Review Article

A doubled down invasion of the northeast Pacific by the Asian mud shrimp, *Upogebia major* and its coevolved bopyrid isopod parasite, *Orthione griffenis*

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Abstract

Dramatic declines of the native northeast Pacific mud shrimp, *Upogebia pugettensis* over the last three decades have occurred in response to intense infestations by the Asian bopyrid isopod parasite, *Orthione griffenis,* that was introduced in the 1980s. We report herein the arrival of the Asian mud shrimp, *Upogebia major*, in San Francisco Bay no later than 2006. Complications of identifying juvenile *U. major* and inefficiencies of collecting mature and readily identified specimens recovered by conventional sampling devices are likely to have delayed its identification and discovery. *U. major* is less vulnerable to *O. griffenis* and is displacing or replacing *U. pugettensis* in its present 200 km range to the north and south of San Francisco Bay. *Upogebia major*, as a coevolved alternative host, assures persistence of *O. griffenis* in this region even where native species extinctions occur and can potentially expand to all habitats that are presently invaded by *O. griffenis* (Alaska to Baja California Norte). The individual and combined *O. griffenis* and *U. major* invasions thus threaten *U. pugettensis* in particular and all other native *Upogebia* species occurring north of Mexico. Our review of *Upogebia* taxonomy for a key to species revealed a previously reported 1912 invasion of San Francisco Bay by *Upogebia affinis* that was in error; hence, the introduction of *U. major* is the first confirmed gebiid invasion in the world. Greater resolution of *U. major* natural history and timing of its invasion is needed to test whether it evaded present vector management efforts. Intervention is warranted to limit the doubled down *U. major* and *O. griffenis* invasion and to conserve *U. pugettensis* and other native *Upogebia* species from ecological or absolute extinction in the coming decades.

Key words: California, vectors, Decapoda, estuary, taxonomy, conservation, extinction

Introduction

San Francisco Bay, California is among the most intensely invaded and modified estuaries in the world (Cohen and Carlton 1998; Nichols et al. 1986). Moreover, nonindigenous species of Northeastern Pacific estuaries pose significant threats to human health, the economy, and the environment and attempts to eradicate these species after they become established are costly and often unsuccessful (Scianni et al. 2019). Vector management remains the most effective first defense from the ecological and economic costs of nonindigenous species (Williams et al. 2013) while nonindigenous species that can escape from vector management efforts and that have the greatest environmental or economic effects are of the greatest concern (Lowe et al. 2000).

Upogebia pugettensis (Dana, 1852) was the only confirmed *Upogebia* species occurring on the western North American coast north of Morro Bay, California (Williams 1986). *Upogebia pugettensis* live in permanent mud lined burrows (Thompson 1972) even in rocky areas, and form dense burrow galleries in intertidal estuary mudflats. *Upogebia pugettensis* are classified as ecosystem engineers (D'Andrea and DeWitt 2009; Dumbauld et al. 2021) due to their intertidal burrows and burrowing activities in estuary mudflats. All *Upogebia,* including *U. pugettensis*, expand effective estuary sediment surface areas (Chapman and Carter 2014) and circulate oxygenated water deep into suboxic subsurface sediments (Thompson and Pritchard 1969; Thompson 1972). *Upogebia* burrowing accelerates sediment remineralization and can dominate estuary biogeochemistry (D'Andrea and Dewitt 2009; Pascal et al. 2019). *Upogebia pugettensis* also support broad diversities of obligate and facultative commensal species (Chapman et al. 2012). Alterations of major burrowing shrimp populations are therefore also major alterations of the estuary ecosystems that they dominate (Dumbauld et al. 2021).

All major *U. pugettensis* populations that have been examined (southern British Columbia to Morro Bay, California) since the early 2000s have declined dramatically due to effective castration and reproductive losses to the introduced Asian bopyrid isopod parasite, *Orthione griffenis* Markham, 2004 (Smith et al. 2008; Griffen 2009; Dumbauld et al. 2011, 2021; Chapman et al. 2012; Repetto and Griffen 2011; Chapman and Carter 2014; Asson et al. 2017; Dumbauld and Bosley 2018). Chapman et al. (2012) concluded that *U. pugettensis* were extinct in the San Francisco Bay area after they did not find them in multiple intertidal surveys. Chapman et al. (2012) did not survey the subtidal benthos, where *U. pugettensis* have seldom been reported. The severe declines of previously abundant intertidal *U. pugettensis* in San Francisco Bay area and all other estuaries from British Columbia to Morro Bay, nevertheless, places *O. griffenis*, the species responsible for its extirpation, also, as an ecosystem engineer.

We discovered a new *Upogebia* species in San Francisco Bay from two mature males recovered from San Pablo Bay (in San Francisco Bay, California) in sediments pumped from a 10 m depth area by US Army Corps dredge, *Essayons,* on 6/10/2010 (McGowan 2010; McGowan et al. 2012). We tentatively identified these subtidal *Upogebia*, that were the second most abundant invertebrate in the *Essayons* spoils and that were clearly not the native *U. pugettensis*, as the Asian *Upogebia major* (de Haan, 1841). Risks of overestimating the distribution ranges of species or of incorrectly assigning species with the status of "non-indigenous" occur however, where identifications are not confirmed by thorough taxonomic investigations (Simon et al. 2019). We therefore attempted a more conclusive identification of this newly discovered species, which required female specimens and a review of the world taxonomy of *Upogebia*. Our review was needed also to test previous conclusions of massive *U. pugettensis* declines, based almost entirely on surveys of intertidal estuary mudflats, and to reexamine a previously assessed "failed introduction" of the western Atlantic, *Upogebia affinis* (Say, 1818) into San Francisco Bay.

With the exception of *U. affinis*, the predominantly intertidal *U. pugettensis* were the only previously reported *Upogebia* in San Francisco Bay (Ricketts et al. 1985; Dumbauld et al. 1996; Kuris et al. 2007; Jensen 2014). *Upogebia affinis* were exceptional because Williams (1986) reported them from the 1912–13 US Fisheries Commission research vessel, "*Albatross*", survey of San Francisco Bay, they were the only subtidal *Upogebia* collected in the *Albatross* survey and also, they were the only species other than *U. pugettensis* reported between Morro Bay, California and Prince William Sound, Alaska (Williams 1986). Cohen and Carlton (1995) included *U. affinis* in their list of "earlier inoculations into the San Francisco Bay estuary". Fofonoff et al. (2021) proposed this same *U. affinis* record was "a failed introduction" (introduced but did not sustain reproductive populations).

Whether the mature, abundant *Essayons Upogebia* were an overlooked native species or a recently exploding population of cryptic origins and history were, initially, open questions. *Upogebia* have been relatively rare in the last 100 years of samples from San Francisco Bay (Shaeffer et al. 2007, herein). Nearly all sampling from the subtidal San Francisco Bay benthos in the last 100 years however, has been by conventional devices which seldom penetrate more than 20 cm below the sediment surface (Nichols 1973). *Upogebia* can burrow to more than two meters below the sediment surface (Thompson 1972; Kinoshita et al. 2002) where they are beyond the reach of conventional sampling devices. The up to 28.6 m reach of the *Essayons* is deeper than all other benthic sampling devices and is therefore more suited for collecting deep burrowing subtidal *Upogebia*.

