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An introduced Asian parasite threatens northeastern Pacific estuarine ecosystems

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Abstract The introduced Asian parasitic bopyrid isopod, *Orthione griffenis*, was first discovered on the Pacific coast of North America in Washington in 1988 and next in California in 1992. The range of *Orthione* presently extends from British Columbia to Baja California, where it infests at least two species of the native estuary mud shrimp, *Upogebia*. Intense *Orthione* infestations are associated with the apparent demise of many local populations of *Upogebia pugettensis* yet nonindigenous origins of *Orthione* in North America and thus the ecological significance of its impacts have remained in doubt. Six criteria reveal that *Orthione* is introduced to North America: its conspecificity with disjunct Asian populations, its earliest (1950s) collections in Asia, its late discovery among symbiotic species associated with *Upogebia*, its historical absence, and its appearance in North America coincident with extensive new ballast water traffic from Asia. *Orthione* is the first recognized bopyrid isopod invasion globally. Coexistence of *U. pugettensis*, which are ecosystem engineers, with its newly acquired parasite cannot be assumed. *Orthione* threatens eastern Pacific estuary ecosystems where *Upogebia* were previously abundant.

Keywords Isopod · Parasite · Estuary · Extinction · Invasion · *Orthione griffenis* · *Upogebia pugettensis*

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Introduction

A persistent assumption is that species are native where they are first recognized, despite extensive evidence to the contrary (Carlton 2009). This perception can lead to the underestimation of the scale of invasions by non-native species. We analyze a dramatic example of this assumption herein.

Markham (2004) described a new species of branchial parasitic bopyrid isopod (*Orthione griffenis*; hereafter *Orthione*) that was collected from the intertidal estuarine mud shrimp (*Upogebia pugettensis*;

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hereafter *Upogebia*) in Yaquina Bay, Oregon in 1999. No isopod parasite had previously been known from the gills of *Upogebia* in western North America. Markham (2004) did not discuss whether *O. griffenis* was introduced or native. Brusca et al. (2007) included *Orthione* in their checklist (but not key) of Northeastern Pacific isopods without comment on its possible origins. Smith et al. (2008) reported *Orthione*'s likely dramatic effects on *Upogebia* reproduction without reference to its possible origins. Dumbauld and Chapman (2008), in a meeting abstract of the same year, however, proposed that *Orthione* was likely introduced. Griffen (2009), for whom the species is named, followed our proposal that *Orthione* is introduced.

Williams and An (2009) next noted the occurrence of *Orthione* in both the eastern and western North Pacific Ocean, and while finding the populations morphologically identical, argued that "until molecular or reproductive cross studies are completed. *O. griffenis* should be labeled as cryptogenic" (Carlton 1996) because "the species may be composed of a complex of morphologically indistinguishable but reproductively isolated species." Williams and An (2009) further noted, however, that *O. griffenis* was unlikely to be native to the eastern Pacific, given that it was absent from historical studies of mud shrimp parasites on the North American Pacific coast, that it was known from Asia long before it was found in America, that it appeared to have undergone a "rapid spread" along the Pacific coast (similar to other introduced species), and that there was a clear mechanism of human-mediated dispersal (ballast water) for this species from Asia to America. They concluded that it is "most parsimonious to conclude that the species had an origin in Asia." Finally, Dumbauld et al. (2011), p. 337 referred to *Orthione* only as "likely introduced" to North America, demurring to two coauthors who maintained "insufficient evidence" of its nonindigenous North American origin pending genetic analysis to confirm the source region.

Retrospective analyses of archived mud shrimp specimens revealed that the first specimens in hand were collected in 1988 in Willapa Bay, Washington (Dumbauld et al. 2011; based upon two specimens [Supplementary Material-Appendix A, and herein]). The next record of *Orthione* is from 1992, in Morro Bay, California (as "California" in Williams and An 2009, p. 121; location from A. Kuris, personal communication). The only other records that we have found prior to the Yaquina Bay 1999 records are for southern Puget Sound in 1995 and Coos Bay, Oregon in 1997, as noted below. In all of these cases the isopods were either not immediately noticed or were initially identified as other species.

Upogebia is a critical ecosystem engineer due to its abundance and extensive suspension feeding and burrowing activities which influence nutrient flux, benthic community structure and functioning of estuaries (Posey et al. 1991; D'Andrea and DeWitt 2009). Effective castration and reproductive losses due to intense *Orthione* infestations since the 1990s appear to drive local *Upogebia* populations to collapse and extinction (Dumbauld and Chapman 2008; Dumbauld et al. 2011). A definitive resolution of whether this recently discovered parasite is introduced or native is critical because of the ecological importance of *Upogebia* and the apparent demise of many of its populations.

Methods

We test a null hypothesis that *Orthione* is a native North American species with six criteria based on taxonomy, field surveys, museum collections, personal interviews and correspondence, analyses of possible vectors and pathways for introduction and 150 years of North Pacific bopyrid taxonomy and natural history literature.

Criterion 1—Distinction of geographically isolated populations

Specific differences between eastern and western Pacific populations are the null hypothesis of criterion 1. We tested for morphological conspecificity of Asian and North American populations identified as *Orthione* by reciprocal examinations of specimens from both regions.

Criterion 2—Geographical precedence

The null hypothesis for criterion 2 predicts an earliest discovery in North America. Precedence of occurrence does not reveal where species evolved since introduced species populations are commonly

discovered before their native populations are known (Carlton 2009). However, precedence can reveal which regions are the latest recipients of expanding invasions. An earliest Asian collection date, in the case of North American *Orthione*, is counter to criterion 2 predictions.

Criterion 3—Precedence among symbionts

The more conspicuous native symbiotic species are expected to be discovered before inconspicuous symbionts regardless of their relative abundances. Criterion 3 thus predicts an early discovery of *Orthione* relative to all other northeast Pacific *Upogebia* symbionts if it is a native species. We used the order in which symbionts were discovered in eastern Pacific *Upogebia* relative to the intensity of research on *Upogebia* symbionts to test criterion 3.

Criterion 4—Taxonomic oversight

Overlooking introductions is more likely when the development and progress of taxonomy is locally or globally incomplete. Criterion 4 predicts that *Orthione* was overlooked by taxonomists prior to 1988 in North America. We partially tested whether *Orthione* was present in North America before 1988 based upon its potential to be misidentified or overlooked, and by comparing the intensity and quality of Asian and North American bopyrid taxonomy. Larger species are expected to be found before smaller species where taxonomic exploration has been continuous and is approaching completion. In contrast, poor correlations of bopyrid lengths with time of discovery or description are expected where taxonomic exploration is incomplete and backlogs of unpublished discoveries are less dependent on additional search efforts. We compared the body lengths of new bopyrid species recognized in Asia and North America since the 1850s for this test. The lack of information available from most of Asia limited our comparison to western North America and Japan and thus, this is a conservative test of criterion 4.

