexico (Table 1, and Singley, 1893; Maury, 1922) include similar-looking sibling species (Rolán and Espinosa, 1995; Rolán et al., 2007, Lee, 2009). *Cerithiopsis greenii* sensu stricto may occur south to Florida (for example, Krisberg, 2009), but this requires confirmation (H.G. Lee, personal communication, September 2010). In more southern waters – Bermuda, the Caribbean, Cuba, Mexico, Costa Rica, Panama, Venezuela, and then south to Brazil, Uruguay, and Argentina, all of which are locations where *C. greenii* has been recorded (Verrill and Smith, 1873; Olsson and McGinty, 1958; Houbriek, 1968; Jensen and Clark, 1986; Figueiras and Broggi, 1988; Britton and Morton, 1989; García-Cubas and Reguero, 1990; Farinati, 1994; Rodríguez et al., 2003; Clavijo et al., 2005; Jensen and Pearse, 2009) – a similar species complex is involved (Rolán and Espinosa, 1995; Rolán et al., 2007). However, this species complex may not include the North American *C. greenii*. Molecular work may be required to resolve the distribution of the *C. greenii*-group in lower latitudes as well as in temperate South America.

Cerithiopsis greenii has been reported from a wide range of habitats. We summarize these in Table 1 (we include all records that we have found, including those in

warmer waters that may well represent sibling species). Sponges are reported in only one case, but it is probable that sponges were either present and not recorded, were nearby, or the records represent dead shells. Rosenberg (2009) notes that while *C. greenii* is reported to 75 meters, living populations of *C. greenii* may occur only as deep as 15 meters. These small shells can drift both offshore and to shallower alloethonous habitats, and their planktotrophic larvae may be carried far afield as well (Jung [1975] and Thiriot-Quévieux [1980] report larval shells from the Cariaco Basin off the north coast of eastern Venezuela, although, as noted above, records of *C. greenii* from this region may represent one or more other species). A number of authors have recorded this snail alive from both marine and estuarine (brackish) waters, as we do here.

While a meticulous work on the mollusks of the Long Island Sound region (Long Island Shell Club, 1988) reported *Cerithiopsis greenii* as “uncommon to rare” (based upon the occurrence of beach drift shells) and while we have found few modern-day records of this species in New England, we report here that it is a common intertidal snail in the summer and fall on the rocky shores of Rhode Island, and that it occurs in the Mystic River Estuary (Mystic, Connecticut) in vessel and other fouling communities. In the first report of its feeding

biology, we detail its predation upon the sponges *Halichondria bowerbanki* Burton, 1930 and *Clathria prolifera* (Ellis and Solander, 1786).

MATERIALS AND METHODS

Cerithiopsis greenii were collected from the edges of colonies of the yellow sponge *Halichondria bowerbanki*, in October and November 2008, from the underside of rocks in the low intertidal zone at Weekapaug Point, Westerly, Rhode Island. Also in November 2008, *C. greenii* were collected from a fouling community with yellow *Halichondria bowerbanki* on the hull of the CHARLES W. MORGAN at Mystic Seaport Museum in the Mystic River Estuary, Mystic; the MORGAN is an exhibit vessel and does not leave the estuary. Temperature and salinity data were collected at all stations.

In the laboratory, snails were maintained in 65 × 57 mm "tea ball" (tea strainer) plastic containers (mesh size 200 μm) in flowing aquaria at 12°C and 28–30‰. The snails were starved for 10 days prior to observational and experimental feeding studies.

Sponges for experimental use included *Halichondria bowerbanki* (yellow and green colonies) from intertidal rocks at Weekapaug Point and from Mystic River subtidal dockside fouling racks, *Chalinula loosanoffi* (Hartman, 1958) (= *Haliclona loosanoffi*), *Cliona* sp., *Clathria prolifera* (= *Microciona prolifera*), and *Halichondria bowerbanki* (orange colonies, which occur on the same racks with yellow colonies in the estuary). We used yellow, orange, and green (which contain zooxanthellae; Hartman, 1958) morphs of *Halichondria* to determine whether the apparent restriction of *C. greenii* to yellow *Halichondria* in the field was due to feeding preference or was a sampling artifact.