The abundant *Upogebia* from the *Essayons* spoils thus potentially contradicted Chapman et al.'s (2012) conclusions of local *U. pugettensis* extinctions. Depending on how long these new *Upogebia* had been overlooked,

their discovery opened to question whether the introduction of the western Atlantic *U. affinis* into San Francisco Bay was a "failed" introduction or whether another new invader had escaped through existing vector management efforts. The *Upogebia* collected by the *Essayons*, if verified to be of Asian origins, were also significant as a previously unrecognized alternative host for *O. griffenis* that could assure persistence of *O. griffenis* even where they extirpate native *Upogebia* species. We partially address these questions in this report.

Materials and methods

We reviewed nearshore northeastern Pacific and global *Upogebia* taxonomy to clearly identify and distinguish the *Essayons Upogebia* from all other *Upogebia* species of the world. Our review included the natural history, ecology and population biology of northeastern Pacific nearshore *Upogebia* to assess the additional risks of this new *Upogebia* to native species if it proved to be introduced. We surveyed *Upogebia* populations in major California estuaries to assess the range of this new species, to establish a baseline for tracking its present and future distribution and to verify the distributions of intertidal *Upogebia* species north of Mexico that are likely to occur within its range. Our field surveys included direct sampling, correspondences, personal communications, published and gray literature, and on-line postings and databases (i.e. GBIF 2019; iNaturalist 2019; UMLAW 2019; Fofonoff et al. 2021; Ahyong et al. 2020). We also surveyed invertebrate collections in the Los Angeles County Museum of Natural History, Los Angeles, CA (NHMLAC), the California Academy of Sciences, Invertebrate Zoology, San Francisco, CA (CASIZ), the Smithsonian Institution, Invertebrate Zoology, National Museum of Natural History, Suitland, MD (NMNH) the Moss Landing Benthic Lab., Moss Landing Marine Laboratory, Moss Landing, CA and the California Department of Fish and Wildlife, Stockton, CA (CDFW 2019) reference collections.

We compared the *Essayons Upogebia* with the other recognized nearshore coastal California species, *Upogebia macginitieorum* Williams, 1986, with *U. pugettensis* with *Upogebia affinis* (as conceived by Williams 1993) and with the 4 San Francisco Bay *U. affinis* specimens reported in Williams (1986). Williams (1993, p. 5) reasserted the possible East Pacific introduction of *U. affinis*. *Upogebia felderi* Williams, 1993, of the Western Gulf of Mexico and *U. paraffinis* Williams, 1993, of Ceará to São Paulo, Brazil, that Williams separated from *U. affinis* narrowed the potential sources of the San Francisco Bay population to the North Atlantic. We reexamined the San Francisco Bay *U. affinis* collection notes and data to verify their specific status within the new *U. affinis* complex and their north Atlantic origins.

We included a photo illustrated key and notes in our correspondences and presentations (Chapman and Breitenstein 2017) that is included herein

to facilitate identifications and public outreach. Photos in the amended key are from a Canon 5D camera focused through an MP-E 65 mm macro lens or through an EF 24-105 mm macro lens attached to a stereo-microscope at 1-20X magnifications. Depth of field was increased by Helicon Focus assemblies of composited, stacked images. We also summarize confirmed and critical *Upogebia* species records in Figure 1, Supplementary material Table S1, confirmed plus reported *U. pugettensis*, *U. macginieorum*, *O. griffenis* and the native bopyrid, *Phyllodurus abdominalis* Stimpson, 1857 in Table S1. The photographs of *U. affinis* from Oyster Bay Harbor, Oyster Bay, New York, in the key (Figure 2) are in place of our low-quality photographs of the San Francisco Bay *U. affinis* specimens in the NMNH collections (Figure S1).

We sampled for *U. major*, *U. macginitieorum* and *U. pugettensis* among California estuaries by yabby pump (Manning 1975), in low density populations ($\sim < 10$ m^{-2}) and by hand held cores or shoveled excavations among higher density ($\sim > 10$ m^{-2}) populations. Appendages of all field collected specimens were preserved on the day of recovery in 70% ETOH for genetic analyses. Voucher specimens from our surveys are deposited in the NHMLAC, CASIZ and the Museum of Natural History, University of Colorado Boulder, Boulder, CO (UCM) museum collections and our notes and reported records of field collected shrimp are summarized in Table S1 and Appendix 1. Field collected shrimp were rinsed of adhering sediments and examined "fresh" or frozen (to fix and prevent escapes of mobile parasites). The shrimp were then thawed and inspected directly for bopyrid isopod parasites and other external commensals, then washed to dislodge parasites under the carapace. The wash water was collected into a 100 mm petri dish where it was examined under 6–10X magnification for small commensals and parasites. We distinguished *Upogebia* sexes from the first pleopods (present on mature females and absent on mature males), and from the female gonopore (on the distal, medial coxa of female pereopod 3) and the male gonopore (on the distal, medial corner of the coxa of male pereopod 5). *Upogebia* bearing both male and female gonopores were classified as hermaphrodites. We estimated size from carapace length (CL) that we measured to the nearest 0.5 mm from the distal tip of the rostrum to the posterior carapace edge. Processed specimens were refrozen or transferred into 70–95% ETOH for long-term preservation.

We used photographs (Figures S2 and S3) to verify juvenile specimens and specimens that were not collected. Our detailed review of San Francisco Bay *U. pugettensis* from 1878 to 2020 is included in Appendix 2.