Criterion 5—Detection confidence relative to sampling efforts

Criterion 4, tests whether *Orthione* might have been collected but misidentified. In contrast, criterion 5 tests whether sampling activities previous to 1988

were sufficient to detect its presence in North America if it was there. Species are most readily discovered during their periods of high abundances (resurgences) or when sampling efforts are sufficiently great to detect them even at their lowest abundances and distributions. Rare species are seldom detected within their habitats in any given sample or time period but the probability that these rare species "are not there" increases exponentially with the numbers and sizes of samples, and sites sampled without success (McArdle 1990). *Orthione* could have been missed previously due to insufficient cumulative research activities and consequent sampling to detect it. We tested criterion 5 three ways: first, by whether *Orthione* populations at present densities could have occurred in the past without detection, second, by the probability of missing *Orthione* relative to the rare eastern Pacific estuarine bopyrid *Ione cornuta* Bate, 1864 (which occurs in the native thalassinid shrimp *Neotrypaea* spp.) and third, by whether *Orthione* could have been missed at its minimum possible prevalence over its present range due to under sampling. A high probability of encountering *Orthione*, even at its minimum prevalence, without finding it in samples prior to 1988, is counter to criterion 5.

Detection confidence

If the frequency of a parasite among hosts is ρ, and the probability of the parasite not occurring in a host is $1-\rho$, then the probability of a parasite not occurring in a sample of N hosts is $(1-\rho)^N$. If all *Upogebia* are equal, the probability of detecting *Orthione*, α, among N *Upogebia* with an infestation frequency, ρ, is:

$$\alpha = 1 - (1 - \rho)^N, \tag{1}$$

the frequency of *Orthione* among *Upogebia*, ρ, detected with a given confidence level, α, among a sample of N *Upogebia* is:

$$\rho = 1 - (1 - \alpha)^{1/N}, \tag{2}$$

and the number of *Upogebia*, N, needed to detect *Orthione* with a given level of confidence for a given frequency of *Orthione* among *Upogebia*, ρ, is:

$$N = \ln(1 - \alpha)/\ln(1 - \rho). \tag{3}$$

However, *Orthione* only infest *Upogebia* of carapace lengths (CL) greater than 12 mm and the

frequency of infestations increases with length (Smith et al. 2008, Dumbauld et al. 2011). The effective *Upogebia* sample size for *Orthione*, *N*, is therefore a function of length-class susceptibility to *Orthione* infestations above 12 mm CL times the numbers of shrimp per length class. The largest *Upogebia* we observed was 38 mm CL. We therefore estimated effective host population sample size, *N*, as the sum of *Upogebia* length frequencies, n_i, times their length dependent vulnerabilities, c_i (Supplementary Material-Appendix A) as:

$$N = \sum_{i=12}^{38} c_i n_i. \tag{4}$$

The effective host population sample size, *N*, is thus also a maximum expected prevalence when *Orthione* are at maximum frequency among all host size classes. Comparisons among populations require *Orthione* prevalence, ρ, normalized by the expected number of infested shrimp, *I*, to the effective vulnerable population, *N*, where:

$$\rho = I/N. \tag{5}$$

We assumed the minimum effective *Orthione* prevalence, ρ_{min}, is the lowest prevalence that it can occur at without extinction.

The power of archival (museum) specimens for detecting *Orthione* depends on their effective host number, *N*, and a minimum expected *Orthione* prevalence, ρ_{min}. We assumed an effective sample size from the vulnerable *U. pugettensis* size ranges collected before 1988, and a minimum likely prevalence, ρ_{min}.

Criterion 6—Trans-pacific dispersal vectors and mechanisms

Introduced species are distinguished, in part, by their associations with human mechanisms of dispersal (Ruiz and Carlton 2003). Criterion 6 predicts that isolated eastern and western Pacific *Orthione* populations are maintained by natural dispersal rather than human-mediated transport vectors and that bopyrid larvae and suitable intermediate hosts do not occur where they can be entrained in or are coincident with trans-oceanic dispersal mechanisms.

We assessed the likelihood of natural ocean current dispersal relative to the potential for trans-oceanic survival in ballast water tanks across the North Pacific and also relative to the supply of *Orthione* pelagic larval stages in a ballast water port. Trans-oceanic ballast water transport potential was assessed from frequency of pelagic bopyrid larvae collected from 159 ships entering Coos Bay, Oregon from Japanese ports between 1986 and 1991 (Carlton, unpublished data). These larvae were sorted from zooplankton samples collected in 80 micron mesh, 0.5-m diameter nets towed vertically from the bottom to the surface of the ballast cargo tanks (Carlton and Geller 1993). We assessed availability of *Orthione* larvae and intermediate hosts for entrainment across the North Pacific in ballast water traffic from the survival and availability of pelagic *Orthione* life stages in the harbor area of Yaquina Bay from 65 zooplankton samples (Supplementary Material-Appendix B) collected between October 2005 and fall of 2006 at high flood, low ebb and mid tide phases. Each of these zooplankton samples consisted of 3–5 m triplicate vertical tows of a 0.2-m diameter, 150 micron mesh net. Each sample was refrigerated until it could be sorted for pelagic *Orthione* larvae within 48 h of collection.

Geographical survey

We estimated the prevalence of *Orthione* over its North American range by sampling *Upogebia* populations between Mexico and Canada in June and July 2008 and in January through March 2009 (Fig. 1). *U. pugettensis* occurs only north of Pt. Conception, California, while *Upogebia macginitieorum, U. lepta* and *U. onychion* occur only south of Pt. Conception (Fig. 1). Our study focused on *U. pugettensis* and did not include *Upogebia lepta* and *U. onychion* of the Channel Islands, California, but did include three *U. macginitieorum* populations in southern California that we sampled (Fig. 1). We supplemented our survey data by correspondence and by interviews with other researchers (Supplementary Material-Appendix A) and from reviews of ecological and taxonomic reports on North Pacific bopyroideans.

