

Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges

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ABSTRACT

Aim To use a comparative approach to understand parasite demographic patterns in native versus introduced populations, evaluating the potential roles of host invasion history and parasite life history.

Location North American east and west coasts with a focus on San Francisco Bay (SFB).

Methods Species richness and prevalence of trematode parasites were examined in the native and introduced ranges of two gastropod host species, *Ilyanassa obsoleta* and *Littorina saxatilis*. We divided the native range into the putative source area for introduction and areas to the north and south; we also sampled the overlapping introduced range in SFB. We dissected 14,781 snails from 103 populations and recorded the prevalence and identity of trematode parasites. We compared trematode species richness and prevalence across the hosts' introduced and native ranges, and evaluated the influence of host availability on observed patterns.

Results Relative to the native range, both *I. obsoleta* and *L. saxatilis* have escaped (lost) parasites in SFB, and *L. saxatilis* demonstrated a greater reduction of trematode diversity and infection prevalence than *I. obsoleta*. This was not due to sampling inequalities between the hosts. Instead, rarefaction curves suggested complete capture of trematode species in native source and SFB subregions, except for *L. saxatilis* in SFB, where infection was extremely rare. For *I. obsoleta*, infection prevalence of trematodes using fish definitive hosts was significantly lower in SFB compared to the native range, unlike those using bird hosts. Host availability partly explained the presence of introduced trematodes in SFB.

Main conclusions Differential losses of parasite richness and prevalence for the two gastropod host species in their introduced range is probably the result of several mechanistic factors: time since introduction, propagule pressure, vector of introduction, and host availability. Moreover, the recent occurrence of *L. saxatilis*' invasion and its active introduction vector suggest that its parasite diversity and distribution will probably increase over time. Our study suggests that host invasion history and parasite life history play key roles in the extent and diversity of trematodes transferred to introduced populations. Our results also provide vital information for understanding community-level influences of parasite introductions, as well as for disease ecology in general.

Keywords

Biogeography, gastropods, *Ilyanassa obsoleta*, intertidal, introduction vector, invasion history, *Littorina saxatilis*, North America, parasite, prevalence.

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INTRODUCTION

Parasites can have strong effects on host populations (Anderson & May, 1978; Hudson *et al.*, 1998), non-host populations (Poulin, 1999; Wood *et al.*, 2007; Grewell, 2008), and ecological processes (Thomas *et al.*, 1998; Mouritsen & Poulin, 2005). However, parasites are often studied across limited portions of their distributions, so a basic understanding of demographic patterns throughout their geographic range is often lacking. Understanding these large-scale patterns is especially important given the global movements of species via human-transport mechanisms (Ruiz *et al.*, 2000).

Empirical evidence demonstrates that human-mediated introductions can strongly limit the abundance and diversity of parasites (Torchin *et al.*, 2003), because the process of introduction filters out some parasite species while enabling others to invade with their hosts (Torchin *et al.*, 2001; Mitchell & Power, 2003; Blakeslee *et al.*, 2009). This process has been termed 'parasite escape'. A recent study by Lafferty *et al.* (2010) concluded that the origin of host taxa (native or introduced) was a key biogeographic predictor of parasite richness and abundance across ecosystems worldwide. Guégan & Kennedy (1993) also found introduction status to be significantly correlated with helminth richness in aquatic fishes of the British Isles.

While there is broad support for introduced hosts escaping the full complement of parasites found in native communities, detailed investigations of the factors influencing the introduction success/failure of individual parasite species are rare. In particular, the means of introduction and points of origin of marine invasions are highly variable among hosts (Carlton & Geller, 1993; Ruiz *et al.*, 1997; Miller, 2000; Geller *et al.*, 2010) and should influence the probability of a parasite species' transfer and establishment in a region of introduction. For parasites that require multiple hosts, absence or rarity of necessary hosts in the introduced range will also restrict that parasite's distribution.

In this study, we examine how factors associated with host invasion history, parasite life history and host-parasite geography affect introduction success. We focus on marine trematodes, which represent a fundamental component of many ecological communities (Lauckner, 1987; Kuris *et al.*, 2008). In addition, trematodes often have long-lived infections in invertebrate hosts, have characteristic life stages useful for morphological identification, and are highly host-specific to their first-intermediate hosts (Lauckner, 1980; Curtis, 2003), making them highly tractable for studies of parasite abundance and diversity. Finally, because trematodes have been studied extensively, they provide a useful model system for informing disease ecology and parasite invasion in general.

To understand how host invasion pathways and parasite life cycles influence parasite introduction, we examine the richness and abundance of infecting trematodes associated with two gastropods: eastern mudsnail, *Ilyanassa obsoleta* (Say, 1822) (Mollusca: Gastropoda: Nassariidae), and rough periwinkle, *Littorina saxatilis* (Oliv, 1792) (Mollusca: Gastropoda:

Littorinidae). Both snails are native to the North American east coast and were introduced to San Francisco Bay (SFB) in the 20th century, although the invasion pathway for each differed (see 'Study system' below). SFB has been the recipient of numerous introductions over the past two centuries and is arguably one of the most invaded estuaries in the world (Cohen & Carlton, 1998); however, few studies have characterized the nature and extent of introduced parasites to the region, or have sought to understand the factors underlying successful establishments. Using knowledge of each snail host's invasion pathway and through an analysis of trematode diversity, distribution and abundance patterns, we present a comprehensive description of parasites infecting these two hosts across their native and introduced ranges. We discuss the results of this detailed demographic study in relation to a number of proposed mechanistic factors associated with observed patterns.

MATERIALS AND METHODS

Study system

Trematodes have complex life histories, requiring transmission through multiple hosts. Larval trematodes reproduce asexually in snail gonads and castrate their first-intermediate hosts. A variety of marine taxa may then serve as appropriate second-intermediate hosts, including 'worms' (segmented worms and flatworms), crustaceans, bivalves and other gastropods. Fish and bird species routinely serve as definitive hosts where the trematode matures and sexually reproduces. While trematodes are typically highly specific to a particular snail (often infecting only a single species), they generally exhibit less taxonomic specificity when infecting second-intermediate and definitive hosts (Lauckner, 1980). In the first-intermediate stage in gastropods, trematodes produce characteristic free-living stages (cercariae) that can be identified to the species level using published keys (McDermott, 1951; James, 1968, 1969; Yamaguti, 1975; Stunkard, 1983), making this stage in the life cycle the most tractable for geographic studies.