Results

The similar morphologies, sizes and colorations of *U. major* and *U. pugettensis* can confuse non-specialists, and initially, ourselves. Gyo Itani, Seto Marine Biological Laboratory, Kyoto University, Shirahama, Wakayama, Japan
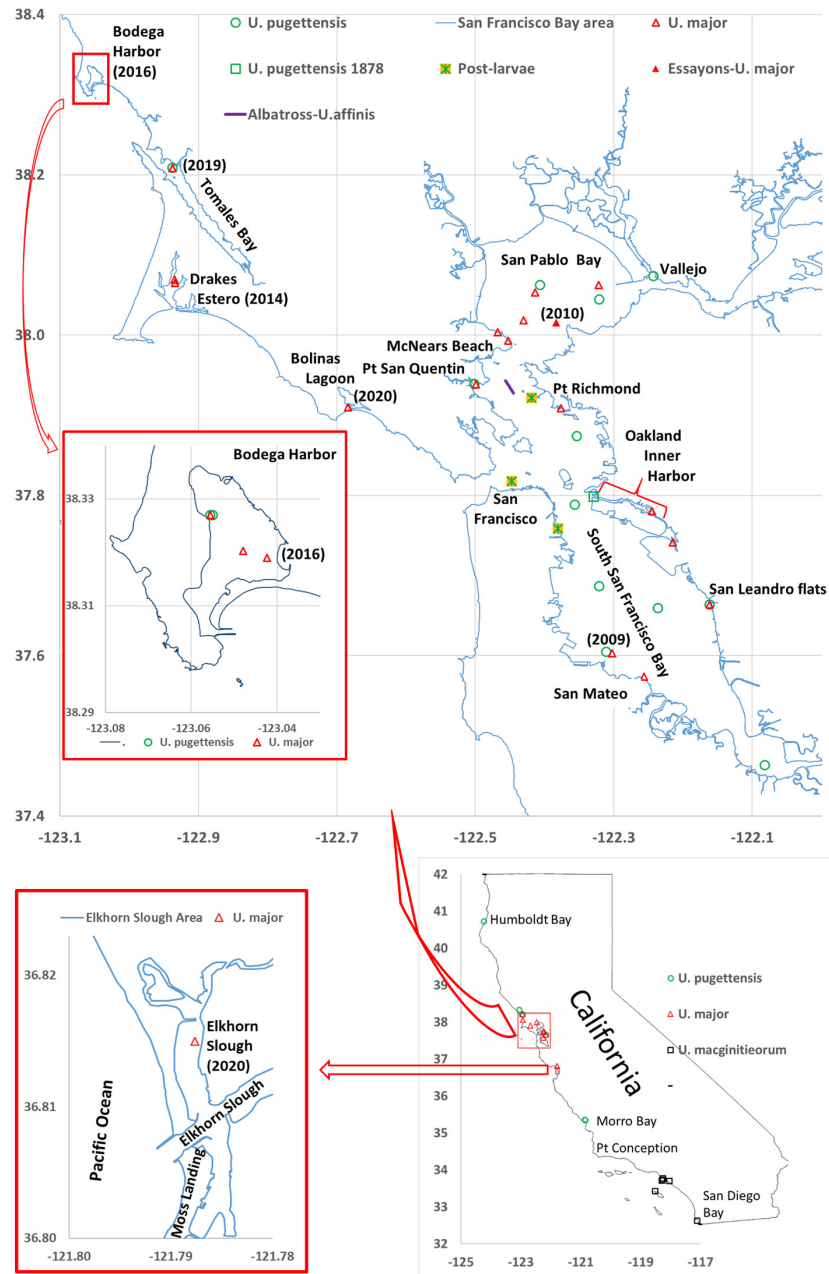
Figure 1. California records and reports of nearshore *Upogebia* (Humboldt Bay to San Diego Bay) including critical *U. major* discovery dates: Bodega Harbor, (upper left inset, 2016 and later records, open red triangles); main map, Tomales Bay (open red triangle, 2019 record), Drakes Estero (open red triangle, 2014 record), Bolinas Lagoon (open red triangle, 2020 record), San Francisco Bay (includes San Pablo Bay and South San Francisco Bay), *Essayons* (solid red triangle, 2010 record), and additional (open red triangles) records – approximately, NW to SW, Bodega Harbor, within San Francisco Bay, CDFW San Pablo Bay survey stations 110, 322 and 323, stations Bullhead Flat at China Camp, McNears Beach, Larkspur mudflat, central bay, San Quintin, Point Richmond, Oakland Inner Harbor, (south San Francisco Bay) San Leandro Bay, San Leandro flats, CDFW station 103 (2009 record), SW San Mateo Bridge and Elkhorn Slough (lower red inset map); *U. pugettensis* critical 1970s to 2020 records and reports (green open circles and square) – (lower right California map) Humboldt Bay, San Francisco Bay area and Morro Bay, (NW to SW San Francisco Bay area map), Bodega Harbor (plus upper left inset), Tomales Bay and San Francisco Bay, approximately north to south, (San Pablo Bay) Napa River entrance, San Pablo Shallow, San Pablo Deep, (central bay) San Quintin, subtidal 1878 Oakland Inner Harbor entrance (green open square), 1984–85 post-larvae from CDFW surveys and Protrero Power intake (green crosshatch and orange squares), (South San Francisco Bay) Bay Bridge, South Bay Deep, San Leandro flats, Coyote Point, Palo Alto and; *U. macginitieorum* (California map, black squares) survey records and recent reports (NW to SW) Cabrillo Marsh, Berth 78 and Domiguez Channel of Los Angeles Harbor and Chula Vista of San Diego Bay. (Details in Appendix S1 and Table S1).
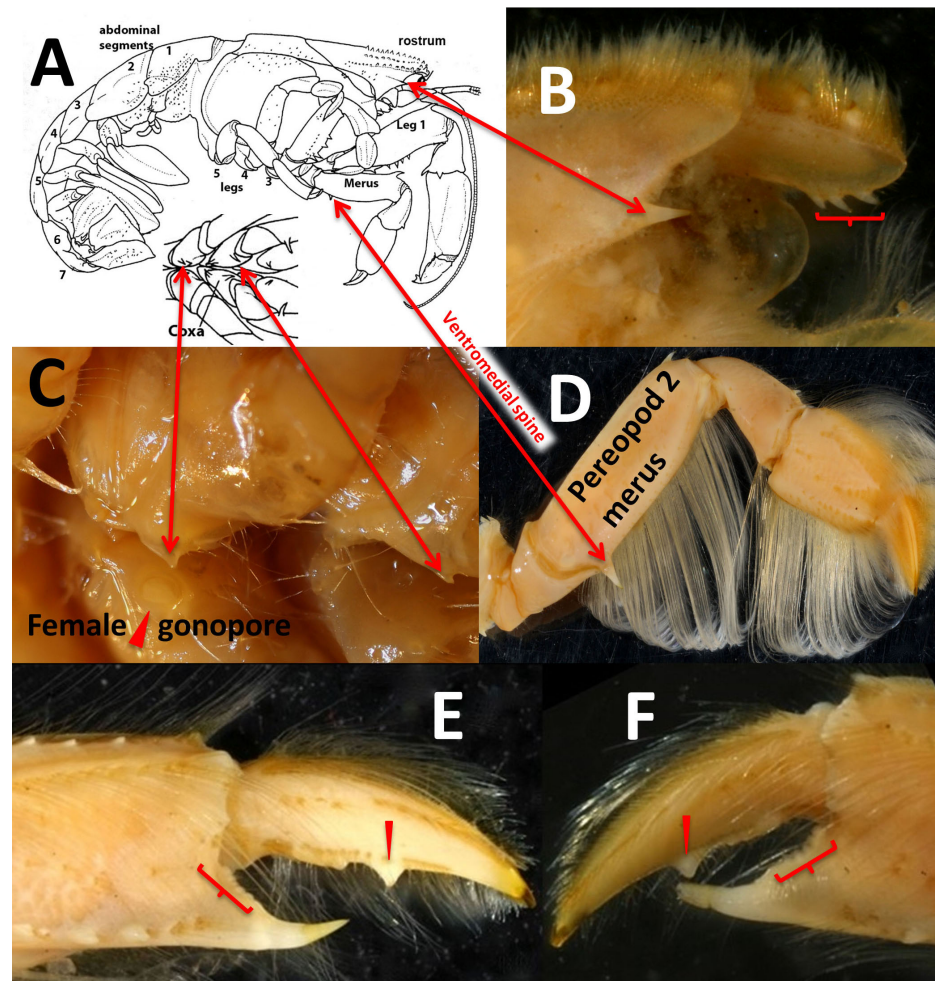
Figure 2. *Upogebia affinis*: A. from Williams (1986): B. Lateral rostrum with post ocular spine (arrow) ventral rostral spines (bracket), C. Ventral-medial spines on pereopod 3 and 2 coxae (arrows) and female gonopore (point), D. Prominent ventral-medial spine of pereopod 2 merus, E. Tooth of medial male cheliped dactyl (point) and broad area of fine teeth of propodus thumb (bracket), F. Tooth of medial female cheliped dactyl (point) and broad area of fine teeth of propodus thumb (bracket). (HMSC Collections). Photomicrographs by R. Breitenstein.

confirmed our initial identification of the *Essayons* specimens as *U. major* from the chela, rostrum, merus and pereopod 2 and 3 merus morphologies described in Sakai's (2006) key to species, Kang et al. (2007) and Hong and Lee (2014). The three nearshore shallow water eastern Pacific *Upogebia* species that can be confirmed north of the California-Mexico border do not include *U. affinis*.