Upogebia populations were initially identified and visually assessed in the field. *Upogebia* are solitary and make Y shaped burrows that have two conspicuous openings to the mudflat surface and have intensely smoothed linings (Thompson 1972). *Upogebia* tubes are thus readily distinguished from other similar sized northeast Pacific invertebrate burrows
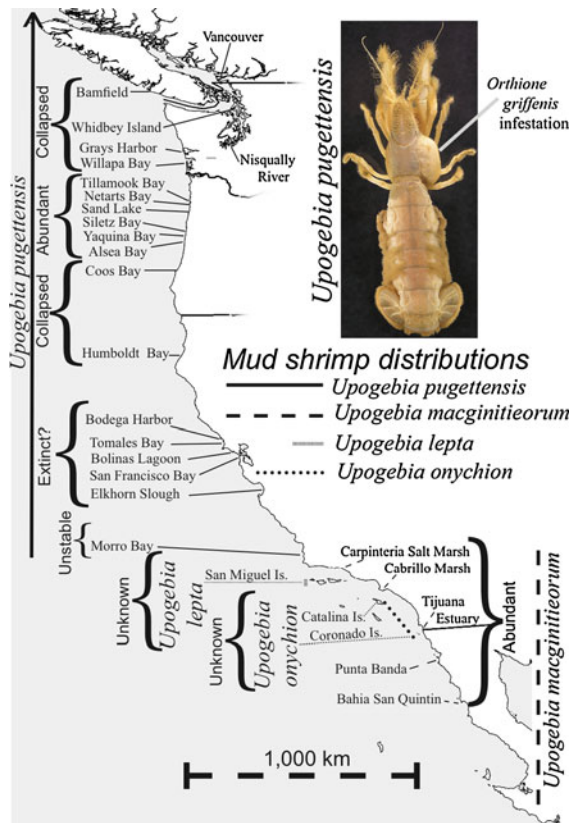
Fig. 1 *Orthione griffenis* survey localities between Vancouver, British Columbia (49° 01′ 35.72″ N, 123° 06′ 10.14″ W) and Bahia San Quintin, Baja California (30° 24′ 54″ N; 115° 57′ 51″ W), status of observed northeast Pacific host populations of *Upogebia pugettensis, U. macginitieorum*, in addition to possible *Orthione* hosts, *U. lepta* and *U. onychion* and photo of *U. pugettensis* infested by *Orthione* (*right side*). (See Supplementary Material-Appendix A notes. Photo credit: Brian Bingham.)

such as the co-occurring intertidal thalassinideans *Neotrypaea gigas* and *N. californiensis*. Juvenile aggregation with adults (Dumbauld et al. 2011) and the adult's inability to construct new burrows (Chapman et al. unpublished observations) results in dense, nearly permanent *Upogebia* beds in estuary mudflats above +0.6 m. Sediment alterations where *Upogebia* burrows exceed 50/m² are easily distinguished from distances greater than 100 m and permit efficient searches of low tide areas covering many ha/hr. *Upogebia* burrow densities as low as 0.05/m² are efficiently surveyed on foot at approximately 10 m²/s.

High density *Upogebia* populations, visually assessed to exceed 8 shrimp burrows m⁻², were sampled quantitatively using a 40 cm inner diameter

(ID) by 60 cm deep "mega core" or by 12.5 cm ID by 70 cm deep "small cores". The lowest density populations were sampled qualitatively, using "yabby guns" (Hailstone and Stephenson 1961) to corroborate whether burrow openings at any density were those of *Upogebia* (Supplementary Material-Appendix A). Surveys of extreme low density *Upogebia* areas were extended over many hundreds of m² to confirm the absence of populations exceeding 0.01/m². Precise locations of all survey sites (Fig. 1) were noted (Supplementary Material-Appendix A).

We classified *Upogebia* populations that occurred at densities greater than 10 m⁻² as "abundant", less dense populations, as "collapsed", populations that fluctuated between merely present and less than 10 m² over time as "unstable", and populations that were apparently extinct as "extinct?" (Fig. 1) when we failed to find any specimens in repeated searches where abundant populations were previously known to occur.

We examined both branchial chambers of each *Upogebia* collected for *Orthione* directly or under 6× magnification. All but newly settled *Orthione* were directly apparent through the transparent *Upogebia* carapace or from the obvious bulges in the host's carapace created by mature *Orthione* (Fig. 1).

Results

All previously known abundant *Upogebia* populations were either absent or at greatly reduced abundances in all California, Oregon and Washington estuaries examined (Fig. 1; Supplementary Material-Appendix A). *Orthione* were present in all examined *U. pugettensis* or *U. macginitieorum* populations between Vancouver, Canada and Bahia de San Quintin, Baja California, Mexico (Fig 1; Supplementary Material-Appendix A) and thus, appear to cover the ranges of both of these eastern Pacific hosts and to be associated with every declining population.

Criterion 1—Conspecific geographically isolated populations

A careful search of the Eheme University museum bopyrid isopod collections (Itani 2004) resulted in the discovery of *Orthione* on the Japanese mudshrimps *Upogebia issaeffi* and *Austinogebia narutensis*. These

isopods had been previously identified only to sub-family "*Pseudioninae* sp. 1" (in part; Itani 2004). Our comparisons of Japanese and North American specimens confirmed their conspecific status, as also reported by Williams and An (2009). The prediction of criterion 1 null hypothesis is thus rejected.

Criterion 2—Geographical precedence

Orthione were collected from northern Chinese estuaries in the 1950s (Williams and An 2009), three decades prior to the earliest North American records. The criterion 2 null hypothesis is thus rejected.

Criterion 3—Precedence among symbionts

Orthione (Fig. 1 photograph) is among the largest, most conspicuous and accessible of northeast Pacific *Upogebia* parasitic or nonparasitic symbionts and thus unlikely to be discovered last if it was always present. The second largest native eastern Pacific bopyrid, *Phyllodurus abdominalis* Stimpson 1857 (Fig. 2a, second open triangle from left) was the second of 17 native eastern Pacific bopyrid species discovered, and the second of 18 eastern Pacific *Upogebia* symbiotic species discovered (Supplementary Material-Appendix C).

New eastern Pacific *Upogebia* symbionts were reported every 7.8 years between 1837 and 1949. A 22 year gap occurred between the report of the kamptozoan *Barentsia discreta* associated with *Upogebia* in southern California (MacGinitie and MacGinitie 1949) and the discovery of the phoronid *Phoronis pallida* associated with *Upogebia* in central California (Thompson 1971, Figure 1 of Supplementary Material-Appendix C). The first report of *Barentsia discreta* was from the South Atlantic Ocean and the earliest report of *P. pallida* was from Europe. The later reports of these species from California may not be of the same species. Neither species is an obligate symbiont or is solely associated with *U. pugettensis*. However, both of these symbionts are cryptic and not easily seen (in contrast to *Orthione*). *Phoronis*, for example, occurs primarily in the deepest sections of *Upogebia* burrows (Thompson 1972; Zimmer 2007).

