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Periwinkle's Progress: The Atlantic Snail *Littorina saxatilis* (Mollusca: Gastropoda) Establishes a Colony on a Pacific Shore

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Abstract. The common ovoviviparous and eurytopic Atlantic Ocean periwinkle *Littorina* (*Neritrema*) *saxatilis* (Olivi, 1792) has established reproducing populations in San Francisco Bay, California, USA. The first population was discovered in 1993. The probable mechanism of introduction into the Bay is the disposal of seaweeds (the brown algae *Ascophyllum nodosum* and *Fucus vesiculosus*) used as transport packing with polychaete worms used for fish bait. These worms, seaweed, and associated periwinkles originate from Maine. An alternative mechanism may be the similar disposal of seaweeds used as packing for imported Atlantic lobsters (*Homarus americanus*) for the restaurant trade. *Littorina saxatilis* could occupy a range on the Pacific American coast from Baja California to western Alaska, and as such it would come into direct contact with the consubgeneric *Littorina* (*Neritrema*) *subrotundata* (Carpenter, 1864) (synonym: *Littorina newcombiana* Hemphill, 1877) and *Littorina* (*Neritrema*) *sitkana* Philippi, 1846, which occur from southern Oregon and north. These latter two species occur in a range of morphological-physiological ecotypes that are closely analogous to those of *Littorina saxatilis*. Eradication of this snail invasion may be possible because the populations are easily accessed and relatively small. However, no tested eradication methods are known, nor are jurisdictional authority or regulatory issues clear relative to initiating potential removal of this species.

INTRODUCTION

The common Atlantic Ocean rough periwinkle *Littorina* (*Neritrema*) *saxatilis* (Olivi, 1792) occurs in North America from Chesapeake Bay north to the high boreal and subarctic waters of Hudson Bay, Baffin Island, Greenland and the Barents Sea, and south along the European coast to the Straits of Gibraltar (Reid, 1996). Outlying populations which occur at the Azores and Canary Islands, at the north end of the Adriatic Sea and at Tunisia in the Mediterranean Sea, and at three sites in the South Atlantic Ocean in Namibia and South Africa, may represent relicts of formerly more widespread populations, transport by migrating birds, or introductions through human activities (Reid, 1996; McQuaid, 1996a). We here report on the introduction and establishment of *Littorina saxatilis* in the Pacific Ocean.

DISCOVERY AND DESCRIPTION OF HABITAT

On 4 October 1993 we discovered a population of *Littorina saxatilis* living intertidally on scattered large rocks (placed here for shoreline stabilization) in the high intertidal zone at a site on the eastern shore of San Francisco Bay, California. This site is adjacent to the Emeryville Marina Launching Facility, a public dock and boat ramp in the city of Emeryville. Subsequent collections from 1993 to 1996 (Table 1) revealed a reproducing and well-established population, with numerous snails occupying crevices and empty barnacle shells. One quantitative sample taken in November 1996 indicated a density of over 1800 snails per square meter (Table 1).

Other species found on and under these same rocks are the native barnacle *Balanus glandula* Darwin, 1854, the native snail *Assiminea californica* (Tryon, 1865), the native isopod *Ligia occidentalis* Dana, 1853, the native crabs *Pachygrapsus crassipes* Randall, 1839, and *Hemigrapsus oregonensis* (Dana, 1851), the Atlantic bryozoan *Bowerbankia gracilis* Leidy, 1855, the Japanese sea anemone *Diadumene lineata* (Verrill, 1873) [synonym: *Haliplanella luciae* (Verrill, 1898)], and the cryptogenic (neither clearly introduced nor native; Carlton, 1996) green algae *Enteromorpha* sp. and *Ulva* sp. In 1993 we found native periwinkles of the *Littorina scutulata* Gould, 1849—*Littorina plena* Gould, 1849, complex on these rocks along with *Littorina saxatilis*. However, in November 1996 no native periwinkles occurred where *L. saxatilis* was found; rather, the native species was found only on rocks commencing about 5 m to the

Table 1

Records of *Littorina saxatilis* in San Francisco Bay.