Upogebia affinis (Say, 1818)

(Figure 2)

Systematics – The exoskeleton of the abdomen, telson and left uropod are all that remain of the Say's type *U. affinis* (Williams 1993). Williams (1993) therefore re-described and illustrated *U. affinis* using a specimen "of size comparable to Say's type when originally described, from South Carolina near the Georgia state line". Williams (1993) separated *U. felderi*, Williams, 1993, from the Gulf of Mexico, and *U. paraffinis*, Williams, 1993, from

Brazil from the originally conceived *U. affinis* by: 1) absence of a strong anteriorly projecting spine near to the dorsal margin of the rostrum in *U. affinis* that is present and, often prominent in *U. paraffinis*; 2) stronger spines on the chelipeds of *U. felderi* and *U. paraffinis* than in *U. affinis*; 3) strongly developed ventral spines on coxa 1 through 5 of *U. affinis* that are reduced in *U. felderi* and *U. paraffinis* and; 4) granules or short spines on the distal margin of *U. affinis* and *U. felderi* uropods that are absent on *U. paraffinis*.

Material examined – Appendix 1.

Description – Rostrum bearing large post-ocular spine (Figure 2A, B) and 0–8 ventral spines (Figure 2B, bracket). Pereopod 2 merus with proximoventral spine, 1 subdistal dorsal spine (Figures 2D and S1B) and prominent ventral coxa spines (Figure 2A, C). Prominent spines on ventral coxae of pereopods 1–5. Male and female dactyl and thumb similar (Figure 2E, F). Fine teeth on proximal dorsal thumb of cheliped opposed by a narrow ridge of similarly fine teeth on ventral proximal dactyl (Figure 2E, F). Ventral medial tooth of the dactyl extending to medial side of the closed thumb.

Remarks – As expected, the four San Francisco Bay *U. affinis* of William's (1986) match William's (1993) conception of *U. affinis* and are distinguished from all northeastern Pacific *Upogebia* species by their ventral distal rostral spines, which are absent on all North Pacific *Upogebia*. The proximal medial ventral spine on the pereopod 2 merus of *U. affinis* are in common with *U. major* and the small teeth on the inner face of the *U. affinis* cheliped thumb (Figures 2E and S1A) could be misinterpreted by non-specialists as bare, and thus, confused with the unadorned inner face of the *U. major* cheliped thumb (Figure 3C, D). However, our examination of William's San Francisco Bay *U. affinis* specimens, collection notes and original collection data revealed that the record itself is in error.

Williams (1986) reported: "The specimens" (of *U. affinis*) "may represent an introduction" and further noted: "Carlton (1979)" . . . (the earliest review of introduced marine and estuarine invertebrates of the North American Pacific coast) . . ."did not list this species from San Francisco Bay and to my knowledge no other specimens have been taken from there." These specimens would thus have been remarkable as the only record of the species in the Pacific, as a possible new introduced species on the coast, and because they were from the subtidal benthos.

Williams' (1986) 4 San Francisco Bay *U. affinis* were from one sample: "USNM-213285, 2 ♂, 2 ♀, middle section of San Francisco Bay, R. Tang. Red Rk., S 48D E Brothers L1. N 13 D E, Lft. Tang. Marine I. N 41 D W (triangulation bearings off P. San Quentin), 12.5 fm, CS5532, *Albatross* sta. 5824A, 18 December 1912, sledge trawl, gooey mud". That *Albatross* sample was 16 km northwest of the only previous subtidal record of *U. pugettensis* in San Francisco Bay, dredged from "3 to 4 fathoms" in Oakland Harbor (Lockington 1878) and 11 km southwest of the *Essayons* sample (Figure 1).

Other than a male *U. pugettensis* collected in June 1942 from offshore of Winchester Bay, Oregon (Williams 1986) and one specimen collected in July 1904 from Prince of Wales Island, Alaska (Appendix 1), we are unaware of subtidal northeast Pacific *Upogebia* records from outside of San Francisco Bay. Other than the 1912 *U. affinis,* subtidal *Upogebia* were not reported from San Francisco Bay between 1878 and the 1980s (Schemel et al. 1988, 1990).

Schmitt (1921) recognized only *U. pugettensis* in the East Pacific and emphasized (p. 10) that *U. pugettensis* was one of only 5 decapod species that were obtained entirely at shore (intertidal) stations from the *Albatross* survey. Schmitt (1921, p. 115) additionally noted that the "three", "shore" specimens of *Upogebia* "were taken in the course of the *Albatross* survey, one at Sausalito, February 8, and two at Tiburon, April 29, 1913", in a "150 foot seine" (p. 353). The validity of Williams' (1986) remarkable "four" *sui generis U. affinis* from *Albatross* survey trawl "5824A" require that they were misplaced or overlooked for 64 years despite extensive, meticulous, comprehensive original survey notes (USBF 1921; Schmitt 1921).

The 12/18/1912, *Albatross* "D" for dredging station "D. 5824A" sample was part of a modified 5 foot wide Tanner beam trawl "towed approximately 2 km between orange peel bucket dredge stations 5824A, 7 fathoms and 5824B, 12.5 fathoms" (USBF 1921, p. 64). The trawl center was approximately (37.9354; −122.4507) (Figure 1, purple line) (also from Plate 1, and p. 338 of Schmitt [1921]). Sediments in these samples ranged from "Soft, gray mud, slightly gritty, not very tenacious, at beginning and shelly, somewhat muddy sand, at end of haul." Schmitt's (1921, pp. 338 and 339) species list for sample 5824 (1 *Crangon* [as *Crago*] *nigromaculata*, 28 *Neotrypaea gigas* [as *Callianassa longimana*] and 1 *Pinnixa franciscana*), does not include *Upogebia*. The Smithsonian Oceanographic Data Set for NMNH Invertebrate Collections 5824A coordinates (Smithsonian Institution 2019), place this trawl section "[37°46′37″N; 122°26′21″W]" or (37.77694; −122.43912), on the 1300 block of Fulton St., in San Francisco (not at Station 5824). Decapod crustaceans were recovered from 285 (116 dredging and 152 hydrographic) stations of the *Albatross* survey within San Francisco Bay (Schmitt 1921). The as yet undetermined origins of Williams' (1986) *U. affinis* specimens do not include San Francisco Bay. The absence of "*Upogebia*" (that would have been the *U. affinis* specimens) from the original collection notes (USBF 1921; Schmitt 1921), the recovery of 4 mature *U. affinis* from only 1 of 285 benthic samples in the *Albatross* survey in which crustaceans were recovered (Schmitt 1921) and the lack of additional *U. affinis* records from San Francisco Bay or outside of the west Atlantic in the following 7 decades preceding Williams' (1986) report, place the source location of these *U. affinis* specimens in extreme, highly significant, doubt.