The two eastern Pacific bopyrid isopod parasites, *Aporobopyrus bourdonis* Markham 2008 and *Discomorphus magnifoliatus* Markham 2008, both reported since the discovery of *O. griffenis*, are based upon
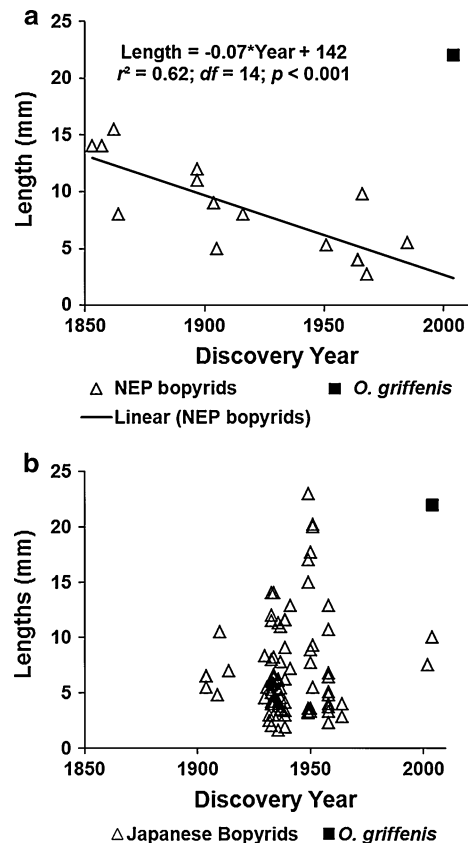

Fig. 2 a Body lengths of northeast Pacific [NEP] and **b** Japanese bopyrid species by their dates of publication or earliest collection date (*triangles*) and *O. griffenis* (*solid square*) with predicted NEP lengths by year [excluding *O. griffenis*] (*line*) (Data in appendices C and D-Supplementary Material)

specimens collected in 1951 and 1964, respectively (Supplementary Material-Appendix C) and thus before the earliest eastern Pacific record of *O. griffenis*. The last northeastern Pacific *Upogebia* parasite discovered before *O. griffenis* was the semi-tropical bopyrid parasite *Progebiophilus bruscei* Salazar-Vallejo and Leija-Tristán in 1989. This latter species is smaller than *Orthione* and is from the less explored Mexican coast (first collected in 1986; Supplementary Material-Appendix C). *P. bruscei* is known only from *Upogebia dawsoni* and *U. macginitieorum* which occur south of *U. pugettensis* and do not overlap its range. The 1988 North American discovery of *O. griffenis* thus followed discoveries of all other North or Central American *Upogebia* parasites by two years (Supplementary Material-Appendix C). *Orthione* was also collected 17 years after the last *U. pugettensis* or *U. macginitieorum* parasite or

symbiont was recognized (Supplementary Material-Appendix C).

Contrary to criterion 3 predictions, *Orthione* does not have precedence among parasites and symbionts. If it were always present in the region, *Orthione* would have been difficult to miss over the last 150 years and among tens to hundreds of thousands of detailed observations required to discover the 34 less obvious decapod parasites and *Upogebia* spp. symbionts that are also present.

Criterion 4—Taxonomic oversight

Excluding *Orthione*, the largest northeast Pacific coastal bopyrids (Supplementary Material-Appendix D) were recognized first (Fig. 2a, triangles, and Supplementary Material-Appendix D). *Orthione* (Fig. 2a, solid square) is an extreme outlier for its length relative to its late discovery in the overall North American trend (*t test*: $t = -8.4$, $p < 0.00004$, df = 13). In contrast, and consistent with the different histories of North American and Asian taxonomy, the largest Japanese bopyrids (Supplementary Material-Appendix D) were not recognized first. Instead, discoveries of large Japanese bopyrid species have continued over time (Fig. 2b).

Previous to 1895, reports of new eastern and western North Pacific bopyrids were from North American and European generalist taxonomists who were more likely to recognize larger bopyrid parasites incidentally with their primary research on large decapods. The majority of Japanese bopyrids were recognized since the 1900s by proficient 20th century specialists (Saito et al. 2000). The Japanese taxonomists began their explorations of the Japanese bopyrids with immediate access to broad diversities of decapod hosts and thus a wider size range of bopyrids available to describe than taxonomists examining eastern Pacific bopyrids since the 1850s (Fig. 2b). Oversight of *Orthione* in North America until 1988 is thus inconsistent with the sizes and diversities of bopyrid species present or likely to be recognized by Asian and North American taxonomists over time.

Markham (1992, 2001) noted lower bopyrid species numbers and lower bopyrid species diversity per decapod host species in the eastern Pacific relative to other regions by the early 1990s. In contrast, Shiino's prolific descriptions of new Japanese bopyrid species resulted in a particularly rapid accumulation of species

between 1933 and 1974 (Fig. 3). Saito et al. (2000) include 5 "preliminary" (probably undescribed) species in their list of Japanese Bopyridae (Supplementary Material-Appendix D). An et al.'s (2009) discovery of 4 new bopyrid species among 8 new records of bopyrids in Chinese mud shrimp further indicates that Japan is a conservative subsample of Asian bopyrid diversity. Nevertheless, 13 western North American taxonomists recognized and reported only 0.098 new bopyrid species per year in 22 publications since 1850 (Markham 1992, 2001, 2008) while 14 resident Japanese or visiting taxonomists discovered 1.02 new Japanese bopyrid per year in 37 publications since 1895 (Fig. 3). The similar numbers of taxonomists are likely to have contributed to similar research efforts. The rate of new bopyrid species recognized per decade in Japan was therefore ten times greater than in all of western North America over the same period (Fig. 3) (1.02/0.098 = 10). The diversity of remaining undescribed bopyrid species is therefore also likely to be at least 10 times greater in Asia alone than in North America.