Date	Search area; search effort (p = person; VT = vertical transects)	Number (height) collector (See lettered footnotes)
	Emeryville Marina, Emeryville	
07 Oct 93	2 m × 5 m; 1 p × 60 min	73 (1–10 mm)[a]
28 Feb 94	2 m × 10 m; 2 p × 30 min	26 (3–10 mm)[b]
22 Jul 94	2 m × 10 m; 4 p × 15 min	3 —[c]
21 Feb 95	2 m × 5 m; 1 p × 30 min	1 (3 mm)[a]
21 Apr 95	2 m × 5 m; 1 p × 30 min	2 (5–9 mm)[a]
27 Apr 95	2 m × 5 m; 1 p × 20 min	1 (10 mm)[a]
19 May 95	2 m × 5 m; 2 p × 20 min	3 (6–8 mm)[d]
20 Jun 95	2 m × 5 m; 1 p × 90 min	14 (3–8 mm)[a]
18 Oct 95	2 m × 10 m; 2 p × 45 min	9 (4–10 mm)[e]
04 Nov 95	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	22* (to 11 mm)[f]
25 Jan 96	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	28* (to 11 mm)[f]
24 Apr 96	7 VT (@ 3 m × 0.6 m); 1 p × 70 min	24* (to 12 mm)[f]
02 May 96	2 m × 5 m; 1 p × 10 min	10* —[a]
24 Nov 96	1 m × 1.5 m; 1 p × 30 min	78 (2–12 mm)[g]
24 Nov 96	12 cm × 14.5 cm area scraped clear (=20 cc barnacle biomass)	32 (1–4 mm, and one 9 mm)[g]
	Coast Guard Island, Oakland	
28 May 96	2 m × 15 m; 2 p × 20 min	11 (3–10 mm)[b]
05 Nov 96	5 m × 45 m; 27 p × 15 min	51 (0.5–9 mm)[h]
05 Nov 96	5 m × 20 m; 3 p × 5 min	16 (4–10 mm)[i]

* Specimens not collected.

Collectors: [a] Andrew N. Cohen (ANC). [b] James T. Carlton (JTC) and ANC. [c] JTC, ANC, John Chapman, and Sarah Cohen. [d] ANC and Jonathan Geller. [e] ANC and Jeanne Yamauchi (JY). [f] JY. [g] JTC. [h] The fall 1996 class and faculty of the Williams College–Mystic Seaport Maritime Studies Program (students Laurel Bastone, Alicyn Campbell, Nicole Dobroski, Antonia Fairbanks, Hillary Frey, Dan Garner, Todd Hunter, Eileen McCullough, Emily Morland, Jan Sarra, Joshua Shapiro, Clarissa Shen, Kate Simmons, Tristan Smith, Jessica Stevens, Joe Street, Kristin Sutherland, Ben Tassinari, Andy Tolonen, Darylanne Villard, Kate Wearn, Kyra Williams, Rob Wittenmyer, and faculty members Fred Dalzell, Glenn Gordinier, Mary K. Bercaw Edwards, and James McKenna). [i] JTC, Anna Fitzgerald, and Lenny Bellet.

west of the *L. saxatilis* populations. Also occurring abundantly with *Littorina saxatilis* at this site in November 1996 was the introduced isopod *Sphaeroma walkeri* Stebbing, 1905.

We searched similar habitats in other areas of the Emeryville Marina and found no other populations of *Littorina saxatilis.* J. Yamauchi (personal communication, 1996) sampled vertical transects along 30 m of shore at this site from November 1995 to April 1996 (Table 1) and found the population to be restricted to 10 m of shore adjacent to the boat dock, as had we earlier.

On 28 May 1996 we found a second population 9 km south of Emeryville on scattered small to medium-sized rocks set in mud, in the mid to high intertidal zone of the Taney Marina beach on Coast Guard Island, Oakland, in the Oakland Estuary on the eastern side of San Francisco Bay (Table 1). The size range collected indicates reproduction at this site. The snails occur on and among the barnacle *Balanus glandula.* As with the Emeryville site, collections here in November 1996 did not include any native *Littorina.*

DESCRIPTION OF POPULATION

Littorina saxatilis shells (size range 1.0–12.0 mm) and animals at both San Francisco Bay sites conform closely with descriptions by Reid (1996). San Francisco Bay shells often have a pale yellow body whorl, occasionally with brown spots or revolving brown stripes and thus conform morphologically with the southern (low boreal Atlantic Ocean, rather than high boreal to subarctic) geographic variety *typica* (Reid, 1996).

Littorina saxatilis is easily distinguished from the native *Littorina scutulata*/*Littorina plena* in San Francisco Bay by its round, yellow shell. *Littorina scutulata*/*Littorina plena* shells are conical, and while they may be dotted or checkered, are not yellow. *Littorina keenae,* another native periwinkle in the San Francisco Bay area, possesses a distinctive flat and polished columella (inner lip).