Distribution – Upogebia affinis are confirmed only from the east coast of North America, the Western Atlantic, from Massachusetts to southern Texas.
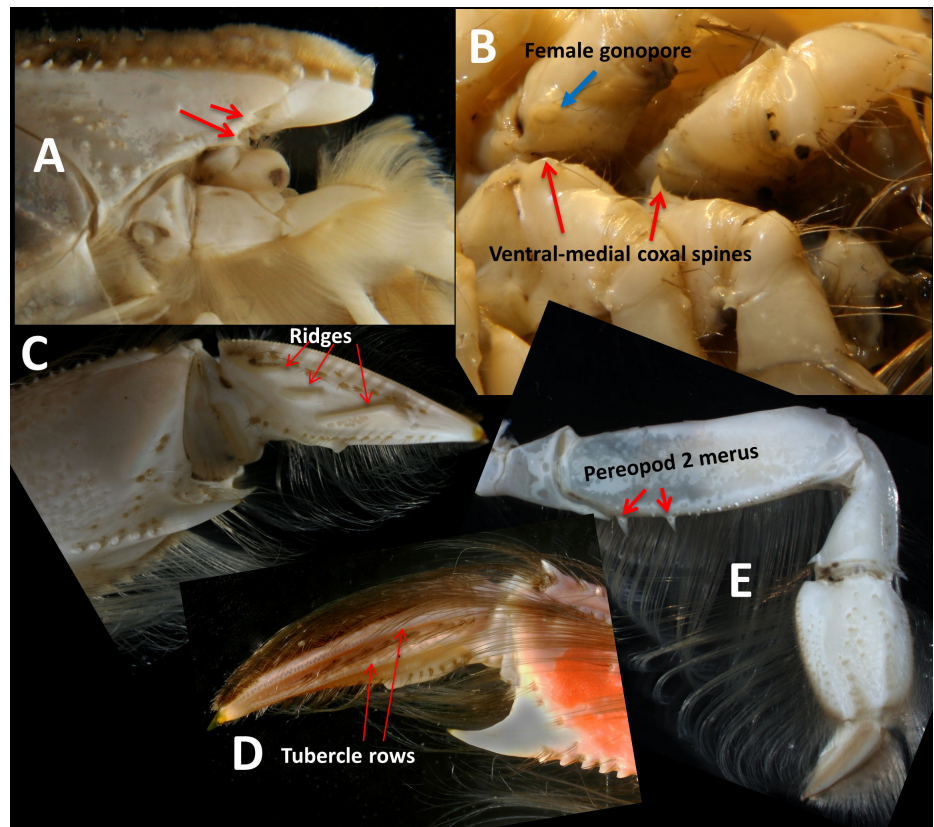
Figure 3. *Upogebia major:* A. Post ocular spines (arrows) and smooth ventral rostrum, B. Ventral pereopods 3 and 4 with coxa spines (red arrows) and pereopod 3 female gonopore (blue arrow), C. Male medial dactyl showing oblique ridges, D. Female medial dactyl with two rows of tubercles (arrows), E. Pereopod 2 merus with two ventral-medial spines (arrows). (Male UCM 48825, Female UCM 48959). Photomicrographs by R. Breitenstein.

There are no confirmed records of *U. affinis* from San Francisco Bay, California or the Pacific Ocean. No subtidal *Upogebia* species were collected in the 1912–1913 *Albatross* survey of San Francisco Bay.

Upogebia major (de Haan, 1841)

(Figure 3)

Material examined – Appendix 1.

Description – Rostrum smoothly rounded ventrally and lacking ventral teeth. One or two ocular spines (Figure 3A, red arrows). Thumb of male and female chela propodus length 1/3 of dactyl length and lacking teeth or tubercles on inner and outer distal surfaces (Figure 3C, D). Cheliped dactyls strongly dimorphic between sexes. Male cheliped dactyl medial surfaces bearing three prominent oblique ridges and a small lateral tooth (Figure 3C). Female dactyl with two longitudinal rows of tubercles (Figure 3D). Pereopod 2 merus with one proximal ventral spine and two large proximal medio-ventral spines (Figure 3E). Weak spines on ventral coxae of pereopods 1–3 (Figure 3B). *Upogebia major* are similar in general morphology and color to *U. pugettensis* but mature *U. major* are readily distinguished in the field by the smooth, unadorned the cheliped thumb inner face (Figure 3C, D).

Systematics – Summarized in Sakai's (2006) key to species, illustrations in Kang et al. (2007) and photographs in Hong and Lee (2014).

Asian Distribution – Liaoning, Bohai Sea and Shandong, Yellow Sea, China (Sakai 2006; Hong et al. 2015), Vostok Bay, Russia (Golubinskaya et al. 2016) and Seto Inland Sea northern Hokkaido, Japan (Sato et al. 2013).

North American Distribution – Bodega Harbor, Drakes Estero, Tomales Bay, Bolinas Lagoon, San Francisco Bay, and Elkhorn Slough, California. Not found in 2/10/2020 to 2/16/2020 searches of San Diego Bay, Mission Bay, Newport Bay, Los Angeles Harbor or Morrow Bay (Figure 1, Appendix 1, Table S1). Not found among extensive annual collections of *U. pugettensis* from Oregon or Washington over the last decade (Smith et al. 2008; Dumbauld et al. 2011; Chapman et al. 2012; Chapman and Carter 2014; Asson et al. 2017; Breitenstein et al. 2017; Li et al. 2020). The 200 km (Elkhorn Slough to Bodega Harbor) range of *U. major* (Figure 1) includes all major estuaries adjacent to San Francisco Bay, where it is most likely to have first established.

Remarks – Agonistic behaviors of in-hand specimens or among multiple *U. major* held in the same containers are minor. The prevalence of solitary or multiple tube occupancy is unclear. The roughly 2:1 *U. major* F:M sex ratio (herein) is consistent with hermaphroditism.

North American *U. major* are a possible "Category 4" introduced species "misidentified initially as a known native species" (Carlton 2009). Pre-reproductive *U. major*, that are most accessible to conventional quantitative sampling devices, are readily confused with *U. pugettensis*. Mature *U. major*, which are more readily identified, can burrow to 2 m depths (Kinoshita 2002) that are beyond the reach of conventional sampling devices. The dredged *Essayons* sediments have seldom been examined by biologists. *Upogebia major* could thus readily have escaped notice, even in dredge spoils, for multiple years previous to McGowan's discovery and at least one *Upogebia* species was abundant in San Francisco Bay in the early to mid-1980s.

Upogebia post-larvae that we could not identify to species were collected from CDFW San Francisco Bay Study station 213, 2/9/1984 and 3/9/1984 and station 216, 4/4/1984 (Hieb, Bay-Delta surveys, Figure 1 and Table S1). The long cheliped dactyl of 3 of these formalin preserved post-larval specimens resemble *U. major* (Konishi 1989) but cannot be distinguished from Hart's (1937) illustrated *U. pugettensis* post-larvae without fresh material.

Associated species – Three of the commensal clams, *Neaeromya rugifera* (Carpenter, 1864) and two solitary juvenile *O. griffenis* (0.9 and 1.4 mm in length), were recovered from 18 *U. major* collected between 5/5/2018 and 5/6/2018 from Bodega Harbor in an approximately 50 m diameter area of the approximately 1 km² overall intertidal survey area. Both *U. pugettensis* recovered in that survey were from the same 50 m diameter area as the
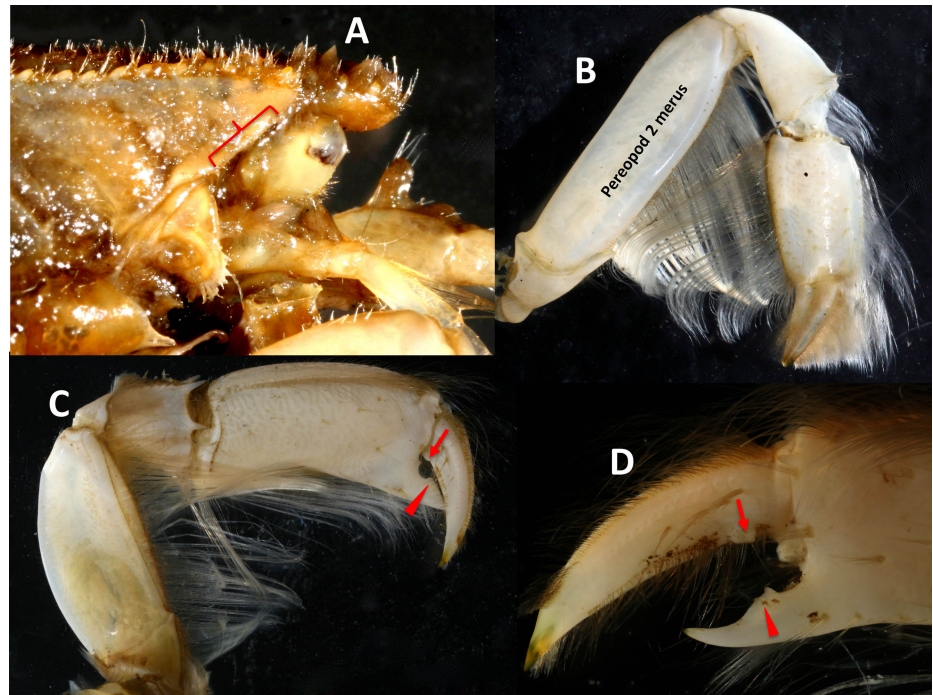
Figure 4. *Upogebia macginitieorum:* A. Smooth ventral rostrum and lateral rostrum without post ocular spines (bracket), B. Pereopod 2 merus without spines. C. Male medial dactyl with small blunt proximal tooth (arrow) and broad tooth on propodus thumb (point), D. Female medial dactyl with small blunt medial tooth (arrow) and broad tooth on propodus thumb (point). (HMSC Collections, Catalina Island). Photomicrographs by R. Breitenstein.