Asia is also the most common source of marine species that are introduced to western North America (Cohen and Carlton 1995, Chapman 2000; Ruiz et al. 2000). Thus, ignoring other geographical sources for introductions, and given that one new introduced species arrives in the eastern Pacific (based only on San Francisco Bay) every 14 weeks (Cohen and
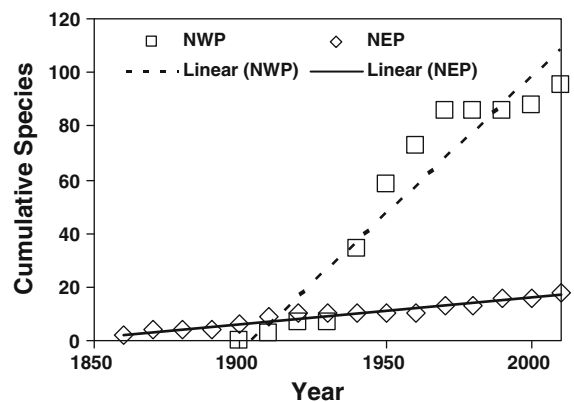

Fig. 3 Cumulative numbers of new bopyrid species per decade from the northeast Pacific [NEP] (Panama to the Bering Sea, diamonds) and Japan, (squares) since 1855 with linear models of Japanese species after 1885 ([Post 1885 NWP] = 1.02*year—1950, df = 10, $r^2 = 0.91$; $p < 0.001$) and northeast Pacific species, 1855–2008 ([NEP] = 0.098 * year—179, $r^2 = 0.95$, df = 14, $p < 0.001$). (Supplementary Material-Appendix C)

Carlton 1998), the rate of recent introductions, just to San Francisco Bay, far outstrips the rate of all new marine macroinvertebrate species being discovered on the eastern Pacific coast in recent decades (Carlton 2007). A new conspicuous bopyrid, such as *Orthione*, discovered in western North America is thus approximately 10 times more likely to be an introduction from Asia or elsewhere than to be a previously overlooked native species. The lesser known but much more diverse Asian complex of bopyrid species are a ready source for undescribed bopyrid introductions to North America.

The earliest Japanese record of *Orthione* (1998, in Itani 2004) was initially misidentified as *Gyge ovalis* (Shiino 1939), a species which is nearly 100 times more prevalent than the combined prevalence of other Japanese branchial mud shrimp (*Upogebia* and *Austinogebia*) parasites, *Progebiophilus filicaudatus* (Shiino 1958), *Progebiophilus villosus* (Shiino 1964) and *Procepon insolitum* Shiino, 1937 (Itani, personal observation). In contrast, abundant and conspicuous *Orthione* are the only branchial mud shrimp bopyrid in western North America. The recognition of *Orthione* in Asia only after it was discovered in North America is thus consistent with the general history of North Pacific marine invertebrate taxonomy and with the pattern of species introductions to North America. The position of bopyrid infestations on hosts is a critical character for the identification of North American bopyrids (Richardson 1905; Schultz 1969; Hatch 1947 p. 223; Kozloff 1973 p. 30; Bourdon 1987 p. 342; Hart 1982 p. 31; Miller 1975 p. 286, 305; Markham 2004). Historical references to bopyrids from Eastern Pacific *Upogebia* include only abdominal infestations (Stimpson 1857; Lockington 1878; Johnson and Snook 1927; MacGinitie 1930, 1935; MacGinitie and MacGinitie 1949; Schultz 1969; Miller 1975; Hart 1982; Kozloff and Price 1987; Jensen 1995). *P. abdominalis* Stimpson 1857 infest *U. pugettensis* and *U. macginitieorum* abdominal pleopods and never infest the branchial chambers. Previous to 1988, no branchial isopods were reported from *U. pugettensis*.

In contrast, unintended reports of *Orthione* are common since 1988. Telnack and Phipps (2005) include a 1995 photograph of *U. pugettensis* with a bulging left carapace from south Puget Sound that we believe represents the presence of an *Orthione* (see Supplementary Material-Appendix A). Lamb and

Hanby (2005), p. 280 identify a photograph of a branchial bopyrid from *Upogebia* collected at Stanley Park, Vancouver Harbor as *Ione* sp., which however, is *Orthione* (reported also in Williams and An 2009). Lamb and Hanby (2005), p. 280 present a bopyrid identified as *Hemiarthrus abdominalis* Richardson, 1909 in another photograph that was extracted from the carapace of a hairy-spined crab, *Acantholithodes hispidus* (Stimpson, 1860) which Williams and An (2009) identify as ?*Ione* sp. Though its identity can not be confirmed without direct examination, this latter specimen was more likely *Pseudione giardi* Calman 1898, which infests lithodid and pagurid crabs (Markham 2003). The photograph confirms for the first time that *A. hispidus* can host bopyrid infestations. Sept (2008), p. 67 includes a 1997 photograph of a male *Upogebia* from Coos Bay that is infested by a male and female *Orthione*.

Zoologists observing large numbers of *U. pugettensis* in their studies before the 1980s did not find thoracic bopyrid infestations (Supplementary Material-Appendix E). Moreover, the numerous naturalists, zoologists and taxonomists investigating eastern Pacific intertidal estuaries and *Upogebia* over the last 150 years (Carlton 2007, Kozloff and Price 1987) would not likely have missed *Orthione* over its present range, even at extreme low frequencies, until the 1980s. The predicted taxonomic oversight of *Orthione* in North America before the 1980s of criterion 4 is thus not evident.

Criterion 5—Detection confidence relative to sampling effort

Increases (or resurgences) to the 50–80% *O. griffenis* infestations presently occurring among reproductive sized *Upogebia* populations (Smith et al. 2008, Dumbauld et al. 2011) between Baja California and Canada would not have been missed at any time by isopod taxonomists or the hundreds of intertidal mudflat collectors and ecologists working in the region since 1852 (when *U. pugettensis* was first reported). *Orthione* are too large and conspicuous on their hosts to have escaped detection for 150 years in North America due to undersampling unless they were rare. We therefore consider detection confidence only for a minimum prevalence of *Orthione* that could have avoided detection.

Minimum likely prevalence (ρ_{min})

This minimum prevalence is comparable and can be related to: (1) the prevalence of the rare and co-occurring native bopyrid, *Ione cornuta* and, (2) *Orthione* at its minimum likely sustainable (Allee) threshold density. *I. cornuta* infests the branchial chambers of the native ghost shrimps, *Neotrypaea californiensis* and *N. gigas* at less than 3% prevalence (Dumbauld et al. 2011) but was independently reported at least 9 times previous to 1988 (Supplementary Material-Appendix F). Eastern Pacific *Upogebia* and *Neotrypaea* are similar in size and abundance and occur in adjacent areas of the same intertidal estuary mudflats, over the same geographical range and are similarly referred to in scores of pre-1988 studies. The lack of pre-1988 references to *O. griffenis*

are expected only if it was absent or significantly less prevalent than *I. cornuta* is among *Neotrypaea*. We therefore tested whether *Orthione* at similar prevalence was likely to be overlooked or whether its persistence was likely at less than 3% prevalence.

