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Research Article

New discoveries of introduced and cryptogenic fresh and brackish water gastropods (Caenogastropoda: Cochliopidae) in the western United States

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Abstract

We report the discovery of a second western Atlantic brackish-coastal cochliopid gastropod in San Francisco Bay [*Spurwinkia salsa* (Pilsbry, 1905)], and detail the first records for a widely distributed member of the family, *Tryonia porrecta* (Mighels, 1845), from artificial lakes (in the Phoenix metropolitan area). These identifications were based on morphological criteria and supported by mitochondrial DNA sequence data that also indicates little or no divergence of the newly reported populations, which is consistent with evolutionarily recent spread or separation. *Spurwinkia salsa* was most likely introduced to San Francisco Bay either in recent decades in bait worm packing or ships' ballast or in the 19th or early 20th century in solid ballast or with oyster imports. The discovery of *T. porrecta* in artificial lakes in the Phoenix area in 1984 and 2014 may be due to either recent arrival in the area or to dispersal into a newly available habitat from a population long present in the area. In either case, the occurrence of *T. porrecta* in the Phoenix area is likely due to transport on birds along an eastern branch of the Pacific Flyway. The discovery of *T. porrecta* in artificial lakes suggests that this species (which is typically distributed in thermal springs) is more broadly tolerant than previously thought. Additional spread of this unusual snail within the highly modified aquatic ecosystem of the Phoenix metropolitan area (which includes more than 900 artificial lakes) would appear likely.

Key words: Mollusca, snails, aquatic, North America, spread, identification, molecular

Introduction

The Cochliopidae (formerly a Hydrobiidae subfamily; Wilke et al. 2001, 2013) is a large (>250 species), predominantly New World family of caenogastropods that occurs in a wide variety of brackish-coastal and inland aquatic habitats (Hershler and Thompson 1992). These tiny snails do not well tolerate desiccation. Inland species typically have an entirely benthic life cycle, although several estuarine species have a free swimming larval stage of short (e.g., *Heleobia australis* (d'Orbigny, 1835); Neves et al. 2010) or long (*Spurwinkia salsa* (Pilsbry, 1905); Mazurkiewicz 1972) duration. This constrains the dispersal of inland species and renders them especially vulnerable to anthropogenic stressors on aquatic ecosystems: for example, 31 of the 45 inland cochliopid species in the United States currently are listed as endangered by the American Fisheries Society (Johnson et al. 2013). In contrast with this prevailing trend of decline, there are a few well documented cases of recent range expansions of cochliopid gastropods, some of which appear to have resulted from anthropogenic transport (e.g., Nasarat et al. 2014).

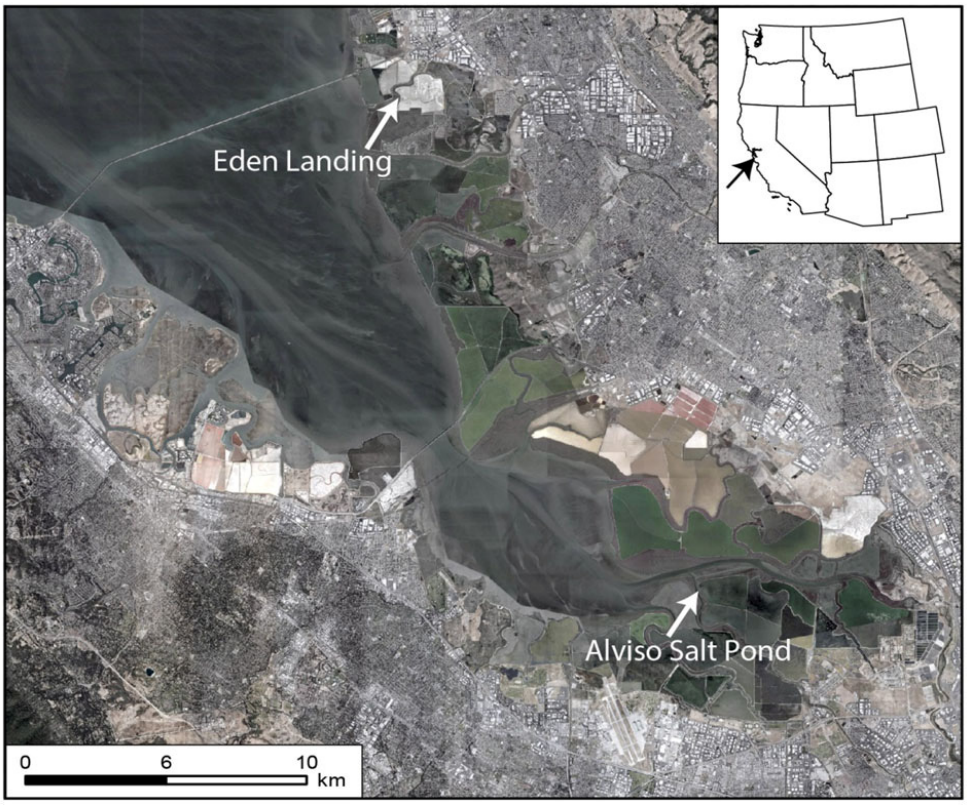

Figure 1. Landsat image (4/9/2013) of southern San Francisco Bay showing the two *S. salsa* collecting localities. Image from Google Earth Pro (data from SIO, NOAA, U.S. Navy, NGA, GEBCO). Insert shows location of image area in the western United States.