U. major (Appendix 1). The approximately 100 m diameter area of Tomales Bay where 40 *U. major* were recovered in 2/23/2020 included all 17 *U. pugettensis* collected in that survey of an approximately 2 km² area (Appendix 1).

Upogebia macginitieorum **Williams, 1986**

(Figure 4)

Material examined and records – Appendix 1.

Description – Rostrum smoothly rounded ventrally, lacking ventral teeth. Postocular spine absent (Figure 4A). Pereopod 2 merus lacking proximal-ventral spine (Figure 4B). Ventral spines on coxae absent. Male chelipeds (Figure 4C) more robust than female chelipeds (Figure 4D), similar overall, with minor row of tubercles extending the length of the medial dactyl face. Powerful tooth (red points) at the base of the dactyl. Dactyl closing over a broad tooth on the thumb that is separated proximally from the main propodus by deep sinus (Figure 4B, F). Dorsal anterior propodus without teeth or spines (Figure 4A).

Systematics – Summarized in Williams (1986).

Distribution – Santa Catalina Island, Los Angeles Harbor, Anaheim Bay, California to Tortugas Bay, Baja California Sur, Mexico (Williams 1986; Campos and Campos 1989; Campos et al. 2009).

Remarks – The vertical distribution of *U. macginitieorum* extends from low intertidal mudflats to high intertidal *Salicornia* marshes (Campos et al.
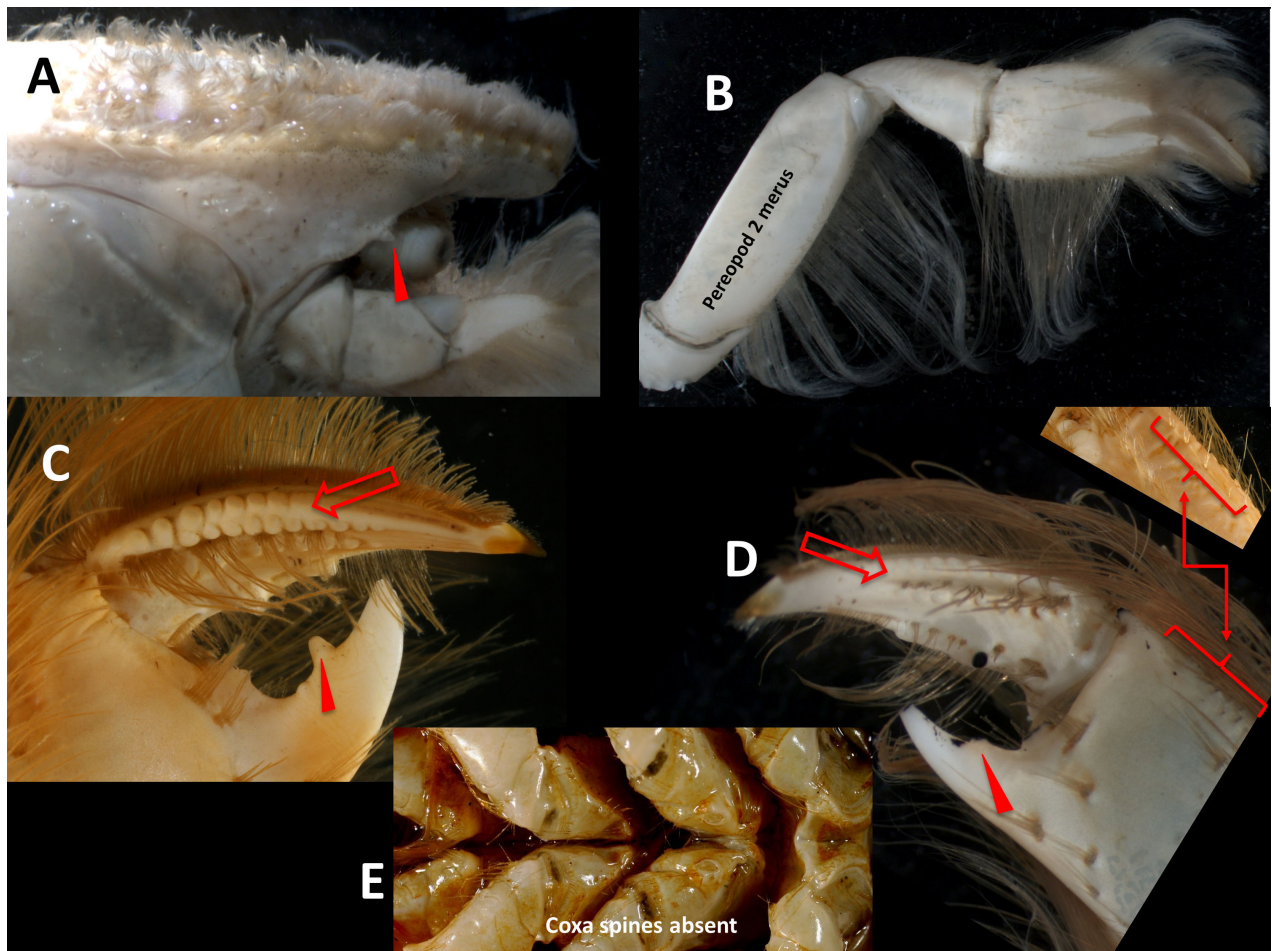
Figure 5. *Upogebia pugettensis:* A. Smooth verntral rostrum and lateral rostrum with post ocular spine (point), B. Pereopod 2 merus lacking spines, C. Male medial dactyl with rows of tubercles (arrow) and large tooth on propodus thumb (point), D. Female medial dactyl with rows of tubercles (arrow) and large tooth on propodus thumb broken off (point), E. Ventral pereopods 2–4 lacking coxa spines. (HMSC collections from Yaquina Bay). Photomicrographs by R. Breitenstein.

2009; J. Chapman *personal observations*), cord grass stands adjacent to marsh channels (R. Appy *personal observations*) and clay banks (Campos et al. 2009). *Orthione griffenis* recovered from San Diego Bay and Los Angeles Harbor populations. *U. macginitieorum* not found in 2/15/2020 searches of lower and upper Newport Bay, California. *Upogebia macginitieorum* female to male ratio (herein) roughly 2:1, consistent with hermaphroditism. Agonistic behaviors minor and burrow cohabitation occurs.