We explored trematode parasitism in *I. obsoleta* and *L. saxatilis*, which have overlapping distributions on the east and west coasts of North America. In the native east coast range, *I. obsoleta* is found from the Gulf of Saint Lawrence, Canada to northern Florida, USA (Abbott, 1974), and *L. saxatilis* has been documented from Hudson Bay, Canada to Chesapeake Bay, USA (Carlton & Cohen, 1998; although recent field surveys did not find the snail south of Long Island, USA, A.M.H.B., pers. obs.). On the west coast, both occur in SFB, and *I. obsoleta* also occurs in Willapa Bay (WB), Washington and in Boundary Bay (BB) along the border of Washington and British Columbia (Demond, 1952; Carlton, 1992; Carlton & Cohen, 1998). Although they have similar geographic ranges, the snails' invasion histories differ significantly. *Ilyanassa obsoleta* was introduced via large-scale transplants of eastern oysters (*Crassostrea virginica*) for aquaculture in the early 1900s (primarily concentrated in SFB), an introduction vector that no longer operates. *Littorina saxatilis* was introduced

Table 1 Comparative information on the North American distribution and invasion history for two snail host species, *Ilyanassa obsoleta* and *Littorina saxatilis* (for detailed descriptions accompanying this table see Appendix S1).

Snail species	East coast native range	West coast introduced range	Date of first recorded observation in introduced range	Purported introduction vector	Introduction vector: open or closed?	Source population(s) for west coast introduction
<i>Ilyanassa obsoleta</i>	Gulf of St Lawrence, Canada to northern Florida, USA	San Francisco Bay (SFB), California, USA; Willapa Bay (WB), Washington; Boundary Bay (BB), Washington, USA and British Columbia, Canada	SFB: 1907 (Carlton, 1992); WB: 1945 (Carlton, 1992); BB: 1952 (Demond, 1952)	Introduced with intentional but ultimately failed attempts at transplanting the eastern oyster, <i>Crassostrea virginica</i> , to the west coast (Carlton, 1992)	Closed	New York (primarily Long Island) bays; in addition, nearby bays in southern New England and the mid-Atlantic. Oysters from Chesapeake Bay were probably an additional indirect source (Kochiss, 1974; Miller, 2000)
<i>Littorina saxatilis</i>	Hudson Bay, Canada to Delaware Bay, USA	San Francisco Bay (SFB), California, USA	SFB: 1993 (Carlton & Cohen, 1998)	Introduced with brown algae (primarily <i>Ascophyllum nodosum</i>) packing materials for the Maine baitworm (bloodworms, sandworms) and live seafood (primarily New England lobster, <i>Homarus americanus</i>) trades (Carlton & Cohen, 1998)	Open	Primarily coastal northern New England (Maine, New Hampshire, Massachusetts) (Miller, 1969; Carlton & Cohen, 1998; Miller <i>et al.</i> , 2004)

in the 1990s with live algal packing materials used in the seafood/baitworm trade, an introduction vector that remains open (see Table 1 and Appendix S1 in Supporting Information for detailed invasion history information for both snails).

Sampling and dissection protocols

The source of introduced populations rarely represents a random sample from the native range because organisms are often selected from a specific area for historical and/or economic reasons (Collins *et al.*, 2002; Voisin *et al.*, 2005; Kolbe *et al.*, 2007; Brawley *et al.*, 2009). For parasites whose abundance and diversities vary across their native distribution, source regions can strongly affect which parasites become introduced. To evaluate spatial variation in trematode diversity and distribution patterns, we explored trematode communities within a number of subregions. On the east coast, we sampled *I. obsoleta* at 49 sites from mid-coast Maine (43° N) to southern Georgia (31° N) and *L. saxatilis* at 29 sites from Newfoundland (51° N) to Long Island, New York (41° N). Along the west coast, we concentrated sampling in SFB (37° N) and performed some additional sampling at the two northern bays, WB (46° N) and BB (49° N). For both snails, we categorized subregions as: the putative source area (see Appendix S1 for source population selection), those areas to the north and south of the source area, and San Francisco Bay (henceforth referred

to as 'source', 'north', 'south' and 'SFB'). We also included WB and BB as two additional introduced subregions for *I. obsoleta* (Fig. 1). Because the native ranges for both snails were much larger than the overlapping introduced range in SFB, we sampled extensively in SFB to ensure numbers were sufficiently large (see Table S1 in Appendix S2); in addition, we performed rarefaction analyses to ensure adequate sampling.

At each site, we haphazardly collected an average of 140 (range = 48–557; mode = 100) adult snails (> 14 mm for *I. obsoleta* and > 6 mm for *L. saxatilis*) while walking 100 m along a rocky shoreline for *L. saxatilis* or in intertidal soft sediments for *I. obsoleta*. Snails were dissected in the laboratory and the presence of infection was determined through visual inspection of snail gonad and digestive tissues beneath a stereo dissecting microscope. Trematodes were identified under a compound microscope with the aid of keys and descriptions found in McDermott (1951), Yamaguti (1975), James (1968, 1969), and Stunkard (1983). Samples were collected primarily in the summer months of 2004–11 (see Table S1b).

Species richness and prevalence analyses

Species richness accumulation and estimation

Because we were unable to sample evenly across all populations, we constructed rarefaction curves (species accumulation



Figure 1 The study area, including sites sampled for *Ilyanassa obsoleta* (IO) and *Littorina saxatilis* (LS) trematodes in native (east coast: a,b) and introduced (west coast: c) regions of North America. (a) Native *I. obsoleta*: the east coast range consists of 49 sites: 18 in the source subregion (orange diamonds) and 12 in the north and 19 in the south subregions (white circles, orange outline); (b) native *L. saxatilis*: the east coast range consists of 29 sites: 14 in the source subregion (green diamonds) and 10 in the north and five in the south subregions (white circles, green outline); (c) introduced *I. obsoleta* (red, white outline) and *L. saxatilis* (red, black outline): the west coast range consists of eight and seven sites in San Francisco Bay (SFB) (stars) for the two snails, respectively, and five additional sites in Willapa Bay (WB) (diamonds) and Boundary Bay (BB) (crosses) for *I. obsoleta*. In panels (a) and (b), the sizes of markers are based on the number of sites sampled in the area: the smallest markers represent a single site, medium markers represent 2–5 sites, and large markers represent 5+ sites. See Table S1 in Appendix S2 for detailed information on sample sites.

and species estimation) using ESTIMATES 8.2 (Colwell, 2009) to quantify the effect of sampling effort on species richness. Based on its recommended use with parasite data (Walther & Morand, 1998), we chose the nonparametric species estimator Chao2 for rarefaction analyses. Chao2 uses the frequency of unique species in samples to estimate the number of missing species in a population (Chao, 2005).