Littoridinops monroensis (Frauenfeld, 1863), a brackish-water cochliopid having a well-established native range along the western Atlantic and eastern Gulf Coasts, was recently reported in the San Francisco Bay estuary (Hershler et al. 2007), which has a long history of species introductions (Cohen and Carlton 1998). This new population was thought to have been introduced by shipping, with snails or egg capsules possibly transported in residual ballast sediment. In the same paper another cochliopid, *Tryonia porrecta* (Mighels, 1845), previously known from thermal springs in western North America (and several sites in Hawaii), was also newly reported in San Francisco Bay, over 250 km distant from its most geographically proximal population (Hershler et al. 2007). The San Francisco Bay population was considered cryptogenic (per Carlton 1996) because the native range of *T. porrecta* has not been well established and because the primarily partheno-genetic mode of reproduction of this species may facilitate a pattern of natural dispersal that cannot be easily distinguished from anthropogenic spread.

Herein we report a second western Atlantic cochliopid species in San Francisco Bay (*Spurwinkia salsa*) that also was likely introduced by shipping, and detail new records for *T. porrecta* from several artificial lakes in the Phoenix (Arizona) metropolitan area. We present analyses of mitochondrial DNA sequence data that confirm our identifications, and discuss possible modes of anthropogenic or natural dispersal that could explain these distributions.

Material and methods

Spurwinkia salsa was discovered in San Francisco Bay in 2008 in a brackish, high *Sarcocornia* marsh along Mount Eden Creek, north of Whale's Tail Marsh and south of the east end of the San Mateo (I-92) bridge, in the Eden Landing Ecological Reserve (Figure 1). In 2009, this species was found in the nearby Alviso Salt Pond complex. This portion of the estuary shoreline consists of highly modified, brackish to hypersaline habitats previously used