A native *Orthione* cannot simultaneously occur at less than its Allee prevalence in all areas. *Orthione* were found at their lowest prevalence at long term monitoring sites at Cedar River and the Palix River in Willapa Bay in 1988, 1990 and 1994. *Orthione* dramatically increased in prevalence at these sites after 1998 (Table 1, Dumbauld et al. 2011). The abrupt increase after 1998 is consistent with an Allee density threshold being exceeded (Table 1). We tested these low density periods (Table 1) for possible Allee density responses at these sites previous to 1998. We estimated ρ_{min} (from Eqs. 1 and 2) on the assumption

Table 1 *Upogebia* collected by year from the Cedar River and Palix River sites of Willapa Bay, Washington, with (Total) infested *Upogebia* (*I*), effective *Upogebia* host number (*N*) (Eq. 4), yearly prevalence, based on infested per effective hosts (ρ) and average prevalence (bold) (Eq. 5), the probability of encountering *Upogebia* in the subsample or the overall sample (α), based on that year's effective *Upogebia* host number and the present or the next previous ρ value greater than zero or the overall sample, the cumulative numbers of uninfested *Upogebia* among years following *Orthione* encounters ($\sum N$) and the estimated confidence of encounter probability with the cumulative sample size ($\sum \alpha$)

Year	Total	I	N	ρ	α	$\sum N$	$\sum \alpha$	Notes
1988	158	2	64.6	0.03	0.87			
1989	26	0	16.4	0.00	0.40	16.4	0.40	*
1990	66	0	37.1	0.00	0.69	53.5	0.81	***
1990a	91	2	61.4	0.04	0.31			**
1991	24	0	14.2	0.00	0.36	67.7	0.88	***
1992	26	0	11.6	0.00	0.70	79.3	0.92	***
1993	96	0	33.4	0.00	0.35	112.7	0.97	***
1994	62	1	17.5	0.06	0.36			
1995	230	0	61.3	0.00	0.03	61.3	0.97	*
1996	99	0	46.7	0.00	0.07	108.0	1.00	***
1997	139	0	72.3	0.00	0.02	180.3	1.00	***
1998	160	1	36.0	0.03	0.36			
1999	90	9	36.1	0.25	1.00			
2000	152	11	82.5	0.13	1.00			
2001	113	57	68.6	0.83	1.00			
2002	6	0	2.9	0.00	0.97			
Overall	**1,447**	**81**	**601.2**	**0.13**			**1.00**	****

* Using ρ of nearest previous year

** Sample from Palix River area

*** Using ρ plus cumulative N of all previous years without infestations

**** The sums of all *Upogebia* and all infested *Upogebia*, the average infested *Upogebia* and total probability of detecting *Orthione* among all years and collections

that minimum *Orthione* prevalence is only slightly greater than its Allee density.

Detection confidence, α, (Eq. 1) is overestimated by samples from decreasing populations and underestimated by samples from increasing populations. The cumulative confidence of encounter, $\sum \alpha$, with accumulating empty samples, $\sum N$, reached 0.97 by 1993 and 1.00 by 1997 (Table 1). Thus, $\sum \alpha$ (Table 1, column 8) overestimated *Orthione* prevalence in the years that it was not collected. *Orthione* would have been collected more often between 1989 and 1997 if its prevalence in non-detection years had remained equal to the years when it was detected. We assume these Willapa Bay populations, occurring at 3% prevalence or less, were failing, that they were at or below their Allee densities and thus yield suitable ρ_{min} estimates. From Eq. 3, using ρ_{min} from above, *Orthione* prevalence in 1988 and 1994 at Cedar River and in 1990 at the Palix River (Table 1) required effective sample sizes of 98.4, 48.4, 98.4 and 73.4 *Upogebia* respectively, for $\alpha > 0.95$ (>95% probability of detection). Thus, even if *Orthione* occurred only at the 3% ρ_{min} before 1988, 50 to 100 suitable *U. pugettensis* would have been sufficient for detecting them with 95% confidence.

Considering *Orthione* relative to *Ione cornuta* among *Neotrypaea*, the minimum *Orthione* prevalence (approaching 3%) exceeds the 2% or lower prevalence typical of *Ione* (Dumbauld et al. 2011). The absence of pre-1988 *Orthione* records compared to 9 *Ione* records before 1988 (Supplementary Material-Appendix F) indicates, by this test, that it was not there.

We tested again for detection confidence based on the 3% ρ_{min} among 82 pre-1988 *U. pugettensis* we found in museum collections that were in suitable condition to retain *Orthione* if they were present (Supplementary Material-Appendix A). These specimens were collected between 1918 and 1977 and from Morro Bay, California to Vancouver, British Columbia and thus sampled most of the present ranges of *U. pugettensis* and *Orthione* over time and included at least 37 effective (suitable) hosts (Eq. 4, and Figure 1 of Supplementary Material-Appendix A). *Orthione* was not found among them. *Orthione* detection confidence, α, from this sample at respective Cedar River Allee prevalence for 1988 and 1998, $\rho = 0.03$ (Figure 1 of Supplementary Material-Appendix A, thin line) and 1994, $\rho = 0.06$ and Palix River in 1990, $\rho = 0.04$, were respectively, 0.68, 0.90 and 0.78

(Table 1). An effective sample size for 95% detection confidence with the average *Orthione* prevalence at Cedar River over the 15 year sample period (Table 1, $\rho = 0.13$) would be 21.5. Thus, the museum samples are sufficient to reject pre-1988 North American *Orthione* with greater than 95% confidence only at recent densities.

A criterion 5 default assumption that *Orthione* is native could only fail rejection if a continuous low prevalence among pre-1988 *Orthione* populations could be demonstrated. However, even then, the present museum sample is sufficient for detection, even at the lowest possible prevalence, with greater than 50% confidence. These three tests of whether *Orthione* "was not there" (McArdle 1990) previous to 1988 will increase in power when more museum collections of *U. pugettensis* can be examined. These tests also do not include the hundreds of specimens Lockington (1878) examined for symbionts from Tomales and San Francisco Bay without finding *Orthione* (Supplementary Material-Appendix A). Predictions of criterion 5 are thus rejected.

Criterion 6—Trans-Pacific dispersal vectors and mechanisms

Natural transoceanic dispersal on ocean currents

That *Orthione* could disperse on ocean currents across the North Pacific between East Asian and North American estuaries has not been demonstrated for any invertebrate species and such a model would be *sui generis*. The time required for direct ocean crossings in North Pacific currents is too great for *Orthione* larvae to survive. Moreover, previous models and interpretations of long distance dispersal by non-teleplanic coastal marine larvae to maintain connectivity among distant populations are increasingly held in doubt (Morgan et al. 2009). Larval distributions of near-shore marine invertebrates appear to be adapted for remaining in local circulation cells even in strong upwelling areas (Morgan et al. 2009) and, not surprisingly, for returning to source populations and habitats (Wooldridge and Loubser 1996; Shanks and Roegner 2007). Behavioral adaptations for restricted larval dispersal are common among decapods, including thalassinid shrimp (Tamaki et al. 2010, Wooldridge and Loubser 1996, Queiroga and Blanton 2005). The lack of mud shrimp host species in the Siberian

Western Pacific Ocean (Williams 1986) also precludes *O. griffenis* dispersal across the North Pacific by island hopping through host populations.