Upogebia pugettensis (Dana, 1852)

(Figure 5)

Material examined and records – Appendix 1.

Description – Small ocular spine (Figure 5A). Pereopod 2 merus without spines (Figure 5B). Chela more robust in males (Figure 5C) than females (Figure 5D) but similar overall, with strong tooth on dorsal medial thumb (Figure 5C, red point) and smaller tooth (Figure 5D, red point) on medial ventral dactyl that does not meet with the closed dactyl (Figure 5C, D). Ventral coxae of pereopods 2 and 3 lacking spines (Figure 5E).

Systematics – Summarized in Williams (1986).

Distribution – Previously, Prince William Sound, Alaska to Morro Bay, California (Williams 1986). All known populations between Ketchikan, Alaska and Elkhorn Slough, California are of uncertain status, collapsed or extinct.

Remarks – Review of *U. pugettensis* in San Francisco Bay from the 19th century to 2020 and our 2020 field survey (Appendix 2) resulted in 6 major findings:

1) *Orthione griffenis* infestations (and probable effective castration) among *U. pugettensis* co-occurring with *U. major* (Bodega Harbor and Tomales Bay) (Appendices 1 and 2) were 9.8 times more frequent than among *U. major*.

2) *Upogebia pugettensis* abundances varied dramatically over the species range in the last century preceding and following the introduction of *O. griffenis* in the 1980s (see also Dumbauld et al. 2011; Chapman et al. 2012; Chapman and Carter 2014).

3) Nearly all subtidal records of *U. pugettensis* are from San Francisco Bay.

4) Subtidal *U. pugettensis* were common or abundant in San Francisco Bay before the 1900s, absent in 1912–1913, common or abundant by the late 1980s and effectively replaced or displaced by *U. major* before 2008.

5) Intertidal *U. pugettensis* in San Francisco Bay were abundant before the 1900s, at least present in 1913, at least common through the mid to late 1980s and vanishingly rare after 2006.

6) *Upogebia pugettensis* are ecologically extinct and possibly entirely extinct in San Francisco Bay (Chapman et al. 2012; Appendices 1 and 2).

The 1:1 *U. pugettensis* sex ratio (Asson et al. 2017, herein) is consistent with gonochorism, which may require greater densities for reproduction and establishing new populations than are required for the possibly hermaphroditic *U. major*. Extreme agonistic behaviors among mature *U. pugettensis* require separation to limit dismembering (*personal observations*). The greater aggression of *U. pugettensis* and their maintenance of solitary burrows are consistent with high territory value and territoriality. All known intertidal *U. major* populations in all estuaries of the San Francisco Bay area occur where *U. pugettensis* previously occurred.

Shallow water Upogebia *from San Diego Bay, California to Alaska*

Exclusion of *U. affinis* from popular guides to East Pacific decapods (i.e., Kuris et al. 2007; Jensen 2014) was logical but, without explanation of the omission, left *U. macginitieorum* and *U. pugettensis* as the default *Upogebia* species north of Mexico. We include *U. affinis* in our key to prevent its confusion with *U. major* by non-specialists, including us initially. *Upogebia major* is distinguished from both confirmed nearshore East Pacific *Upogebia*

species occurring north of Mexico (*U. pugettensis* and *U. macginitieorum*) by the combination of smooth, toothless inner face of the cheliped thumb and the proximal medial ventral pereopod 2 merus spine.

1. Pereopod 2 merus with proximal medial-ventral spine (Figures 2A, D, 3E) and ventral spines on coxae of pereopods 2 and 3 (Figures 2A, C, 3B)......2
–. Proximal medial-ventral spine of pereopod 2 merus absent (Figures 4B, 5B) and lacking ventral coxa spines (Figure 5E)...3
2. Rostrum ventrally toothed (Figure 2B), cheliped thumb bearing fine teeth (Figure 2E and F, brackets) and dactyl with large ventral tooth (Figure 2E, F, points) .... *U. affinis* (NW Atlantic only. Reports of this species in the northeast Pacific are in error).
–. Rostrum ventrally smooth (Figure 3A), propodus thumb of both sexes smoothly pointed, without teeth (Figure 3C, D, red points), medial male dactyl flattened, with three oblique ridges (Figure 3C, arrows), female medial dactyl with two fine longitudinal tubercle rows (Figure 3D, arrows)...*U. major*
3. Postocular spine tiny or absent (Figure 4A), male and female dactyl with blunt medial-ventral tooth on dactyl (Figure 4C, D), dorsal propodus smooth (Figure 4C, D) ....*U. macginitieorum*
–. Prominent postocular spine (Figure 5A), prominent tooth on propodus thumb (Figure 5C, D, arrows), dorsal propodus finely toothed (Figure 5D). .... *U. pugettensis*

Northeastern Pacific *Upogebia* species occurring south of California that lack a proximal spine on the pereopod 2 merus: *U. burkenroadi* Williams, 1986, *U. lepta* Williams, 1986, *U. maccraryae* Williams, 1986, *U. onychion* Williams, 1986, *U. tenuipollex* Williams, 1986, and *U. veleronis* Williams, 1986. Northeastern Pacific *Upogebia* occurring south of California that bear a proximal spine on the pereopod 2 merus: *U. acanthops* Williams, 1986, *U. aestuari* Williams, 1993, *U. dawsoni* Williams, 1986, *U. galapagensis* Williams, 1986, *U. jonesi* Williams, 1986, *U. longipollex* Streets, 1871 and *U. schmitti* Williams, 1986.

Discussion

The combined *O. griffenis* and *U. major* invasion threat is greater than their independent sums and places them among the most consequential marine invasions that have occurred in the East Pacific. *Orthione griffenis* effectively place its coevolved host, *U. major*, at competitive advantage over every native *Upogebia* species where they both invade. *Upogebia pugettensis* within the *U. major* range occur at lower densities than *U. major* and carry approximately 10 fold or greater *O. griffenis* infestation intensities. As an alternative host, *U. major* assures persistence of *O. griffenis* even where native *Upogebia* extinctions occur. *Upogebia major,* occurring in subtidal

and intertidal habits (Figure 1, Appendix 2) overlap the almost exclusively intertidal *U. pugettensis* and thus are adapted to all known *U. pugettensis* habitats within its present range. *Orthione griffenis* and *U. major* reveal, once again, the long-term values of controlling invasion vectors (vector management, Williams et al. 2013; Ruiz et al. 2015) and of limiting ongoing invasion impacts (Pyšek et al. 2020).

Vector management can most effectively prevent introductions "by managing the many vectors that deliver them, rather than by focusing efforts on the management of individual species or even individual vectors" (Williams et al. 2013). Vector management requires species by species knowledge to identify likely vectors and information on prevention effectiveness. The second defense requires information on invasion risks and possible responses based on estimated present and future ranges, impacts and mechanisms controlling invasions underway.

Vector effectiveness assessed from invasion timing

Upogebia major and *O. griffenis* could have established in San Francisco Bay together from unsanctioned live seafood releases (Cohen and Carlton 1997; Chapman et al. 2003) or independently as larvae and pre-settlement decapodids, respectively, that arrived in ballast water traffic. Chapman et al. (2012) were unaware of *U. major* in North America when they reported the *O. griffenis* invasion. They inferred that *O. griffenis* directly caused the collapse of San Francisco Bay *U. pugettensis* that were abundant up to the late 1980s (Schemel et al. 1988, 1990). Information on whether *U. major* can re-burrow and the coincidence of *O. griffenis* and *U. major* invasion dates will be critical for determining the timing of these invasions and their likely seafood or ballast water introduction vectors.