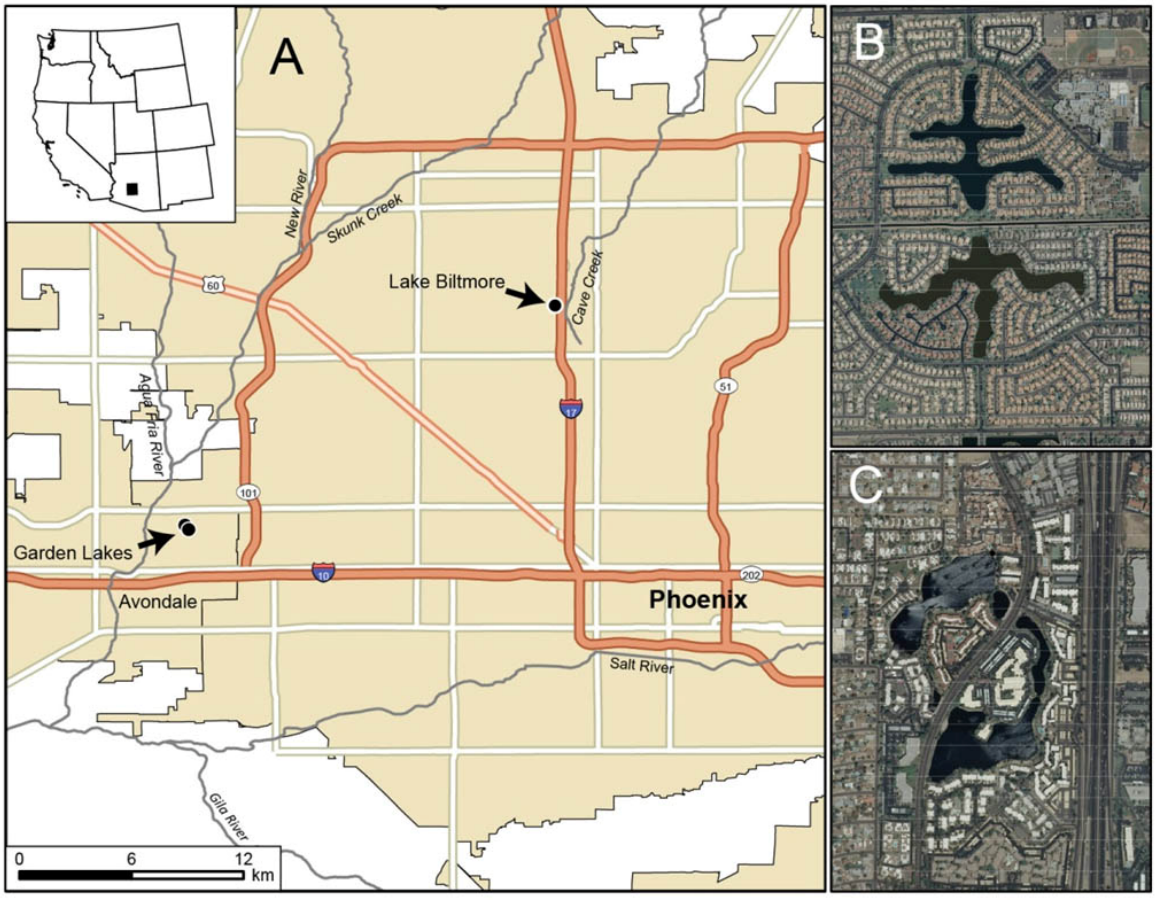

Figure 2. Phoenix collection localities for *T. porrecta*. A. Street map (data from Esri) showing the locations of the two artificial lakes. Phoenix urban area shaded light brown. B, C. 2010 NAIP 1-m orthoimagery (from Arizona Imagery Server, http://sco.azland.gov/imagery.htm) showing Garden Lakes and Lake Biltmore, respectively. Insert shows location of map area in the western United States.

for solar salt production and that are being restored to tidal wetlands (Lonzarich and Smith 1997; Life Science!, Inc. 2003).

Tryonia porrecta was discovered near Phoenix, Arizona in the northwest segment of Lake Biltmore in 1984 (briefly mentioned by Hershler et al. 2005) and in Garden Lakes during 2014 (Figure 2A). Garden Lakes (Figure 2B), occupying about 15 ha (Larson and Grimm 2012) and consisting of two closely proximal but physically separated water bodies (both containing snails), was constructed around 1986, while Lake Biltmore (Figure 2C), occupying ca. 8 ha (Larson and Grimm 2012), was constructed between 1969 and 1979. Lake Biltmore receives water from the Salt River Project canal system; Garden Lakes is also supplied from this project via underground feed pipes (Garden Lakes Community Association 2014).

Snails were collected by hand or using a small sieve or dip net and directly preserved in 90% ethanol for molecular analysis, or relaxed with menthol crystals, fixed in dilute formalin and preserved in 70% ethanol for morphological study. Specimens were identified based on study of shells using light microscopy and a scanning electron microscopy, and examination of diagnostic aspects of soft part anatomy (e.g. penis and female oviduct). Voucher material was deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Pertinent material in the collections of the Academy of Natural Sciences of Philadelphia (ANSP) and University of Michigan Museum of Zoology (UMMZ) was also studied.

Four specimens from Eden Landing identified as *S. salsa*, and four specimens from Garden Lakes (north) identified as *T. porrecta* were

sequenced for mitochondrial DNA. Genomic DNA was extracted from entire snails using a CTAB protocol (Bucklin 1992); each specimen was analyzed for mtDNA individually. LCO1490 and HCO2198 (Folmer et al. 1994) were used to amplify a 710 base pair (bp) fragment of cytochrome c oxidase subunit I (COI). Amplification conditions and sequencing of amplified polymerase chain reaction product were from Liu et al. (2003). Sequences were determined for both strands and then edited and aligned using SEQUENCHER™ version 5.0.1. New sequences were deposited in GenBank (*Spurwinkia salsa,* KP057916; *Tryonia porrecta*, KP057915). The haplotype detected in San Francisco Bay specimens of *S. salsa* was compared to previously published COI sequences of this monotypic genus from two western Atlantic localities (Liu et al. 2001; Wilke et al. 2001); this collective dataset was also analyzed phylogenetically together with representatives of 18 other cochliopid genera from the New World; *Ipnobius robustus* was used as the root of the tree (per Liu et al. 2001). The haplotype delineated in Arizona specimens of *T. porrecta* was compared to the large number of previously published COI sequences from across the entire geographic range of this species in western North America (Hershler et al. 2005; Hershler et al. 2007).