Sponges were kept in a temperature-controlled aerated incubator chamber at 5°C in 28–30‰ water for 24 hours before use. Sponges were identified using the diagnostic characters of Hartman (1958); sponge nomenclature follows that of the World Porifera Database (<http://www.marinespecies.org/porifera/>, accessed September 2010).

In the laboratory detailed observations of predation by *C. greenii* on sponges were made, and feeding was recorded through still and video photography, using a Motic Digital Microscope (DM 143, NTSC system) supported by Motic Images Plus software, Version 2.0. To observe feeding behavior, *C. greenii* were placed in 60 × 15 mm plastic Petri dishes in seawater at room temperature (21°C) with 2 mm² pieces of *H. bowerbanki* (yellow colonies from Weekapaug) for 3 to 4 days. The dish was later searched for fecal pellets that might further demonstrate prey consumption. Fecal pellets were examined under the compound microscope at 400× for the presence of spongin tissue and spicules.

Choice experiments similar to those performed by Becerro et al. (2003) were used to determine prey preference. Four snails (two from Weekapaug, and two from

Mystic) were each offered 2 mm² pieces of six different sponge colonies, for a total of 4 controls and 20 treatments as follows: *H. bowerbanki* (Weekapaug, green colonies; yellow colonies from Weekapaug served as the control because *Cerithiopsis* is commonly associated with these in the field), *H. bowerbanki* (Mystic, orange colonies), *Chalinula loosanoffi*, *Cliona* sp., and *Clathria prolifera*. The snails were placed in separate 60 × 15 mm plastic Petri dishes with seawater; these trials were also conducted at room temperature (21°C). Observations were made for 10 minutes in order to establish if initial contact by a snail with the sponge would induce a feeding response (defined as proboscis moving and probing in a pumping fashion in order to scrape sponge tissue); if it did, snail behavior and prey consumption were recorded.

A separate experiment was conducted to examine potential predation given longer periods of prey availability. Twelve 2 mm² fragments of *Clathria prolifera* were placed in separate 60 × 15 mm Petri dishes filled with sea water and held at room temperature (21°C). A single snail was placed directly on top of each sponge fragment. Because *C. prolifera* tissue is red, we hypothesized that a snail which consumed the sponge tissue might produce red fecal pellets. At 24 and 48 hours the presence or absence, and color, of fecal pellets were recorded. At the end of the first 24 hour interval the few snails which had departed the sponge were placed back on the sponge fragments.

RESULTS

Our largest specimens of *Cerithiopsis greenii* from Weekapaug Point were 5.0 mm in height; our largest specimen from the Mystic River Estuary was 3.49 mm. The body is translucent-white, and, when extended across its sponge prey, can appear almost transparent against the spongin and spicules of *Halichondria*. A pedal gland on the posterior lobe of the foot produces mucus (Fretter, 1951), which then runs along the lobe's longitudinal furrow; the mucus assists the snail's locomotion (for example, we observed *Cerithiopsis* gliding on surface water tension in the laboratory), and may also play a role in securing the snail to its sponge prey, as noted by Fretter (1951) for *Cerithiopsis tubercularis* (Montagu, 1803) in England.

Habitat and Phenology: *Cerithiopsis greenii* was found in two habitats: the rocky intertidal of Rhode Island and subtidal fouling communities in Connecticut. At Weekapaug Point, Rhode Island, the snails were found under rocks in the low intertidal zone, alone or in pairs, exclusively associated with the yellow sponge *Halichondria bowerbanki*. Sponge colonies in October were commonly 10 cm in width, but by late November were 3 to 5 cm in width, with winter regression having commenced; concomitantly, snail abundance declined. In the Mystic River, Connecticut, other sponges occurring with yellow *Halichondria bowerbanki* include

orange-colored *H. bowerbanki*, *Chalinula loosanoffi*, *Clathria prolifera*, and *Cliona* sp. *Cerithiopsis greenii* was found only on yellow *Halichondria*.