Anthropogenic dispersal across the Pacific: ballast water traffic

Epicaridia and cryptoniscans (the first and last bopyrid swimming stages) and microniscans (the nonswimming parasite of the intermediate zooplankton hosts) of at least two bopyrid species were found in 29 of the 31 planktonic isopod samples collected from 18 different ships arriving from Japan during a Coos Bay, Oregon ballast water survey (Carlton and Geller 1993). These pelagic dispersal stages survived 11–21 days ballast water transits from Japan to Coos Bay in at least 11% of the ships sampled. Moreover, the tiny 0.3–0.6 mm length epicaridia, microniscan and cryptoniscan larval stages may have been undercounted in these samples (Carlton, personal communication). The absence of *Orthione* in Carlton and Geller's (1993) samples is consistent with the lack of abundant *Orthione* source populations in Japan (Itani, personal observation). The appearance of *Orthione* on the Washington coast also did not coincide with changes in Japanese ballast water traffic but closely followed the onset of major western North American trade from China, which steadily increased after 1986 (Carter and Rozelle 2002). *Orthione* are common among *Upogebia wuhsienweni* from the mudflats of Qingdao (Williams and An 2009), a major Chinese seaport of the Shandong Peninsula. The Bohai and Yellow Seas, which are separated by the Shandong Peninsula, are the busiest shipping lanes in the world (Rongfen and Guozheng 2007).

Orthione epicaridia or cryptoniscans were in all 65 zooplankton samples collected from the harbor area of Yaquina Bay between March and September 2006 (Supplementary Material-Appendix B, Figure 1). *Orthione* epicaridia were most abundant in low tide samples and cryptoniscans were most abundant in high tide samples while microniscans were absent in the estuary at all times (Supplementary Material-Appendix B, Figure 2).

Thus, counter to predictions of criterion 6, its earliest North American appearance closely followed the onset of ballast water traffic from China where the largest known Asian *Orthione* populations occur (Williams and An 2009); pelagic epicaridia, microniscan and cryptoniscans occur in ballast water arriving in the Pacific Northwest from Asia (Carlton 1985, Carlton and Geller 1993 and herein) and *Orthione* larvae survive well where ballast water entrainment and discharge occurs. A new source of ballast water traffic is thus the likely mechanism and vector that connected Asian *Orthione* to North America.

Other mechanisms

Pernet et al. (2008) note the transport of *Upogebia* as bait along the American Pacific coast, and *Upogebia* is a seafood item in Asia (Yuji et al. 2008). However, we know of no intentional transport of living *Upogebia* from Asia to North America. Even if live *Upogebia* were to arrive in North America as part of bait or live seafood trade, *Orthione* infest only reproductive sized *Upogebia* (Smith et al. 2008), which cannot reburrow (Chapman et al., unpublished data). Rapid reburrowing by *Upogebia* after release would be critical for even brief survival, and released *Upogebia* and their parasites would thus most likely quickly perish.

Discussion

Probability of indigenous origins

The recent discovery of *Orthione* in Eastern Pacific *Upogebia* provided an ideal opportunity for a multiple criteria based analyses of its origins. Ranking criteria as binomials (Table 2), rather than as cumulative Bayesian probabilities, is a more conservative test of *Orthione* origins. The binomial ranks of these 6 criteria nevertheless include a 95% chance of mixed outcomes (cryptogenic species) and less than 5% chance of either all positive (native species) or all negative (introduced origins). Counter to all null predictions *Orthione*: (1) has geographically isolated Asian and North American populations; (2) was first collected in Asia; (3) was discovered last among symbiotic species of North American *Upogebia*; (4) is absent in published North American records before 1988 but appears in several reports after 1988 where it was misidentified; (5) is absent in early museum collections, reports, surveys and research activities that were sufficiently extensive for detection if it was there in addition to being discovered late in North

Table 2 The one tailed binomial probability (*p*) of 6 criteria for a native species failing to predict observed characteristics of *Orthione griffenis* in North America

Criteria	Predicted	Observed
Geographically isolated species	Distinct	Conspecific
Precedence of first record	North America	Asia
Precedence among North American symbionts	Early	Last
Previous misidentified North American records	Yes	No
Early North American museum samples	Yes	No
Appearance and potential introduction mechanism	Dissidence	Coincidence
Binomial probability for 6 predictions	0 of 6	*p < 0.02*

America relative to the sizes and diversity of all other North American Bopyridae and; (6) appeared in North America coincident with the onset of its most likely vector of introduction. The simplest hypothesis, even by a conservative binomial probability estimate (Table 2) ($p < 0.02$), is that *Orthione* is introduced to North America.

The specific identities of nearly all marine bopyrid microniscans are unknown. However, all Asian and North American microniscan records (Saito 2002 and herein) are from coastal marine calanoid copepod hosts. The abundant ebb tide epicaridia, abundant flood tide cryptoniscans (Supplementary Material-Appendix B, Figure 2) and the absence of microniscans in plankton samples from within Yaquina Bay are consistent with these observations. *Orthione* epicaridians must emigrate from the estuary on ebb tides, cryptoniscans must return to the estuary on flood tides and the microniscans must reside in the coastal ocean where copepod species that are larger than the resident estuarine copepod species are available (Bill Peterson, Alan Shanks, personal communications). Temperate Asian and North American estuary tidal circulation systems are similar. However, Asian coastal oceans are predominantly downwelling systems while eastern Pacific coastal oceans are predominantly upwelling systems (Peterson 1998; Morgan et al. 2009). How adaptations of introduced Asian microniscan permit them to navigate back into eastern Pacific estuaries is unclear. Perhaps these Asian microniscans find the right native hosts: the North American copepods

Calanus marshallae and *C. pacificus* may be ecological equivalents of the Japanese bopyrid host *Calanus sinicus* (Saito 2002). *Calanus marshallae* and *C. pacificus* migrate close to shore for reproduction (Peterson 1998; Hoof and Peterson 2006) and could carry introduced microniscans to adjacent circulation cells of estuaries (Frick et al. 2007). Moreover, four of the eight identified Japanese copepod hosts of bopyrid microniscans (*Acartia omorii*, *Paracalanus parvus*, *Centropages abdominalis* and *Oithona davisae*) (Saito 2002) also occur on the North American coast, at least two of which (*Acartia* and *Oithona*) are likely ballast-mediated introductions.