Phylogenetic relationships of San Francisco Bay specimens of *S. salsa* were inferred by Bayesian analysis using MRBAYES 3.1.2 (Huelsenbeck and Ronquist 2001). MrModeltest 2.3 (Nylander 2004) was used to obtain an appropriate substitution model (using the Akaike Information Criterion) and parameter values for this analysis. Metropolis-coupled Markov chain Monte Carlo simulations were run across four chains (using the model selected through MrModeltest) for 2,000,000 generations, and Markov chains were sampled at intervals of 10 generations to obtain 200,000 sample points. Multiple runs were performed to assess that parameters were not considerably different. We used the default settings for the priors on topologies and the GTR + I + G model parameters selected by MRMODELTEST as the best fit model. At the end of the analysis, the average standard deviation of split frequencies was less than 0.01 (0.003) and the Potential Scale Reduction Factor (PSRF) was 1, indicating that the runs had reached convergence. The sampled trees with branch lengths were used to generate a 50% majority rule consensus tree with the first 25% of the samples (50,000) removed to ensure that the chain sampled reached a stationary position based on the log likelihood values of the trees.

Results

Species accounts

Spurwinkia salsa (Pilsbry, 1905)

Distribution: western Atlantic coast from New Brunswick south to Georgia (Hershler and Thompson 1992; McAlpine et al. 2005).

Referred material: California. *Alameda County*: USNM 1120373, salt marsh, Eden Landing, south San Francisco Bay (37.6117°N, 122.1335°W), 13 October 2008 (coll. JTC, ANC). *Ibid*., USNM 1136372, 12 October 2009 (coll. JTC, ANC, David Kim, Linda McCann). *Santa Clara County*: USNM 1135761, Alviso Salt Pond #9, south San Francisco Bay (37.4582°N, 122.0193°W), 8 October 2009 (coll. CD). *Ibid*., USNM 1136466, 11 January 2010 (coll. CD).

Snails were found in low abundance at Eden Landing on the undersides of damp wood debris and on the soil/organic debris underneath these materials. Snails were collected along the edges of the Alviso Salt Pond #9 on fine sediment (in association with *Tryonia porrecta*). These estuarine habitats are similar to those occupied by *S. salsa* along the western Atlantic coast (e.g., Davis et al. 1982; McAlpine et al. 2005). Specimens were identified as *S. salsa* based on the broadly conical shell having medium sutures and a relatively large body whorl and aperture (Figure 3A; Table 1); the presence of a broad, non-glandular, distal lobe on the inner edge of the penis (Figure 4A-B); and details of the female reproductive anatomy (per Davis et al. 1982; Hershler and Thompson 1992).

Tryonia porrecta (Mighels, 1845)

Distribution: Great Basin, lower Colorado River basin, San Francisco Bay, Hawaii (Holocene only) (Hershler et al. 2007).

Referred material: Arizona. *Maricopa County*: USNM 1152012, Lake Biltmore, Deer Valley (33.591904°N, 112.120027°W), 10 August 1984 (coll. James Jerry Landye). *Ibid*., USNM 847207, 16 August 1985 coll. RH, JJL). USNM 1248613, Garden Lakes (north), Avondale (33.4864°N, 112.2981°W), 31 January 2014 (coll. JS). USNM 1248614, USNM 1252055, Garden Lakes (south), Avondale (33.4843°N, 112.2965°W), 31 January 2014 (coll. JS), 1 July 2014 (coll. JS and DW), respectively.

The Lake Biltmore population of *T. porrecta* was discovered in 1984 during an informal visit to evaluate possible pond management issues (James Jerry Landye, email to RH, 26 July 2014).

Table 1. Shell characteristics of *Spurwinkia salsa* and *Tryonia porrecta*. Measurements are in mm. WH=number of shell whorls, SH=shell height, SW=shell width, HBW=height of body whorl, WBW=width of body whorl, AH=aperture height, AW=aperture width.

	WH	SH	SW	HBW	WBW	AH	AW	SH/SW	AH/AW	WH/SH
Spurwinkia salsa, USNM 1120373 (*n*=6)										
Mean	6.00	4.26	2.51	2.85	2.15	1.76	1.43	1.70	1.24	1.41
S.D.	0.16	0.14	0.10	0.17	0.10	0.11	0.05	0.05	0.06	0.06
Range	5.75–6.25	4.10–4.46	2.30–2.59	2.58–3.08	1.97–2.25	1.59–1.89	1.34–1.46	1.63–1.78	1.16–1.31	1.29–1.47
Tryonia porrecta, USNM 1152012 (*n*=20)										
Mean	5.84	8.14	3.64	4.64	3.36	2.55	2.14	2.23	1.19	0.72
S.D.	0.25	0.57	0.20	0.23	0.17	0.19	0.10	0.11	0.06	0.03
Range	5.25–6.50	7.37–9.48	3.31–4.09	4.20–5.07	3.02–3.66	2.32–3.00	1.99–2.33	2.07–2.39	1.10–1.28	0.66–0.78
Tryonia porrecta, USNM 1252055 (*n*=20)										
Mean	6.24	4.15	1.78	2.26	1.61	1.21	1.02	2.34	1.20	1.51
S.D.	0.34	0.40	0.11	0.14	0.10	0.08	0.06	0.12	0.06	0.07
Range	5.75–7.00	3.65–4.92	1.61–1.95	2.05–2.49	1.46–1.85	1.10–1.36	0.90–1.15	2.11–2.59	0.97–1.27	1.39–1.65