Although the undersurfaces of rocks at Weckapaug Point are covered with an encrusting fauna, including the bryozoans *Schizoporella unicornis* Johnston, 1874 and *Cryptosula pallasiana* (Moll, 1803), the ascidians *Botrylloides violaceus* (Oka, 1927) and *Botryllus schlosseri* (Pallas, 1766), and the serpulid polychaetes *Hydroides dianthus* (A. E. Verrill, 1873) and *Circeis spirillum* (Linnaeus, 1758), no *C. greenii* were found associated with these other species. Other gastropods found near *C. greenii* under rocks included *Astyris lunata* (Say, 1826), *Costoanachis transhirata* (Ravenel, 1861), *Costoanachis avara* (Say, 1822), *Lacuna vineta* (Montagu, 1803), and *Littorina littorea* (Linnaeus, 1758).

On the Rhode Island rocky shore temperatures ranged from 14.5° to 6°C in October and November 2008, and salinities were approximately 30‰. In the Mystic River in November 2008 snails were found in water of 10.9°C and a salinity of 26.9‰.

Feeding Biology We observed *Cerithiopsis greenii* feeding readily upon yellow *Halichondria bowerbanki* collected from both Rhode Island and Connecticut; unlike Fretter's (1951) report that she found *C. tubercularis* "reluctant to feed in captivity," such was not the case with *C. greenii*. Within minutes of initial contact with *H. bowerbanki*, *C. greenii* commenced feeding. In contrast, the other species of sponges presented to this snail elicited a distinctly different behavior: the anterior portion of the snail's foot would flail upon initial contact with non-*Halichondria* sponges, rapidly rising off the sponge, and no direct feeding was observed (but see below).

When feeding upon *H. bowerbanki* the extension of the snail's proboscis into the spongin was clearly visible (Figure 1). Feeding bouts during which *C. greenii*



Figure 1. *Cerithiopsis greenii* feeding on the sponge *Halichondria bowerbanki*. The snail's proboscis is extended into the sponge tissue.

consumed sponge tissue lasted for up to 15 minutes, and occasionally somewhat longer. Proboscis movement alternated between rasping the spongin with a grating motion, and sucking loose tissue into the mouth with a strong pumping motion; tissue could be clearly seen entering through the proboscis. When viewed from above snails can appear to be almost motionless although feeding actively. Translucent yellow fecal pellets, approximately 200–300 µm in length, were found in the dishes with snails that were observed feeding. Pellets contained spongin only; no spicules were found therein.

After 24 hours in dishes with the red sponge *Clathria prolifera*, 3 (of 12 trial snails) had produced red fecal pellets, and after 48 hours, 7 (of 12) snails had produced red pellets, suggesting consumption of the red-colored spongin tissue of this sponge. In addition, one Mystic River snail was observed, in the 10-minute feeding bouts, to briefly consume green *H. bowerbanki* from Weckapaug.

DISCUSSION

We provide the first observations of the native Northwestern Atlantic snail *Cerithiopsis greenii* feeding upon the sponge *Halichondria bowerbanki*. While it has been proposed that *H. bowerbanki* is either introduced or cryptogenic in New England (Pederson et al., 2005; Connecticut Sea Grant 2010), the apparent feeding preference of *C. greenii* for this sponge, and its common association with *Halichondria* in the field, suggest that the sponge, too, may be native, in agreement with the conclusions of Vethaak et al. (1982).

Our observations that *Cerithiopsis* can also feed on the native sponge *Clathria prolifera* in the laboratory suggests, however, a potentially broader dietary range that may come into play when *Halichondria* is less available, or not available, as a food resource. In general, we observed predation in the laboratory only on yellow *Halichondria* and not on other color morphs, with a single exception of one snail that fed briefly on a green colony. More work needs to be undertaken relative to the presence of *C. greenii* in the field on the range of color morphologies of *Halichondria* (Hartman, 1958) and the ability of this snail to utilize non-yellow colonies.

The presence of *Cerithiopsis* in the Gulf of St. Lawrence since at least the 1880s (Winkley, 1888), well north of the known range of *Halichondria bowerbanki* at that time, suggests that some populations may rely on other prey species. *Halichondria panicea* occurs in the Gulf of St. Lawrence (Whiteaves, 1901), and may function as an alternative prey, although we note that this species also occurs in the Gulf of Maine (Hartman, 1958), where *Cerithiopsis* has not been reported (save for one 1850s Boston record, noted above and discussed below). Mitchell (1999) reports *Halichondria bowerbanki* from Northumberland Strait in the Gulf of St. Lawrence, based upon collections in the 1990s, and it is not impossible that it was historically present (as are a number of

otherwise-southern taxa in the southern Gulf of St. Lawrence, as noted earlier) but long overlooked.