San Francisco Bay *L. saxatilis* are heavily infected with a marine fungus (presumably *Pharcidia balani* (Winter) Bauch, 1936 [see Lindberg, 1977]) that also infests native littorines and barnacles. A subsample of 62 *L. saxatilis* (size range 3.7–12.0 mm) collected at the Emeryville site on 24 November 1996 was 95% infected ($n = 59$). The more infected specimens show extensive surface decalcification and pitting when viewed microscopically. Heavy infestations, consisting of numerous pits filled with black fruiting bodies, turn the shell dark; new shell growth on the same individuals is yellow in color. Some snails have, in addition, a bright green unicellular alga on the upper body whorls.

Reid (1996) summarized the literature on the development of this periwinkle, which is the only ovoviviparous *Littorina* on the Pacific coast of North America (Behrens Yamada, 1992; Reid, 1996). Three Emeryville females collected on 24 November 1996 were dissected and found to contain embryos ranging from undifferentiated eggs to shelled snails about 0.5 mm in size: a 4 mm snail contained 18 embryos (14 of which were shelled); two 9 mm snails contained 135 embryos (95 shelled) and 194 embryos (125 shelled).

Voucher specimens of *Littorina saxatilis* from San Francisco Bay have been deposited at the California Academy of Sciences, San Francisco (catalogue number CASIZ 113210) and at the Natural History Museum, London, England (BMNH Reg. No. 1996149).

MECHANISM OF INTRODUCTION

Either of the *Littorina saxatilis* populations in San Francisco Bay could have been derived from the other, or they could each be the result of independent inoculations. In either case it seems likely that the initial inoculation(s) into the Bay were the result of anglers discarding the Atlantic brown algae *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1829, which is used as packing material for live marine baitworms shipped from southern Maine (Carlton, 1992; Cohen et al., unpublished observations). *Littorina saxatilis* is common on *Ascophyllum* in New England (JTC, personal observations), and it has been found alive in boxes of *Ascophyllum*-packed worms from bait shops in the San Francisco Bay area (W. Lau, personal communication, 1995; Cohen et al., unpublished observations) and Newport Bay (Carlton, 1992). The two populations found in San Francisco Bay are adjacent to a public dock and boat ramp and to a small boat marina, and thus are likely sites for the discarding of unused bait and the bait's seaweed packing at the end of a day of fishing. We suggest that similar sites in temperate climate regions that import marine baitworms from New England would bear searches for *Littorina saxatilis* as well as the other snail species noted herein.

An alternative and closely related introduction mechanism may be seaweeds, including *Ascophyllum*, that are used as packing material for imported Atlantic lobsters (*Homarus americanus* H. Milne Edwards, 1837) in the restaurant trade and then occasionally discarded into San Francisco Bay (Miller, 1969). The Coast Guard Island site is adjacent to an officers' club where meals are served. In 1993 we found the empty shells of the edible New Zealand green-lip mussel *Perna canaliculus* (Gmelin, 1791) in the intertidal zone below the club. This mussel is sold alive in San Francisco Bay area markets. The presence of these discarded shells suggests that other seafood-associated debris—such as the seaweed packing for lobsters—may be discarded into the Bay at this site.

Molecular genetic comparisons of the San Francisco Bay populations with Atlantic populations would provide evidence for or against an introduction via baitworms or lobsters imported from New England. Berger (1973) has shown that *Littorina saxatilis* demonstrates distinct gene pool differentiation along the Atlantic coast, as would be expected from an ovoviviparous species, making subpopulations recognizable. Genetic characterization of these two populations would further provide data by which to assess potential founder effects and thus to provide a basis against which to measure future genetic changes. Of particular interest here will be comparisons of the role of local population extinction and population bottlenecks (in terms of colonization ability) as observed on occasion in Swedish *Littorina saxatilis* populations (Johanneson & Johanneson, 1995), and of the role of founder effects (in terms of the resulting levels of genetic variation) as observed in other distant and isolated populations of *Littorina saxatilis* (such as in South Africa, where populations are highly inbred [Knight et al., 1987]; see also Johanneson, 1988).