These secondary copepod hosts may thus have played an important role in secondary dispersal of *Orthione* along the Pacific coast. Willapa Bay is an unlikely entry port for new ballast water introductions due to its lack of international or coastal shipping traffic. Ballast water introductions are therefore more likely to reach Willapa Bay by secondary dispersal in coastal currents from international shipping ports to the north and south. The low *Orthione* infestations discovered in Willapa Bay in 1988, 1994 and 1998 (Dumbauld et al. 2011) followed El Niño years (1987, 1993 and 1997), when reversals of summer currents increased marine larval dispersal from the south (Yamada and Kosro 2010). The 1998 onset of increasingly intense *Orthione* infestations in Willapa Bay (Dumbauld et al. 2011) coincided with the largest northern expansions of the introduced European shore crab, *Carcinus maenas* from San Francisco Bay in coastal currents in 1997 (Yamada and Kosro 2010). *Orthione* microniscans could similarly have arrived in Willapa Bay on their new copepod hosts.

Introduced parasites can cause extinctions of their new hosts, even if they become extinct themselves as a result. Parasites contribute particularly to extinctions when their abundances are sufficient to destabilize host populations (Boots and Sasaki 2001). Castration seldom increases host mortality (Lafferty and Kuris 2002; Kuris et al. 2008; Dumbauld et al. 2011). However, the hosts of parasitic castrators can compete with uninfected neighbors while increasing the potential for new infestations on broader scales. *Orthione* infest *U. macginitieorum* in Bahia San Quintín and Estero Punta Banda, Baja California estuaries and in Carpinteria Marsh, California (Supplementary Material-Appendix A) where marked influences of marine parasites on host populations

and communities are well known (Kuris et al. 2008). Cymothoidan isopods, including the Bopyridae, in these estuaries are the second largest biomass components of the parasite groups that Kuris et al. (2008) speculate may control most of their decapod host biomass. Thus, natural, co-evolved parasite dominance in these systems remains unclear. Pre-adaptations of *Orthione* to both new final and new intermediate hosts in a dramatically different oceanographic system from where it evolved, is unexpected and was unpredictable.

Predator–prey oscillations consistent with coexistence are not apparent between eastern Pacific *Upogebia* and *Orthione*. *Upogebia* populations have collapsed in British Columbia, Washington, Oregon and California since the appearance of *Orthione* (Figure 1, Supplementary Material-Appendix A, Dumbauld et al. 2011). *Upogebia* populations in Bolinas Lagoon, San Francisco Bay and Elkhorn Slough, California (Figure 1, Supplementary Material-Appendix A) populations appear to be extinct. We assume the Bodega Harbor to Elkhorn Slough populations are likely to be extinct (Fig. 1) rather than "collapsed" even though a few isolated specimens have been recovered in recent years. All but one specimen recovered from these estuaries have been infested (Bruce Pernet, Greg Jensen, personal communications) and unlikely to be reproductive. We consider the Tomales Bay population (Fig. 1), where only one uninfested but non-reproductive individual was found after two extensive searches (Supplementary Material-Appendix A) also likely to be extinct.

Thus, *Orthione* persist even in collapsing *U. pugettensis* populations and effective castration by *Orthione* appears to be the cause of these collapses (Dumbauld et al. 2011). Although *Orthione* have not been collected from Tomales Bay, Bolinas Lagoon, San Francisco Bay or Elkhorn Slough (Fig. 1), we assume the collapse of *Upogebia* in these estuaries is due to *Orthione*. *Orthione* occurs in all remaining *Upogebia* populations north and south of these estuaries and *Upogebia* were present in all of these estuaries until the 1970s, only a few years before *Orthione* was discovered in North America.

The least numerous and thus perhaps most vulnerable potential eastern Pacific hosts for *Orthione* are likely to be *Upogebia onychion* Williams 1986, known only from San Miguel Island, California and *Upogebia lepta* Williams 1986, known only from Santa Catalina

Island, California and Coronado Island, Baja California Norte (Figure 1). These latter two species are within the range of pelagic dispersal stages of *Orthione* due to the south-flowing California Current and north flowing Southern California Eddy currents, which reach these islands from coastal California and Mexico in different seasons (Hickey 1998). Investigations of the absence or presence (and if the latter, the prevalence) of *Orthione* in these potential southern *Upogebia* hosts is urgently required.

Implications of *Orthione* being introduced are manifold. First, the eastern Pacific is, of course, a new dispersal hub for export of *Orthione* to all other *Upogebia* populations around the world. Moreover, as with other introductions (Carlton 2009 and references therein) *Orthione* appears capable of reordering its new ecosystems and reducing biodiversity. The combined per capita effects, broad range and continued abundances of *Orthione* place it among the most significant introduced marine species discovered anywhere. The prevalence of *Orthione* in *U. pugettensis* populations has fluctuated among years but these shrimp populations continue to decline with no clear recoveries to date (Dumbauld et al. 2011).

Functional and absolute losses of *Upogebia* species reduce their ecosystem services and dependent symbionts. *Upogebia* previously dominated eastern Pacific estuary mudflat communities (Swinbanks and Luternauer 1987; Posey et al. 1991; Griffen et al. 2004; D'Andrea and DeWitt 2009). *Upogebia* beds covered 40% of the intertidal Yaquina Bay mudflats in 2002 (D'Andrea and DeWitt 2009). *Upogebia* also comprised the largest biomass of any other invertebrate in Yaquina Bay in 2002 but by 2008, their numbers had declined by 65% (Dumbauld, personal observation). *Upogebia* larvae were also important prey of juvenile salmon (Chapman et al., unpublished manuscript). Ignoring tidal exchange and vertical water movement, *Upogebia* filtered the entire water column overlying its burrows in Yaquina Bay daily (Griffen et al. 2004; D'Andrea and DeWitt 2009). Significant changes in sediment and benthic community dynamics are likely to occur in estuaries where these shrimp populations are lost (Dumbauld et al. 2011).

The nonindigenous origins of *Orthione* in North America and the absence of refuges for its new hosts preclude assumptions of the hosts' resilience, equilibrium domains or otherwise long-term persistence.

Orthione is a critical threat to North American *Upogebia* species. Delayed responses are ineffective for conserving complex systems with long time lags (Sterman 2008). The unnatural arms races between *Orthione* and each of its new *Upogebia* hosts in North America can only result in unpredictable *Orthione* extinction, coexistence, or *Upogebia* extinction. The federal Endangered Species Act includes critical habitat designations and protections from human exploitation, but does not provide for introduced species and their effects on native marine invertebrates, including mud shrimp (Lund 2011). The Oregon State Endangered Species Act similarly excludes invertebrates from protection (Lund 2011). Nevertheless, urgent, immediate responses, including captive breeding programs for the most impacted *Upogebia* populations and species are warranted.

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