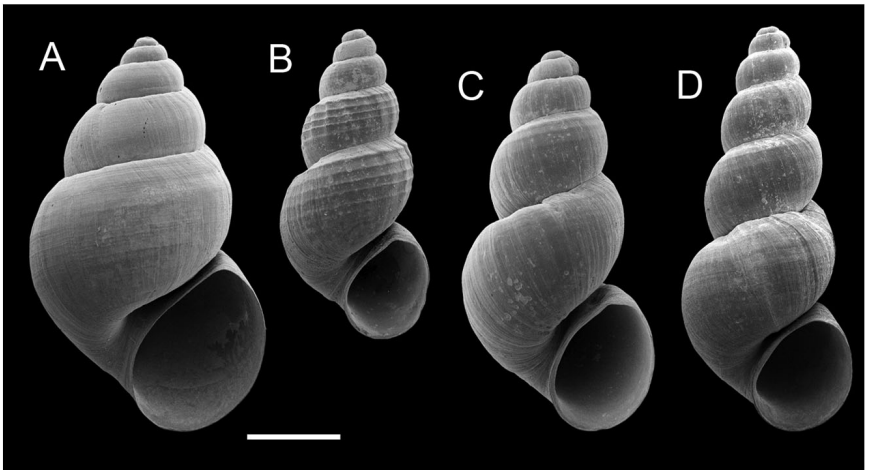

Figure 3. Scanning electron micrographs of shells. A. *Spurwinkia salsa*, Eden Landing, USNM 1120373. B-C. *Tryonia porrecta*, Lake Biltmore, USNM 1152012. D. *Tryonia porrecta*, Garden Lakes (south), USNM 1252055. Scale bar = 1 mm.

Snails were abundant on all substrates along the edges of the lake. During a subsequent visit in 1985 few living specimens of *T. porrecta* were found and empty shells formed a narrow (ca. 10 cm) windrow along the lake's perimeter (JJL field notes). No snails or shells were found during subsequent visits on 26 December 1998 (JJL field notes) and more recently on 1 July 2014 (JS field notes). The appearance of the water in the lake during the most recent visit suggests that it is being chemically treated with copper sulfate. *Tryonia porrecta* was discovered in Garden Lakes south in 2014 by a local homeowner who observed large numbers of snails living on a partly submerged tarpaulin covering his boat. This species was subsequently found in Garden Lakes north near a private boat ramp.

Originally these specimens were thought by Arizona Game and Fish staff to be the invasive New Zealand mudsnail, *Potamopyrgus antipodarum* (email from Kami Silverwood to Robert Dillon, 16 January 2014). They were subsequently identified as *T. porrecta* based on the elongate-conic shells frequently having strong spiral sculpture (Figure 3B-D; Table 1), smooth inner side of the operculum (lacking a calcareous smear), darkly pigmented seminal receptacle, and other details of female reproductive anatomy (per Hershler 2001). The samples (totaling >100 specimens from the two localities) were composed entirely of females, which is typical of this primarily parthenogenetic species (Hershler 2001).

Tryonia porrecta was previously reported in a northern embayment of San Francisco Bay at

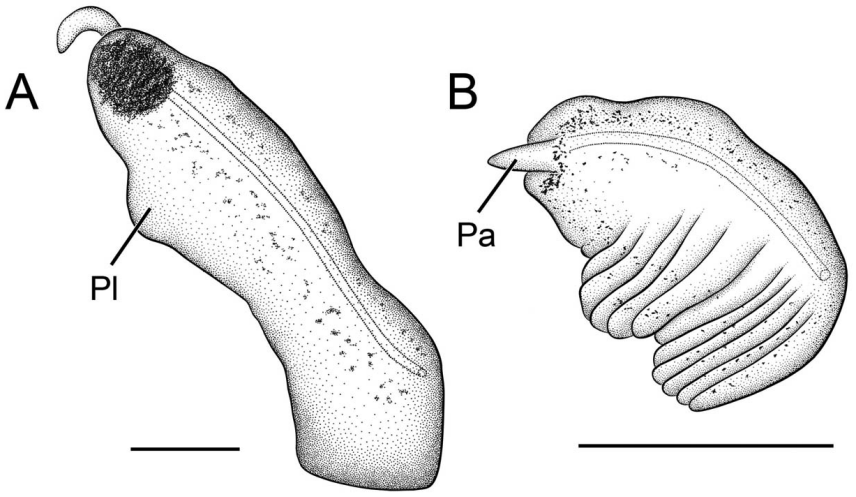

Figure 4. Penes of *Spurwinkia salsa*. A. Alviso Salt Pond (anaesthetized specimen), USNM 1135761. B. Eden Landing (contracted specimen), USNM 1120373. Pa, papilla; Pl, penial lobe. Scale bar = 250 µm.