POTENTIAL GEOGRAPHIC DISTRIBUTION AND HABITAT BREADTH

The latitudinal range of *Littorina saxatilis* in the Atlantic Ocean suggests a potential range in the northeastern Pacific Ocean from Baja California to western Alaska. However, since *L. saxatilis* is ovoviviparous, natural dispersal is likely to be slow. It has been estimated that *Littorina saxatilis* may colonize new habitats within a range of about 1 km or less in about 2–10 yr (references in Reid, 1996). Reid (1996) notes that natural dispersal might be accomplished by adults being rolled along the bottom by currents or by the occasional release of encapsulated embryos, but the likeliest method is probably by transport on drifting algae. One of us (JTC) observed on rare occasions living *Littorina saxatilis* up to 5 mm in height on floating brown algae (*Ascophyllum nodosum* and *Fucus vesiculosus*) 160 km offshore of the coast of Maine. Ingolfsson (1995) also found *Littorina saxatilis* to be uncommon on floating brown algae in nearshore waters of Iceland; specimens ranged from about 3 to 10 mm in height (A. Ingolfsson, University of Iceland, personal communication, 1996).

It is difficult to predict whether *Littorina saxatilis* will spread naturally out of San Francisco Bay; several other nonindigenous species with apparently greater dispersal abilities remain restricted to the bay decades after their establishment (Cohen & Carlton, 1995, Appendix 4). However, while ovovivipary may restrict the potential of *Littorina saxatilis* for short distance dispersal, it has been argued that it may provide an advantage over longer distances (Johannesson, 1988; Reid, 1996). The nonplanktonic young resulting from the introduction of even a single fertilized female might be more likely to produce the critical adult population density needed for successful reproduction and establishment than would the introduction of a large number of planktonic larvae. Indeed, such may have been the case in the founding of these new populations in San Francisco Bay.

Littorina saxatilis has the greatest habitat range of all *Littorina* species, which Reid (1996) related to its ovoviviparity. In the Atlantic Ocean *Littorina saxatilis* occurs intertidally on highly exposed coasts on hard substrates (where it may be restricted to sheltered microhabitats such as crevices), intertidally on moderately exposed coasts, and intertidally or subtidally in protected lagoons or estuaries, where it may also attach to submerged vegetation (Reid, 1996; McQuaid, 1996b). It occurs in salt marshes on stems of the cordgrass *Spartina* and on firm mud, and on beaches on scattered stones, shells, and debris. It is tolerant of brackish conditions, surviving salinities of 5 to 7 parts per thousand. In favorable habitats population densities may range in the 1000s, and sometimes the 100,000s, per square meter (Reid, 1996).

ECOLOGICAL IMPACT OF *LITTORINA SAXATILIS*

The establishment of *Littorina saxatilis* in San Francisco Bay raises the question of what role this snail will play as predator, prey, parasite host, or competitor, and as a new hermit crab shell resource.

In the North Atlantic Ocean, *Littorina saxatilis* is an abundant non-selective grazer on diatoms, cyanobacteria (bluegreen algae), and filamentous green and red algae (literature summarized in Reid, 1996). *Littorina saxatilis* also consumes newly settled barnacles on high intertidal rocky shores in Massachusetts and Connecticut (J. T. Carlton, personal observations). In November 1996, fecal pellets of *L. saxatilis* at the Emeryville site (two samples of 10 combined, 1.0 mm fecal pellets crushed and examined under the compound microscope, and 35 additional pellets examined individually) contained algal cells, diatoms, numerous bacteria-sized particles, crustacean fragments, and many rock grains. Individual pellets contained similar items, as well as a chironomid fly larva (Diptera), a mite (Acarina), and a rotifer (Rotifera).

Littorina saxatilis in San Francisco Bay will likely provide a ready food item for both introduced and native crabs as it does in New England (J. T. Carlton, field observations). Both in New England and elsewhere in its Atlantic range, *Littorina saxatilis* is a common prey of the European green crab *Carcinus maenas* (Linnaeus, 1758), a crab which was first found in San Francisco Bay in 1989–1990 (Cohen et al., 1995). It will be of interest to observe whether the prey handling and selection activities of *Carcinus maenas*, and elicitation of predator-response reactions, differ between *Littorina saxatilis*, with which it evolved, and the native Pacific Coast littorines, which it has never before encountered. The converse applies to native Pacific coast crabs.