Calculation of infection prevalence

Prevalence is the proportion of infected hosts within a population. In most cases, snails are infected with a single trematode species; however, infections containing multiple species were occasionally noted. We calculated pooled species prevalence as the proportion of snails infected with any trematode species. Species-specific prevalence was calculated as

the proportion of snails infected with a particular species of trematode (in cases of multiple infections, the sum of species-specific prevalence for a site will be slightly greater than the combined species prevalence). For each snail, we also calculated pooled prevalence of those trematodes that use either birds or fish as definitive hosts (see Table 2). We calculated prevalence at the subregional level (north, source, south, SFB) by averaging across sites. Prevalence data were normalized using Anscombe arcsine square-root transformation prior to statistical analyses (as advised by Zar, 1999).

Statistical analyses of richness and prevalence

Because sampling at sites was unequal, we also standardized species richness at the site level (as opposed to the regional level as above), using ESTIMATES 8.2. For this, 83 observations

Table 2 Observed trematode species and average prevalence (\pm SE) of trematodes that infect *Ilyanassa obsoleta* and *Littorina saxatilis* in native and introduced subregions of North America. Subregion abbreviations refer to: SFB, San Francisco Bay; WB, Willapa Bay; BB, Boundary Bay.

Trematode species of <i>Ilyanassa obsoleta</i> *	Native source	Native north	Native south	SFB	WB	BB
<i>Zoogonus rubellus</i> (Zr) ^F	7.79 (\pm 2.23)	13.00 (\pm 3.36)	7.95 (\pm 1.80)	1.43 (\pm 0.48)	0.09 (\pm 0.09)	0
<i>Lepocreadium setiferoides</i> (Lse) ^F	5.56 (\pm 1.29)	5.31 (\pm 1.69)	5.81 (\pm 2.22)	1.03 (\pm 0.46)	0	0
<i>Stephanostomum tenue</i> (St) ^F	3.50 (\pm 1.10)	7.08 (\pm 2.19)	0.54 (\pm 0.18)	0.36 (\pm 0.36)	0	0
<i>Stephanostomum dentatum</i> (Sd) ^F	3.73 (\pm 1.86)	4.14 (\pm 2.27)	0.82 (\pm 0.31)	0	0	0
<i>Himasthla quissetensis</i> (Hq) ^B	2.40 (\pm 0.69)	4.68 (\pm 1.63)	0.24 (\pm 0.12)	4.74 (\pm 3.65)	2.20 (\pm 2.20)	0.73 (\pm 0.32)
<i>Austrobilharzia variglandis</i> (Av) ^B	0.55 (\pm 0.14)	0.62 (\pm 0.35)	0.05 (\pm 0.05)	0.91 (\pm 0.74)	0.64 (\pm 0.44)	3.07 (\pm 2.37)
<i>Gynaecotyla adunca</i> (Ga) ^B	0.72 (\pm 0.28)	1.00 (\pm 0.39)	0.15 (\pm 0.11)	0	0	0
<i>Diplostomum nassa</i> (Dn) ^B	0.26 (\pm 0.12)	0.05 (\pm 0.05)	0	0	0	0
<i>Pleurogonius malaclemys</i> (Pm)	0	0	0.70 (\pm 0.27)	0	0	0
Bird-using trematodes ^B	3.95 (\pm 0.97)	7.72 (\pm 3.33)	0.44 (\pm 0.18)	5.65 (\pm 3.77)	2.84 (\pm 2.33)	3.80 (\pm 2.62)
Fish-using trematodes ^F	22.11 (\pm 4.75)	30.74 (\pm 8.28)	15.35 (\pm 3.35)	2.72 (\pm 1.19)	0.09 (\pm 0.09)	0
Trematode species of <i>Littorina saxatilis</i>	Native source	Native north	Native south	SFB	WB	BB
<i>Microphallus similis</i> (Ms) ^B	3.00 (\pm 1.10)	2.39 (\pm 1.55)	0.45 (\pm 0.28)	0.08 (\pm 0.08)	–	–
<i>Cryptocotyle lingua</i> (CrL) ^B	2.34 (\pm 0.71)	2.24 (\pm 1.32)	0.16 (\pm 0.16)	0	–	–
<i>Renicola roscovita</i> (Rr) ^B	1.10 (\pm 0.47)	0.31 (\pm 0.16)	0.53 (\pm 0.33)	0	–	–
<i>Cercaria parvicaudata</i> (Cp) ^B	0.27 (\pm 0.16)	0.11 (\pm 0.11)	0.61 (\pm 0.26)	0	–	–
<i>Himasthla elongata</i> (He) ^B	0.26 (\pm 0.16)	0.10 (\pm 0.10)	0	0	–	–
<i>Maritrema arenaria</i> (Ma) ^B	0.22 (\pm 0.11)	0	0	0.05 (\pm 0.05)	–	–
<i>Cercaria lebouri</i> (Cl) ^B	0.21 (\pm 0.16)	0.09 (\pm 0.09)	0.63 (\pm 0.63)	0	–	–
<i>Himasthla littorinae</i> (Hl) ^B	0.10 (\pm 0.08)	0.10 (\pm 0.10)	0	0	–	–
<i>Podocotyle atomon</i> (Pa) ^F	0.08 (\pm 0.08)	0.66 (\pm 0.38)	0	0	–	–
<i>Cercaria littorinae saxatilis</i> IV (Cls4) ^B	0.07 (\pm 0.07)	0.11 (\pm 0.11)	0	0	–	–
Pygmaeus microphallid group (PYG) ^B	0.02 (\pm 0.02)	1.07 (\pm 0.50)	0	0.05 (\pm 0.05)	–	–
<i>Cercaria littorinae saxatilis</i> I (Cls1) ^B	0.02 (\pm 0.02)	0	0	0	–	–
<i>Cercaria littorinae saxatilis</i> VI (Cls6) ^B	0.02 (\pm 0.02)	0	0	0	–	–
<i>Cercaria littorinae saxatilis</i> II (Cls2) ^B	0	0.09 (\pm 0.09)	0	0	–	–
Bird-using trematodes ^B	7.51 (\pm 1.97)	6.39 (\pm 2.35)	2.37 (\pm 0.99)	0.18 (\pm 0.18)	–	–
Fish-using trematodes ^F	0.08 (\pm 0.07)	0.66 (\pm 0.38)	0	0	–	–

*F, trematodes that use fish as definitive hosts in their infection cycles (fish-using); B, trematodes using birds as definitive hosts (bird-using). The rows for 'bird-using' and 'fish-using' trematodes reflect the pooled prevalence of trematode species that infect birds or fish as definitive hosts for each snail species (note: *L. saxatilis* has just one fish-using trematode, while *I. obsoleta* has a mix of bird-using and fish-using trematodes and one trematode, *Pleurogonius malaclemys*, that uses a terrapin as a definitive host; see Table 3). The pygmaeus microphallid group associated with *L. saxatilis* consists of four morphologically indistinct species, which are commonly identified as only one species, *Microphallus pygmaeus* (see discussion in Blakeslee & Byers, 2008).