Point Edith Marsh in 1999 (Hershler et al. 2007). Three shells tentatively identified as *T. porrecta* were collected at Eden Landing, 50 km to the south, in January 2009 (coll. ANC), and live *T. porrecta* were found in the Alviso Salt Pond complex, 20 km further south, in October 2009 (USNM 1135751) and January 2010 (USNM 1136465) (both coll. CD).

Molecular analyses

The single haplotype detected in specimens of *S. salsa* from San Francisco Bay differed from previously published sequences of this species by 3–9 bp. Collectively these formed a strongly supported (100% posterior probability) clade in the Bayesian tree (Figure 5), providing further evidence of conspecificity. The single COI haplotype detected in specimens from Garden Lakes is identical to the most common haplotype (I) of *T. porrecta* (Hershler et al. 2005).

Discussion

The discovery of the western Atlantic species *S. salsa* in San Francisco Bay closely parallels that of *L. monroensis*, another cochliopid recently found in the upper tidal zone in San Francisco Bay (Hershler et al. 2007). The Pacific Coast haplotype of *S. salsa* differs from the most similar reported Atlantic Coast haplotype by 3 bp (0.46%) of the 658 bp mtCOI fragment analyzed, corresponding to an estimated divergence of 250,000 years based on a geologically calibrated molecular clock estimate of 1.83% per million years for the closely related Hydrobiidae (Wilke 2003). This is too short a time period to be explained by vicariant separation of the populations due to closure of the Central American Seaway, which occurred 3.1–2.8 million years ago (Lessios 2008). Given that only two Atlantic Coast sites were sampled for haplotypes, there may well be Atlantic Coast haplotypes that are more closely similar or even identical to those detected in the San Francisco Bay snails, which would result in a correspondingly shorter divergence estimate.

There is also no natural transport mechanism that could reasonably explain *S. salsa*'s bi-coastal distribution. The long distance migrations of North American birds are along north-south trending flyways; no coastal waterbird, such as might possibly carry a small snail for some distance in its gut or attached externally, migrates across the continent from one coast to the other, nor could *S. salsa* likely survive such a journey, internally or externally (Boag 1986; Van Leeuwen et al. 2012a, b). Since *S. salsa* has never been reported in inland waters, a gradual, stepping stone dispersal across the continent is also not feasible.

Thus, *S. salsa*'s presence on the Pacific Coast must be due to anthropogenic transport. If this took place in recent decades, the most likely mechanism would be transport in the seaweed [*Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863] packing used to ship live marine bait worms from Maine to California (Cohen 2012a), or less