Our observations are in agreement with those of Fretter (1951), who reported the European *Cerithiopsis tubercularis* feeding on the sponge *Hymeniacidon sanguinea* (Grant, 1826) [now known as *Hymeniacidon perlevis* (Montagu, 1818)] in England, and of Collin (2004), who observed *Cerithiopsis gemmulosum* (C. B. Adams, 1850) feeding on the sponge *Halichondria melanadoeia* de Laubenfels, 1936 in Panama. Fretter and Graham (1962) later expanded the prey diversity of *C. tubercularis* to also include *Halichondria* sp. and *Grantia* sp., and noted that another British species, *Cerithiopsis barleei* Jeffreys, 1867 fed on *Suberites domuncula* (Olivi, 1792). In the Northeastern Pacific, *Cerithiopsis stejegeri* Dall, 1884 has been observed feeding on the edges of the sponge *Hymeniacidon ungodou* de Laubenfels, 1932 in the rocky intertidal of Oregon (J. T. Carlton, unpublished). Through gut content analysis and direct observation of feeding, Fretter (1951) found that *C. tubercularis* used spongin for food and reviewed earlier observations that *C. tubercularis* deposited its eggs in sponge tissue, as does *C. gemmulosum* in Panama (Collin, 2004, who further demonstrated that snail larvae metamorphose when exposed to sponge tissue).

Halichondria becomes dormant (degenerates) in the winter (Hartman, 1958; Fell et al., 1984), which our observations along the Rhode Island rocky shore further confirm. Where *Cerithiopsis* “over winters” is not known; they are absent from the undersurface of rocks along Connecticut and Rhode Island winter shores (J. T. Carlton, L. Haram, personal observations). It is possible that the snails embed themselves into the gravel-shell base underneath rocks in the intertidal, as does the snail *Littorina littorea*, which bury themselves along boulder edges in winter (J. T. Carlton, field observations). The discovery of *C. greenii* in a hull fouling community on the CHARLES W. MORGAN (albeit a stationary vessel) is reminiscent of Verrill and Smith’s (1873) report of it from “wharf piles” (Table 1). That its occurrence in fouling communities is likely not uncommon is indicated by our finding it (2 January 1999) on *Halichondria* on experimental fouling panels at Noank (mouth of Mystic River) and on *Halichondria* in float (pontoon) fouling at a marina in the Mystic River (October 2010). We regard the few reports of it from fouling communities as representing under-sampling, or simply under-reporting, of small snails in this habitat [the record of *Cerithiopsis terebralis* by Hutchins (1952) from “buoy fouling” refers to another cerithiopsid now known as *Seila adamsii* (H. C. Lea, 1845)]. Its widespread occurrence on oyster beds (Table 1, Canada, New York, North Carolina, and perhaps Florida) suggests that there are a number of potential human-mediated dispersal vectors for this snail, including both vessel fouling and the movement of commercial oysters, and we suggest that the one-time report of *C. greenii* in Boston in the 1850s is likely due to transport by ships or oyster movements from southern waters.

Finally, we note that changing climatic conditions may potentially play a role in the distribution of *C. greenii*. Its host sponge, *Halichondria bowerbanki* was not known north of Cape Cod prior to the 1950s (Sorte et al., 2010; J. T. Carlton, unpublished). *Halichondria bowerbanki* spread north to the Bay of Fundy by the 1970s, in concert with a number of other southern taxa whose range expansions appear to be linked to warming coastal conditions (Sorte et al., 2010). We predict that, with both warming trends and with prey expansion, *Cerithiopsis greenii* may have already moved, or will move, into northern New England. In turn, in concert with predicted patterns of northward retreat of cooler-affinity taxa (Carlton, 2000; Sorte et al., 2010), the as yet uncertain southern border of *C. greenii* may be now shifting north as well.

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