(the minimum number of snails sampled across all sites for both snail species) were randomly selected for each replicate run, and the species richness across 500 runs was averaged as the adjusted site-level species richness [mean \pm standard error (SE)] for each site. Two *L. saxatilis* sites where the number of dissected snails was < 83 were excluded in analyses of species richness.

ANOVAs at the subregional level determined differences in trematode richness and prevalence for the two snail–parasite systems. When significant differences were found at the subregional level, a Fisher's *post-hoc* test was used to determine which subregions differed. These analyses were performed for all pooled trematodes (total prevalence) in each subregion, species-specific trematodes, and pooled trematodes that use birds as definitive hosts (bird-using) or those that use fish as definitive hosts (fish-using). Analyses were performed separately for each snail host.

Finally, we calculated the index of parasite escape (Torchin *et al.*, 2003) to compare overall species richness between the native region and SFB. We also compared the source subregion to SFB for both snails, and the native region and source subregion to both BB and WB, respectively, for *I. obsoleta*. The index of parasite escape is calculated as: $(n - i)/n$, where n = the total parasite species richness of the native region and i = total parasite species richness of the introduced region. The index ranges from 0 (no escape) to 1 (complete escape).

Trematode infection cycles and hosts

Trematode species require different combinations of second-intermediate and definitive hosts for completion of life cycles, and the absence of suitable hosts at any stage will prevent these parasites from establishing. To understand how the presence of hosts affects establishment of introduced trematodes of

I. obsoleta and *L. saxatilis*, we gathered second-intermediate and definitive host information by extensively searching the literature and two relevant databases: the *Encyclopedia of Life* (<http://www.eol.org>) and the *Nonindigenous Aquatic Species* database (<http://nas.er.usgs.gov>). We compiled information on the presence of natural hosts (those species found infected under natural field conditions) and experimental hosts (those infected in a laboratory setting). When no evidence of a known host species was found in either snail's introduced range, it was designated as 'absent'.

RESULTS

Snail sampling and trematode identifications

For *I. obsoleta*, 6662 snails were examined in the native region: 2660 in the source (18 sites), 2047 in the north (12 sites) and 1955 in the south (19 sites). In the introduced SFB subregion, we examined 1364 *I. obsoleta* snails from eight sites with an additional 540 and 669 snails from WB and BB (five sites each), respectively (see Table S1 for site-level information). Nine species have been documented to infect *I. obsoleta* in the native region (Curtis, 1997). In our sampling, we observed all nine species; however, not all were present in each of the native subregions (Table 2). A total of five trematode species were found in SFB, representing a subset of those present in the

native range. We observed three species in WB and two in BB (Table 2).

For *L. saxatilis*, 3653 snails were examined in the native region: 1958 in the source (14 sites), 1025 in the north (10 sites) and 670 in the south (five sites). In SFB, 1893 snails (seven sites) were examined (see Table S1). Fourteen trematode species are known to infect *L. saxatilis* on the native east coast (Blakeslee & Byers, 2008). All were observed in our study, but not all were present in each native subregion (Table 2). In SFB, three trematode species were observed in *L. saxatilis* (representing a subset of native populations) from just a single site (MLK Regional Shoreline, Oakland; Table S1b).

All of the trematodes observed in SFB are also found on the east coast; thus no native west coast trematodes infected either *I. obsoleta* or *L. saxatilis* in SFB. However, for all trematode species identified, we also examined the literature to assess taxonomic questions regarding west coast trematodes, especially for cosmopolitan records, which may represent true distributions of a single species, misidentification of separate species, or genetically distinct cryptic species (Huspeni, 2000). In our review of the literature, we did find cosmopolitan records for three identified trematodes, which warrant further study; however, these records do not influence our overall data or analyses (see Appendix S3 for detailed results of this investigation).

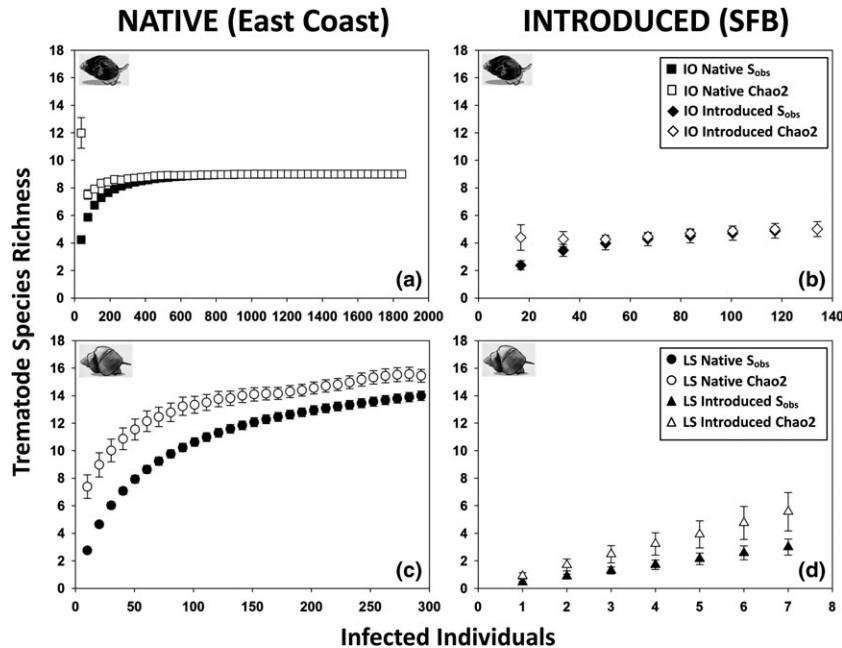


Figure 2 Rarefaction curves for *Ilyanassa obsoleta* (IO: a, b) and *Littorina saxatilis* (LS: c, d) individuals infected with trematode species in the native east coast range and San Francisco Bay (SFB), where both host species have established introduced populations. Species accumulation curves (S_{obs}) reflect the observed number of species as a function of sampling effort; species estimator curves reflect the predicted number of species based on the selected estimator algorithm (Chao2). Error bars are SE for 500 runs in ESTIMATE S 8.2 (Colwell, 2009). Convergence of S_{obs} and Chao2 at an asymptote provides strong evidence that continued sampling within a region would be unlikely to reveal additional species. Although our data were sample-based, we rescaled species accumulation curves to accumulated individuals in order to compare species richness across our data sets in a standardized manner (Gotelli & Colwell, 2001).