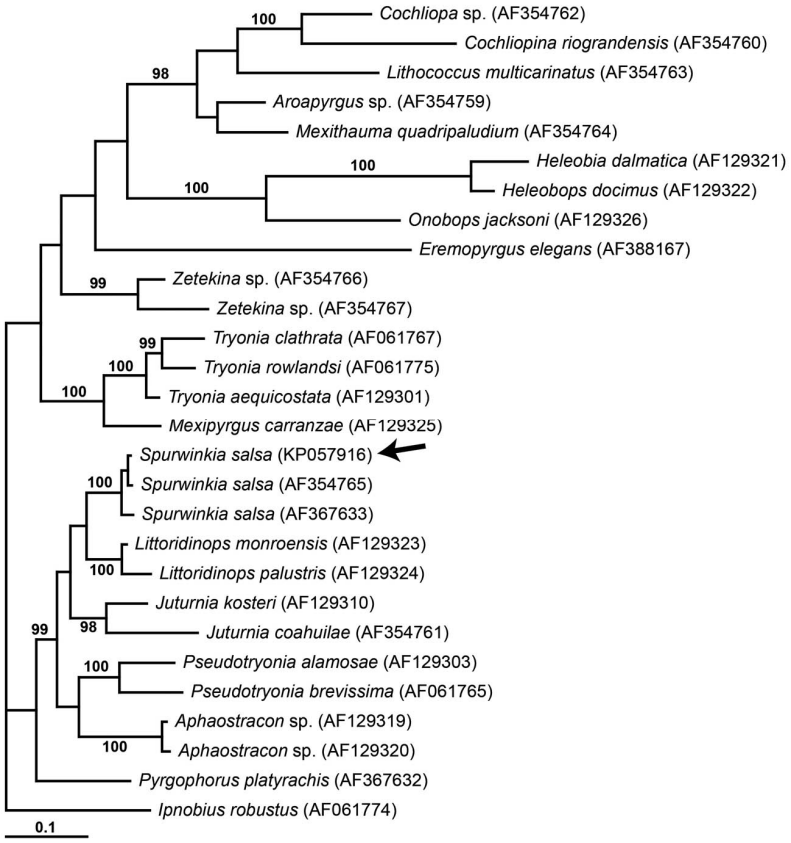

Figure 5. Bayesian tree (based on COI sequences) depicting the relationships of the cochliopid snails that were recently discovered in south San Francisco Bay (terminal identified by arrow). Posterior probability values are shown when >95%.

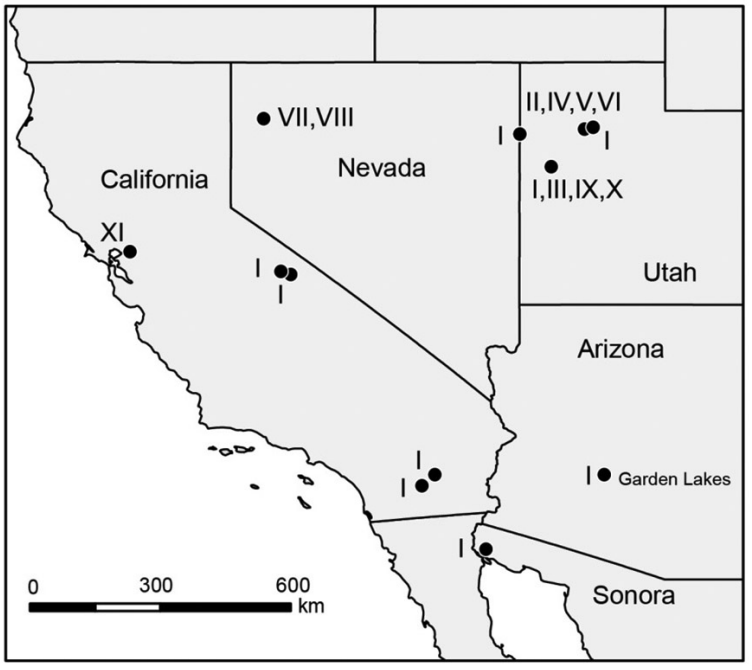

Figure 6. Geographic distribution of *T. porrecta* COI haplotypes (modified from Hershler et al. 2005). Haplotype XI is the "estuary" haplotype reported by Hershler et al. (2007).

Table 2. Possible time lag (in years) between introduction and collection of selected Atlantic species in San Francisco Bay (Carlton 1979; Cohen and Carlton 1995).

Species	Date first collected	Possible time lag (years)	Reason for absence of early collections
Bivalve			
Petricolaria pholadiformis	1927	50+	Poorly explored habitat
Protist			
Ancistrocoma pelseneeri	1930s	50+	Required specialized expertise
Polychaete			
Polydora cornuta	1933	60+	Group poorly collected
Polychaete			
Streblospio benedicti	1932	60+	Group poorly collected
Crab			
Rhithropanopeus harrisii	1937	60+	Poorly explored habitat
Amphipod			Group poorly collected; specimens captured incidental to other collections; not
Melita nitida	1938	60+	identified until 1977
Protists			
Cochliophilus depressus			
Cochliophilus minor	1940s	60+	Required specialized expertise
Polychaete			
Asychis elongata	1950s	80+	Group poorly collected
Sponge			
Clathria prolifera	1950	80+	Group poorly collected; required specialized expertise for recognition
Amphipod			
Ampelisca abdita	1951	80+	Group poorly collected
Bryozoan			
Conopeum tenuissimum	1951	80+	Group poorly collected
Sponge			
Prosuberites sp.	1953	80+	Group poorly collected; required specialized expertise for recognition
Amphipod			
Transorchestia enigmatica	1962	40+ to 110	Poorly explored habitat
Bryozoan			
Victorella pavida	1967	30+ to 100	Poorly explored habitat

likely in the *Ascophyllum* similarly used as packing for live lobsters shipped from New England to California (less likely because less seaweed is transported with the smaller lobster trade and a smaller portion is discarded into the water; Cohen 2012b). Snails reported as unidentified hydrobiids were found among the *Ascophyllum* in bait worm shipments from Maine arriving in the San Francisco Bay area in a 1994–98 study and arriving in the Connecticut/New York region in a 2007–08 study (Cohen 2012a). Although *S. salsa* has been reported in the high intertidal zone on non-fucoid algae, *Ruppia maritime* Linnaeus, 1753, marsh grasses, and sticks (Davis et al. 1982), it is not known whether this snail occurs on *Ascophyllum*. In addition, *S. salsa*'s long planktonic larval stage (45–60 days; Mazurkiewicz 1972) could make establishment by this mechanism difficult. Of three congeneric gastropods that were common in *Ascophyllum* packing [*Littorina obtusata* (Linnaeus, 1758), *L. littorea* (Linnaeus, 1758), *L. saxatilis* (Olivi, 1792)], only the species with non-planktonic larvae (*L. saxatilis*) became established on the Pacific Coast (Cohen 2012a).