Several specimens of *Littorina saxatilis* from both the Emeryville and Coast Guard Island populations show evidence of crab attacks, very likely produced by the native crabs *Hemigrapsus oregonensis* or *Pachygrapsus crassipes*. A total of four shells from 1993, 1995, and 1996 Emeryville collections show evidence of previous attack (breakage) scars (a V- or U-shaped notch in an earlier and now repaired apertural edge [outer lip], as illustrated by Raffaelli [1978]). A total of four specimens from 1993, 1994, and 1996 Emeryville collections and a total of five specimens from 1996 Coast Guard collections show evidence of fresh crab attacks, with the body whorl of the shell being torn back and around in a "can opener" fashion. Shells as small as 3.0 and 4.5 mm were attacked. A snail 6.0 mm in height from Emeryville (24 November 1996) that had been newly attacked had the shell body whorl torn back, leaving much of the animal exposed but still alive.

Competitive interactions that may occur between *Littorina saxatilis* and native periwinkles on the Pacific Coast remain to be studied. In this regard, particular focus could be given to the potential interactions between *Littorina saxatilis* and closely related species in the subgenus *Neritrema* (D. G. Reid, personal communication, 1997). While the native littorines (*L. scutulata*/*L. plena* and *L. keenae*) in San Francisco Bay are in the subgenera *Littorina* and *Planilittorina*, respectively, more closely related to *L. saxatilis* on the Pacific coast are the periwinkles *Littorina* (*Neritrema*) *subrotundata* (Carpenter, 1864) (synonym: *Littorina newcombiana* Hemphill, 1877) and *Littorina* (*Neritrema*) *sitkana* Philippi, 1846. These latter two species occur from southern Oregon north to Alaska, as well as in the Western Pacific Ocean (Reid, 1996) and occur in a range of morphological-physiological ecotypes, that are closely analogous to those of *Littorina saxatilis* (D. Reid, personal communication, 1997). Should *Littorina saxatilis* reach these northern waters, which are well within their physiological range as noted earlier, competition between *L. saxatilis* and *L. sitkana* and *L. subrotundata* could well occur, given (1) the success in the North Atlantic Ocean of *L. saxatilis*, in terms of habitat breadth, rates of population increase, colonizing ability, and dietary range, and (2) evidence of habitat partitioning among the rock-dwelling *Neritrema* species in the North Atlantic Ocean, offering support for the hypothesis of potential competition (Reid, 1996, and D. Reid, personal communication, 1997).

Parasite loads, particularly trematodes, in these newly established California populations have not yet been analyzed. In this regard, it will be of interest to determine which parasites may have accompanied *L. saxatilis* from the Atlantic Ocean compared to which parasites *L. saxatilis* may gain from Pacific littorines. Of particular interest would be determining long-term shifts in introduced versus native trematode infections.

Finally, if it becomes widespread and common, *Littorina saxatilis* may provide a new shell resource for juvenile hermit crabs (pagurid anomurans) on the Pacific coast. While small native littorines are abundant in San Francisco Bay, it will be of interest to see if hermit crabs exhibit shell selection preferences when offered a choice between native littorines and *Littorina saxatilis*.

OTHER POTENTIAL LITTORINE INVASIONS IN SAN FRANCISCO BAY

We have found two other North Atlantic Ocean periwinkles, *Littorina littorea* and *Littorina obtusata* Linnaeus, 1758, on seaweed imported with baitworms to the San Francisco Bay area (Cohen et al., unpublished observations) and Newport Bay (Carlton, 1992). Living individuals and small groups of *Littorina littorea* were found on occasion in the late 1960s and 1970s on the eastern shore of San Francisco Bay, and a living specimen was found by one of us (ANC) on the western shore of the Bay in 1995, but no established populations are known (Carlton, 1969; Cohen & Carlton, 1995, page 203). No living *Littorina obtusata* have been found in the Bay. However, there appear to be no ecological or physiological limitations that would prevent establishment of these two species on the North American Pacific coast.

ERADICATION?

The eradication of *Littorina saxatilis* from San Francisco Bay might be possible. The two known populations are intertidal, readily accessible, and between them occupy an area of less than 50 square meters. However, it is unclear what government entity would have jurisdictional authority to conduct such an eradication or what regulatory issues would need to be addressed (J. Yamauchi, personal communication, 1996). No tested eradication methods are known to us. Possible methods would include covering the sites with sediment, removing the rocks and sediment (along with the snails), or treating the sites with steam. Continuous harvesting of the population by hand would likely be unsuccessful, as this fecund and often cryptically colored (when fungus infections turn the shell dark and black-spotted) snail hides deeply in inaccessible crevices on large rocks, and tiny individuals are nearly impossible to find among thousands of living and empty barnacles.

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