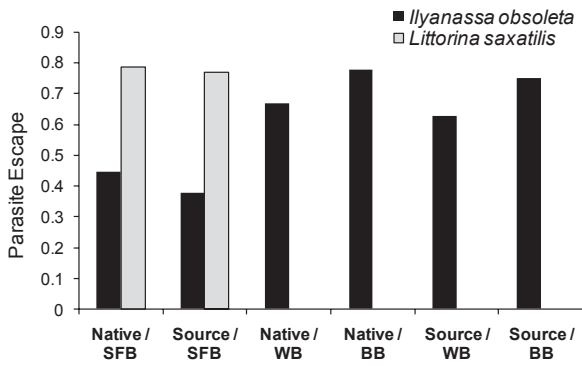


Figure 3 Parasite escape in *Ilyanassa obsoleta* and *Littorina saxatilis* for different comparisons: native versus San Francisco Bay (SFB) and source versus SFB for both species. Parasite escape in *I. obsoleta* from the two additional introduced subregions, Willapa Bay (WB) and Boundary Bay (BB), is also provided. *Littorina saxatilis* exhibits 1.8 and 2.1 times greater parasite escape than *I. obsoleta* in native versus SFB and source versus SFB, respectively.

Species estimation, richness and prevalence

Convergence of the species accumulation (S_{obs}) and species estimator (Chao2) rarefaction curves at an asymptote provides strong evidence that sampling was sufficient to reveal the underlying species richness across samples (Gotelli & Colwell, 2001). For *I. obsoleta*, the S_{obs} and Chao2 curves converged at an asymptote of nine trematode species in the native region [Chao2 95% confidence intervals (CI) = 9–9; Fig. 2a] and five

species in SFB (Chao2 CI = 5–6; Fig. 2b). For *L. saxatilis*, the S_{obs} and Chao2 curves converged near an asymptote of 14 trematode species in the native region (Chao2 CI = 14–29; Fig. 2c), but there was no indication of convergence at an asymptote in SFB (Chao2 = 6, CI = 3–14; Fig. 2d).

Based on the index of parasite escape (Torchin *et al.*, 2003), *L. saxatilis* escaped more parasites than *I. obsoleta* for both the native/SFB and source/SFB comparisons (1.8 times and 2.1 times greater, respectively). The WB and BB comparisons for *I. obsoleta* also showed high levels of parasite escape when compared qualitatively with SFB trematodes (Fig. 3).

For each snail–trematode system, we also explored differences in species richness and prevalence at the subregional level for pooled trematodes using ANOVAs (see Table S2). For both snails, trematode richness was significantly lower in SFB compared with native north and source subregions, but not with the native south. Also, *I. obsoleta* from WB and BB had significantly lower trematode richness compared with native subregions, but were not different from SFB. Further, *L. saxatilis* displayed significantly lower prevalence in SFB compared with native subregions, but for *I. obsoleta*, prevalence was only significantly lower in SFB versus the native north. Finally, WB was the only introduced subregion that was significantly lower than all native subregions (Fig. 4).

For species-specific prevalence, we found that of *I. obsoleta*'s five introduced trematodes, the three that use fish as definitive hosts (*Lepocreadium setiferoides*, *Stephanostomum tenue* and *Zoogonus rubellus*) had significantly lower prevalence

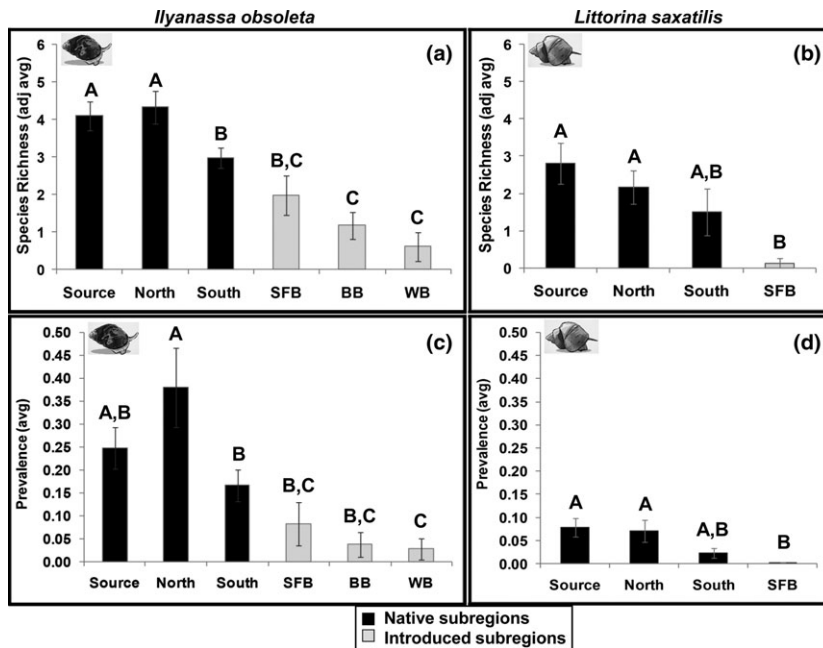


Figure 4 Average (\pm SE) site-level species richness (standardized for sampling differences) and Anscombe-transformed site-level prevalence for subregions in the native region (source, north and south) and the introduced region [San Francisco Bay (SFB), Willapa Bay (WB) and Boundary Bay (BB)] in *Ilyanassa obsoleta* (a, c) and *Littorina saxatilis* (b, d). Letters denote significance at the $P < 0.05$ level for *post-hoc* Fisher's pairwise comparison tests following ANOVAs.