Another possible mechanism for a recent introduction is in ships' ballast water. However, ship arrivals in San Francisco Bay from the Atlantic were common only in the 19th century, before there was any significant ballast water use. Also, there are no clear records of ballast water introductions from the Atlantic to San Francisco Bay (or to anywhere on the Pacific Coast), although there are numerous clear examples of ballast water introductions across the Atlantic and across the Pacific along shipping routes that have been heavily used in recent decades. Thus, ballast water appears to be a less likely mechanism for transporting *S. salsa* to the Pacific Coast than in bait-worm packing. Occasional transport of these small benthic snails by being caught up in hull fouling cannot be ruled out, but seems even less likely.

No other recent mechanism—aquarium animals, scientific specimens, nursery plants, the few experimental oyster plantings made in San Francisco Bay in the second half of the 20th Century, or coast-to-coast overland transport on a trailered boat or equipment—seems a likely explanation for the arrival of these snails in San Francisco Bay.

The remaining possibility is that *S. salsa* was introduced a long time ago, in the 19th or very early 20th century, but only recently discovered and identified. Except for one thesis on the native

estuarine cochliopid *Tryonia imitator* (Pilsbry, 1899) (Kellogg 1985), there has been little sampling in appropriate habitats in California in the 20th or 21st centuries that would have been likely to collect and recognize *S. salsa*. Related to this is a pattern of long lag-times in the detection and identification of early introductions of Atlantic species in San Francisco Bay (Table 2). If *S. salsa* is an old introduction, the likeliest mechanism is with solid ballast. It might also have been transported with the Atlantic Coast oyster, *Crassostrea virginica* (Gmelin, 1791), which was shipped across the country and planted in San Francisco Bay in large numbers from 1869 to around 1910, although *S. salsa* has not been reported from oyster beds.

The *T. porrecta* populations in the southwestern United States are found in hydrographically separated habitats, primarily in thermal springs. Except for possible anthropogenic introductions, this distribution is probably the result of dispersal on migrating waterfowl (Hershler et al. 2005). In the Phoenix area, in addition to the records in artificial lakes reported here, live specimens (identified as *T. protea*, a junior synonym of *T. porrecta*) were collected in 1962 from an irrigation ditch (Bequaert and Miller 1973) and there are museum records of dry shells found in the Tempe area in 1910 (ANSP 112044, UMMZ 119262). Thus, the artificial lake records may not represent a recent introduction into the Phoenix area, but might instead reflect dispersal into a newly available habitat from a population long present in the area. The closest extant populations of *T. porrecta* are in southeastern California, but maps of the Pacific Flyway show it branching in this region, with one segment passing down through northwestern Nevada and eastern California to the Colorado River delta at the head of the Gulf of California, and a separate segment passing through Utah and Arizona (e.g., Hawkins et al. 1984). In a previous investigation, all five populations in northwestern Nevada and eastern California that were studied were composed of a single allozyme genotype (genotype 1), while none of the four populations in Utah that were analyzed contained this genotype (Hershler et al. 2005; 20 to >50 snails were analyzed for each population). Thus the distribution of allozyme genotypes in *T. porrecta* closely parallels the common avian migratory pathways, so that the Phoenix area population may be more likely to contain genotypes found in Utah (700 km to the north) than genotype 1 (found in the closest California population, 325 km to the west). The COI haplotype (I) detected in Garden Lakes snails has been reported from most *T. porrecta* populations (Hershler et al. 2005; this study) and thus is not very informative, especially since the sample size was small.

The discovery of *T. porrecta* in several artificial lakes, together with the recent report from the San Francisco estuary (Hershler et al. 2007), indicates that this species may be more broadly tolerant ecologically than previously thought. Further spread of this snail within the highly modified aquatic ecosystem of the Phoenix metropolitan area, which includes more than 900 artificial lakes (Larson and Grimm 2012), would appear likely.

This paper provides a baseline for evaluating future changes in the distribution of these two species. Our identifications may also assist the ongoing efforts of western land managers and conservation biologists to track the spread of the New Zealand mudsnail (*Potamopyrgus antipodarum*), a highly invasive pest that is easily confused with other small caenogastropods (ANS Task Force 2005).

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