Table 3 Summary results of literature and database searches to identify second-intermediate and definitive hosts of *Ilyanassa obsoleta* and *Littorina saxatilis* trematodes in the introduced region (west coast, USA, primarily San Francisco Bay). See Table 2 for full trematode species names.

Trematode species	Present in introduced range?	First-intermediate host species	Second-intermediate hosts*				Definitive hosts*			
			Type of host	No. of identified host species	No. of identified hosts in introduced range	Percentage of identified hosts in introduced region	Type of host	No. of identified host species	No. of identified hosts in introduced range	Percentage of identified hosts in introduced region
<i>Av</i>	Yes	<i>I. obsoleta</i>	Rock, shell	–	–	–	Bird	2	2	100.0
<i>Hq</i>	Yes	<i>I. obsoleta</i>	Molluscs	11	4	36.4	Bird	2	2	100.0
<i>Lse</i>	Yes	<i>I. obsoleta</i>	Worms	12	6	50.0	Fish	4	0	0.0
<i>St</i>	Yes	<i>I. obsoleta</i>	Fish	2	0	0.0	Fish	7	1	14.3
<i>Zr</i>	Yes	<i>I. obsoleta</i>	Worms	6	0	0.0	Fish	3	0	0.0
<i>Dn</i>	No	<i>I. obsoleta</i>	Fish	2	1	50.0	Bird?	†	†	†
<i>Ga</i>	No	<i>I. obsoleta</i>	Crustaceans	4	0	0.0	Bird	7	3	42.9
<i>Pm</i>	No	<i>I. obsoleta</i>	Vegetation, hard surfaces	–	–	–	Terrapin	3	0	0.0
<i>Sd</i>	No	<i>I. obsoleta</i>	Fish	1	0	0.0	Fish	2	0	0.0
<i>Ma</i>	Yes	<i>L. saxatilis</i>	Crustaceans	5	1	20.0	Bird	4	2	50.0
<i>Ms</i>	Yes	<i>L. saxatilis</i>	Crustaceans	4	1	25.0	Bird	17	8	47.1
PYG	Yes	<i>L. saxatilis</i>	Snail‡	1	1	100.0	Bird	9	3	33.3
<i>Cl</i>	No	<i>L. saxatilis</i>	Rock, shell	–	–	–	Bird	3	2	66.7
<i>Cp</i>	No	<i>L. saxatilis</i>	Molluscs, worms	13	3	23.1	Bird?	†	†	†
<i>CrI</i>	No	<i>L. saxatilis</i>	Fish	27	2	7.4	Bird	23	11	47.8
<i>He</i>	No	<i>L. saxatilis</i>	Molluscs, worms	17	4	23.5	Bird	14	6	42.9
<i>HI</i>	No	<i>L. saxatilis</i>	Molluscs	5	3	60.0	Bird	1	1	100.0
<i>Pa</i>	No	<i>L. saxatilis</i>	Crustaceans	17	0	0.0	Fish	27	7	25.9
<i>Rr</i>	No	<i>L. saxatilis</i>	Molluscs	10	5	50.0	Bird	1	1	100.0

*Second-intermediate and definitive host columns describe the following: the general taxonomic group associated with hosts; the total number of species identified as documented hosts; the number of documented host species present in the introduced region; and the percentage of host species present in the introduced range relative to total number of documented hosts. See Table S3 for detailed information on host species and citations. Four rare trematode species (*Cercaria littorinae saxatilis* I, II, IV and VI; see Table 2) that infect *L. saxatilis* in the native but not in the introduced range are not included in the table because there is no known information concerning their life cycles beyond the first-intermediate snail stage.

†May use a bird as its definitive host, but information is incomplete.

‡Uses its snail host as both a first- and second-intermediate host.

(individually and pooled) in all three west coast subregions compared with native north and source subregions, where prevalence was often very high (Fig. S1; see Table S2 for *P* values). The other two trematodes (*Austrobilharzia variglandis* and *Himasthla quissetensis*) use birds as definitive hosts, and these species did not show any reductions (individually or pooled) in prevalence in introduced subregions versus native subregions. The three *L. saxatilis* trematodes (*Maritrema arenaria*, *Microphallus similis* and the pygmaeus microphallid) all use birds as definitive hosts and, when pooled, showed significant reductions in prevalence in SFB compared with the source subregion for *M. arenaria* and *M. similis*, and compared with the north for the pygmaeus microphallid (see Fig. S1).

Trematode infection cycles and hosts

Database and literature searches to determine the presence of hosts for *I. obsoleta* and *L. saxatilis* trematodes in west coast bays (Table 3, details are given in Table S3) indicate that four of five introduced trematodes in *I. obsoleta* have at least one documented second-intermediate or definitive host species available on the west coast. Moreover, the species exhibiting the highest prevalence of infection in SFB, *Himasthla quissetensis* (Table 2), has a full complement of documented hosts available. Of the four *I. obsoleta* trematodes that have not invaded SFB, none had a full complement of hosts (Tables 3 & S3a). For *L. saxatilis*, all three trematode species observed in SFB had at least one second-intermediate and definitive host species present. However, this was also true for all of *L. saxatilis*' absent trematode species for which entire life cycles are known (Tables 3 & S3b).

DISCUSSION

Significantly decreased infection prevalence and species richness of trematode parasites in SFB indicate that both snail hosts have escaped several parasites common in native populations. This is apparent when comparing the entire native region with SFB, or when focusing on the more relevant source subregion compared with SFB. The only non-significant comparison between the source subregion and SFB occurred for pooled prevalence in *I. obsoleta* – and this is likely due to *I. obsoleta*'s greater time since introduction and propagule pressure. Rarefaction analyses indicate that our results are unlikely to have been affected by sampling artefacts. However, the extreme rarity of *L. saxatilis* infection in SFB populations (only seven infected of 1893 individuals) made it difficult to pinpoint the underlying species richness of trematodes in SFB. Even so, predicted richness in *L. saxatilis* SFB was significantly lower than in the native region, and the magnitude of this reduction was more pronounced for *L. saxatilis* than for *I. obsoleta*. Similarly, *L. saxatilis* has a much higher parasite escape index (approximately twice that of *I. obsoleta*) and a larger reduction in trematode prevalence. These findings indicate that introduced *L. saxatilis* is experiencing a greater degree of parasite escape compared with *I. obsoleta*. There are a

number of non-mutually exclusive explanations for why this has occurred.

Time since introduction

Ilyanassa obsoleta was introduced to SFB nearly a century earlier than *L. saxatilis*, an important difference given that time since introduction/colonization is a strong positive predictor of parasite richness in aquatic systems (e.g. Guégan & Kennedy, 1993; Torchin & Lafferty, 2009). *Ilyanassa obsoleta* trematodes have therefore had nearly 100 more years for transport and establishment in the introduced region than trematodes of *L. saxatilis*. Notably, the five species we found infecting introduced *I. obsoleta* is the same number as found by Grodhaus & Keh (1958), suggesting that trematode species richness has possibly been stable for more than 50 years (a more specific comparison of species between the two studies is limited by the fact that only one species, *Austrobilharzia variglandis*, was identified in the older study). In contrast, given the more recent introduction of *L. saxatilis* and the rarity of trematode infections observed in introduced populations (< 0.5% throughout the bay), it is unlikely that trematode richness has stabilized for *L. saxatilis*, especially given its open introduction vector.

Propagule pressure

Propagule pressure is a key determinant underlying successful establishment of non-native species, and is a measure integrating both the number of individuals released in an introduction event and the frequency of introduction events (Lockwood *et al.*, 2005). Propagule pressure is also influenced by the abundance of species in source populations and characteristics of the invasion vector related to entrainment and transfer of propagules to non-native populations (Kolar & Lodge, 2001; Miller *et al.*, 2007). Of the two snail hosts, *I. obsoleta* exhibits consistently higher pooled species prevalence in populations throughout the native region. In source populations, *I. obsoleta*'s prevalence of infection was more than three times greater than *L. saxatilis*' prevalence (25% compared with 8%; Table S1a). Thus, based on prevalence alone, *I. obsoleta* trematodes would generally have a much greater likelihood of transport to the west coast than trematodes of *L. saxatilis*. In addition, similar to other host–parasite systems, the prevalence of individual trematode species in source regions helps explain which trematodes were introduced to SFB (Torchin *et al.*, 2003). Specifically, introduced trematode species were generally those associated with the highest infection prevalences in native, and especially source, populations.

Characteristics associated with a specific transfer mechanism (the vector of introduction) will also affect the likelihood that a parasite is successfully transported to a novel region with its host (Miller & Ruiz, 2009). In particular, the number of host individuals transported, frequency of transport events, and transport conditions are important characteristics that affect entrainment, transfer, and ultimately introduction success.

Ilyanassa obsoleta was introduced to the west coast as a hitchhiking species with commercial shipments of the eastern oyster (*Crassostrea virginica*) in attempts to establish a west coast fishery (Carlton, 1992). This introduction vector would have provided strong entrainment and transfer of *I. obsoleta* trematodes, for a number of reasons. First, shipments of oysters from the east to west coast occurred on a massive scale that was sustained over many years, resulting in billions of oysters being transported (Miller, 2000). SFB, in particular, was the main receiving area for transcontinental shipments of oysters during the industry's peak (Carlton, 1979), probably contributing to the significantly greater trematode diversity in SFB compared with northern west coast bays (WB and BB). Second, because the main harvesting method for oyster extraction, dredging, was very unselective (Ingersoll, 1881; Carlton, 1992), it would have resulted in the capture of numerous *I. obsoleta* across a full spectrum of sizes, including older/larger snails, which are the most likely portion of the host population to be infected (Curtis & Hurd, 1983; Curtis, 1997). Third, commercial oysters were packaged for transcontinental shipping in a manner that ensured their survival, and this would have benefited the survival of hitchhiking organisms, including snails and associated parasites (Carlton, 1979). Commercial shipments of the eastern oyster largely ceased by the early 1900s, effectively closing the introduction vector for *I. obsoleta*; still it remains possible that additional trematode propagules could be introduced through other hosts moving into the system with alternative introduction vectors.

Littorina saxatilis was introduced to SFB via the live baitworm and seafood trade, through its relationship with algae used as packing materials (Carlton & Cohen, 1998). Similar to oysters, transfer conditions linked to this introduction vector should promote the survival of associated *L. saxatilis* hosts and parasites, because live baitworms and seafood are packaged in a manner ensuring their health during transport. However, the magnitude of transport for baitworms and live seafood is far less than for commercial oysters, given the sustained attempts at introducing oysters from 1869 to the 1920s. Furthermore, snails associated with algal packing materials are typically few in number and small in size (A.W.M. and G.M.R., pers. obs.), reducing the likelihood of parasite introduction. A final difference is that *L. saxatilis*' introduction vector remains open. Thus continued opportunities for transfer of trematode propagules remain in operation and could result in an expansion of *L. saxatilis* trematode fauna in SFB.

Host availability

For successful establishment and spread, invasive species must be able to survive and reproduce in novel regions (Miller & Ruiz, 2009). For obligate, multi-host parasites like trematodes, this depends on the presence and abundance of suitable hosts. Trematodes are highly specific to snail hosts (typically infecting only one or few species), but infection of second-intermediate and definitive hosts is often more general (Graczyk, 1997);

even so, specific groups of species are typically targeted. For example, a trematode species infecting 'crustaceans' may not infect all available crustaceans in habitats where the trematode exists (see Stunkard, 1983; Curtis, 2002, and references therein; also see Table S3). Therefore, the availability of suitable hosts could help explain the presence or absence of specific parasite species in SFB for both snail–host systems. Although we were unable to obtain consistent information on host abundance in introduced areas, and therefore can draw no conclusions based on this important determinant of trematode prevalence (Smith, 2001; Huspeni & Lafferty, 2004; Hechinger & Lafferty, 2005; Byers *et al.*, 2011), our presence–absence data for known hosts do provide some clues to understanding the presence of trematodes in SFB.

For *I. obsoleta*, we found that having at least one documented second-intermediate or definitive host in SFB was generally consistent with a trematode's successful introduction there (e.g. 80% of *I. obsoleta*'s introduced trematodes had more than one documented host species in SFB). These documented second-intermediate and definitive hosts include both species native to the west coast and those that have been introduced there [see Table S3a for host species lists and status as native, introduced or cryptogenic (= origin uncertain)]. Furthermore, the two trematodes (*A. variglandis* and *H. quissetensis*) that possessed a full complement of hosts in the introduced region were also the trematodes found in all three west coast bays. This suggests that both establishment and spread are enhanced by having a familiar group of host species in introduced regions. Prevalence of *H. quissetensis* in SFB was also the highest observed of any introduced *I. obsoleta* trematode, and *H. quissetensis*' prevalence in SFB was markedly higher than in its native regions, suggesting that second-intermediate and definitive hosts are not only present on the west coast, but occur in sufficient numbers for successful life-cycle completion. While this high prevalence could also suggest a release from interspecific competition of native trematodes, this seems unlikely because redial species such as *H. quissetensis* tend to dominate in trematode competitive hierarchies (e.g. Kuris, 1990; Lafferty, 1993; Sousa, 1993); in addition, Curtis & Hubbard (1993) found no evidence for competitive hierarchies in native populations of *I. obsoleta* trematodes. Interestingly, *H. quissetensis*' lack of a prevalence reduction in SFB was also observed in another species introduced to the west coast, *A. variglandis*, which, like *H. quissetensis*, uses birds as definitive hosts. This is in stark contrast to prevalences in *I. obsoleta*'s three introduced fish-using trematodes (*L. setiferoides*, *S. tenue* and *Z. rubellus*), which were significantly reduced (individually and pooled) in SFB versus native subregions (Fig. S1). This could point to a greater number and/or abundance of suitable bird definitive hosts in west coast bays compared with fish definitive hosts (as also suggested by our species lists in Table S3).

Finally, for *L. saxatilis*, our literature/database search revealed the presence of many suitable hosts in SFB for its native east coast trematodes; yet only three have been introduced there, suggesting that factors other than host

availability (such as propagule pressure and time since introduction) are more strongly limiting these trematodes from establishing in SFB.

Temporal sampling

Our samples were collected over several years in the native and introduced regions (Table S1b). Both trematode species richness and prevalence within populations have been shown to be affected by temporal sampling due to a number of biological and physical factors (changing abundance of host populations, temperature and salinity, among others; Kube *et al.*, 2002; Huspeni & Lafferty, 2004; Gerard *et al.*, 2008). However, for both snail–parasite systems, we believe that gross-level comparisons among subregions should not be overly biased by temporal differences in sampling because we sampled over approximately the same range of years in native and introduced populations; we focused our sampling in summer months; and we resampled many of the same populations. Furthermore, the full time-scale over which we sampled did not exceed the maximum life span of either species of snail host, thus the observed patterns still reflect distribution of parasites associated with a single host generation, especially given the long-term nature of trematode infections in gastropod hosts (e.g. Curtis, 2002, 2003). In addition, some studies (e.g. Kube *et al.*, 2002; Blakeslee & Byers, 2008) have shown trematode richness to be fairly robust to temporal sampling, and anecdotal evidence from our study suggests the same. For example, when we compared our 2009–10 *I. obsoleta* data from the same Cape Henlopen, Delaware site sampled by Curtis & Hurd (1983) nearly 30 years earlier, we found species richness and composition of trematodes were identical, and total prevalence differed by only 13% [the absolute prevalence in Curtis & Hurd (1983) was 62% compared with our absolute prevalence of 49%]. We believe these factors in combination limit the effect of temporal variability on the patterns in our two snail–parasite systems.

Invasion implications and conclusions

Consistent with other studies of introduced versus native populations, we show that *I. obsoleta* and *L. saxatilis* have escaped parasites in SFB. Parasite escape is important because the loss of natural enemies is one mechanism by which introduced hosts are thought to become highly successful (Keane & Crawley, 2002; Torchin & Mitchell, 2004; Liu & Stiling, 2006). In snails, trematode infection results in castration and can confer physiological costs. Thus introduced species and populations with lowered infection rates are bestowed a direct fitness advantage compared with more highly infected natives (Byers & Goldwasser, 2001; Torchin *et al.*, 2005; Blakeslee *et al.*, 2009). *Littorina saxatilis* has very quickly (within 20 years) established itself in high abundance across SFB (I.A., A.M.H.B., A.W.M. and G.R., unpublished data), and the fact that it is nearly parasite-free may be contributing to its rapid invasion.

Introduced parasites can be highly influential in marine communities, altering community structure (Wood *et al.*, 2007), affecting host health (Lauckner, 1980; Torchin *et al.*, 2001, 2005; Thieltges, 2006), influencing host behaviour (Poulin, 1995; Lafferty & Morris, 1996; Thomas *et al.*, 1998; Curtis, 2007), and having an adverse impact on host reproductive fitness (Lauckner, 1984; Torchin *et al.*, 2001; Mouritsen & Poulin, 2002). It is not yet known which (if any) of these influences are affecting the SFB communities we investigated here.

Documenting the biogeographic tracks of parasites and pathogens is also relevant to understanding disease ecology, because the global movement of humans and associated organisms can result in novel host and parasite/pathogen establishments that could be highly detrimental to human health and agriculture (Slingenberg *et al.*, 2010). In fact, one of *I. obsoleta*'s trematodes (*A. variglandis*) has human health effects in its own right by causing cercarial dermatitis ('swimmer's itch'). This trematode was first documented in SFB by Grodhaus & Keh (1958) in response to outbreaks of cercarial dermatitis in the Alameda area, where they found moderate levels of infection by *A. variglandis*. We also observed *A. variglandis* to be moderately prevalent in several populations throughout SFB as well as in the two northern west coast bays. Continued monitoring of this trematode is important considering its human health effects.

Due to their less visible nature, introduced parasites may go unrecorded for years (especially those with no direct human health connection). Our study documents seven new trematode species in SFB from both snail–parasite systems, and these new records add to a growing list of introduced species in the Bay, consistent with other studies demonstrating this estuary to be one of the most invaded in the world (Cohen & Carlton, 1998). The relatively high diversity of established trematodes in SFB emphasizes that, given appropriate environmental conditions and host communities, parasites can flourish in introduced communities. Our work also evokes concerns for the still active live seafood/bait introduction vector responsible for transporting *L. saxatilis* to SFB, which could introduce new host species (e.g. amphipods, worms, bivalves) and/or novel parasites of already established host species (e.g. *L. saxatilis*, *Carcinus maenas*) to the region. Continued monitoring and in-depth studies such as this one are needed to resolve the many questions that remain regarding introduction vectors and their influence on parasite biogeographies worldwide.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Snail historical ecology and invasion histories.

Appendix S2 Additional results from statistical analyses and literature surveys (including summary statistics, sampling information, species-specific prevalence, *post-hoc* tests and trematode host surveys) (Tables S1–S3 & Fig. S1).

Appendix S3 Taxonomic assessment of west coast trematodes.

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