Upogebia major infested with *O. griffenis* could have been introduced to San Francisco Bay together as live seafood or bait. The Chinese mitten crab, *Eriocheir sinensis* Edwards, 1853, and the green crab, *Carcinus maenas* (Linnaeus, 1758), were introduced initially into San Francisco Bay as unsanctioned releases of, respectively, seafood (Cohen et al. 1995) and bait (Cohen and Carlton 1997). *Upogebia major* are a popular Asian seafood (Hooper 2006; Inoue et al. 2002; Inoue et al. 2008). *Upogebia pugettensis* were a popular bait species (Chapman and Carter 2014) and live seafood species are commonly purchased in North America for consumption but released later as bait (Chapman and Miller 1999; Chapman et al. 2003). The probabilities of both seafood or bait vectors depend on whether *U. major* are competent to reburrow. *Upogebia* cannot survive outside of their burrows where they are vulnerable to predation by fish (Dumbauld et al. 2008) and birds (Figure S2C; Stenzel et al. 1976). Released mature *Upogebia* can thus survive only by quickly re-burrowing. Burrowing competence of *U. major* however, is unknown. Reproductive size *U. pugettensis* cannot re-burrow (Thompson 1972; Jackson et al. 2011; *personal observations*) while other *Upogebia* species can (Pascal et al. 2019).

A likely alternative transoceanic vector of *U. major* and *O. griffenis* would be as larvae entrained in transoceanic ballast water traffic. *U. major* and *O. griffenis* larvae would not likely be transported in the same seasons or years. *Upogebia major* produce larvae, in late winter that settle by late spring (Konishi 1989). *Orthione griffenis* produce larvae through summer that settle in fall (J. Chapman *personal observation*). The first in-hand *O. griffenis* place them in North America by the early to mid 1980s (Chapman et al. 2012). The first in-hand *U. major* was a reproductive size, 30.5 mm CL, (2–5 year old) male from CDFW station 103 in South San Francisco Bay, collected in December 2009 (Figure 1, Table S1, Appendix 1) (that was initially misidentified as *U. pugettensis*). The next earliest in-hand *U. major* were the two 6/10/2010 (23.4 mm CL and 33.5 mm CL) no less than 2 year old reproductive size *Essayons* males. Depending on their ages, these early specimens place *U. major* in San Francisco Bay between 2004 and 2007, with widespread populations no later than 2008. A conservative "earliest in-hand estimate" of *U. major* presence from these specimens, based on their minimum likely 2+ year ages is at least by 2006. *Upogebia major* would thus have been overlooked for around 20 years if *O. griffenis* was a seafood or bait introduction among infested *U. major*. A 20 year discovery gap for these two invasion thus, would be remarkable if they came with seafood or bait but not if they came as larvae in ballast water. A later introduction of *U. major* via ballast water traffic however, would have occurred after ballast water restrictions were in place.

Ballast water treatment and seafood vector management efforts were minor before the 1990s. Greater ballast water or seafood management efforts may thus be warranted only if *U. major* established in the East Pacific in the early to mid-1980s with *O. griffenis* before management efforts were in place (Chapman et al. 2012). The State of California, effective Jan 2000, mandated the exchange of ballast water from ships traveling outside the US Exclusive Economic Zone and entering California ports to stem future biological invasions (Scianni et al. 2019). The California Marine Invasive Species Act of 2003 extended the Ballast Water Management Act of 1999 to prevent the discharge of nonindigenous species into the waters of the state (CDFW 2008, 2011; Scianni et al. 2019). San Francisco Bay nevertheless, received nearly 3 million m^3 of "treated" (exchanged in open ocean) and untreated ballast water from foreign countries between January 2000 and June 2002 (Choi et al. 2005). Surveys of commensal clams could narrow the 20-year knowledge gaps between when the *U. major* invasion began (in the 1980s or after 2004) and whether *U. major* are likely to have arrived when vector management efforts were in place.

Marine mollusk shell deposits can indicate mollusk population dynamics over time (i.e., Schopf 1978). The native clam, *Cryptomya californica* (Conrad, 1837) is commensal with *U. major* and *U. pugettensis*. Deposits of

C. californica in the overlapping *U. major* and *U. pugettensis* distributions (Figure 1) may indicate the abundances of these two shrimps through time, even where they were not collected. Analyses of *C. californica* shell remains could thus address the decades wide information gaps between when *O. griffenis* invaded and decimated *U. pugettensis* populations and when *U. major* established and became abundant. *Cryptomya californica* are abundant in the burrows of all mature native and introduced *Upogebia* species in California and north and are readily collected in conventional sampling devices. The distributions and size structures of live and deposited *C. californica* valves collected in past or new surveys can reveal the sizes, ages and distributions of their extinct or recently arriving shrimp hosts.

Cryptomya californica, for example, were absent from stations D41A–C "San Pablo Bay, near the mouth of Petaluma River-Center" (38.053, −122.4138) between 1996 and 2006 and present in all following years (IEP 2019) (Figure S4). *Upogebia major* were not collected from San Pablo Bay until June 2010. A year or more would have been required after *Upogebia* arrived for *C. californica* to settle and grow to large enough sizes to be collected and identified in the IEP survey. *Upogebia* therefore established at the IEP D41A-C station a year or more before *C. californica* could appear. The appearance of *C. californica* in 2007 is roughly consistent with the 2006 estimate from our 2009 in-hand *U. major* from South San Francisco Bay (Figure 1). The presence of *C. californica* also, again, place *U. major* as widely established and abundant in San Francisco Bay no later than 2007 or 2008 but no earlier than 2006.

The absence of *C. californica* at stations D41A–C between 1996 and 2006 (Figure S4) also place the decline or extinction of *U. pugettensis* in San Francisco Bay previous to 1996, when *O. griffenis* are likely to have been present for at least a decade, and before the first "in-hand evidence" of *U. major* in the bay at around 2006. Aging live and deposited *C. californica* shells at this and other San Francisco Bay area stations would provide another method for the invasion sequence analyses.

Assessing risk

Estimates of present and future impacts and knowledge of how these impacts occur or could be mitigated are needed for a second defense against established and expanding invasions. The impacts of this double invasion appear to be severe. All of our records of *U. major* in Drakes Estero, Bolinas Lagoon, San Francisco Bay and Elkhorn Slough mudflats are from where *U. pugettensis* were abundant but also no longer occur. *Orthione griffenis* infest a broad diversity of, and possibly all, *Upogebia* and *Austinogebia* species within its Asian range (Itani 2004; Chapman et al. 2012; Hong et al. 2015). *Orthione griffenis* have infested all *U. pugettensis* populations and most *U. macginitieorum* populations examined over its

3,000 km Alaska to Punta Banda, Baja California Sur, Mexico range (Campos et al. 2009; Chapman et al. 2012 and herein). The less vulnerable *U. major* are a refuge for *O. griffenis*, that assures its persistence even where extinctions of native *Upogebia* species occur. Conservation, a second level defense, will benefit from information on whether or when *Upogebia* populations within the present *O. griffenis* range will not be invaded by *U. major*.

The present 200 km range north and south of San Francisco Bay place the initial North American origins of *U. major* within San Francisco Bay. San Francisco Bay is surrounded by the greatest human populations in the region and is the only international shipping port among the presently invaded estuaries (Figure 1). Estuaries outside of San Francisco Bay receive little or no ballast water traffic and are likely to have been invaded by pelagic *U. major* larvae that dispersed from San Francisco Bay via coastal currents. The geography and order of *U. major* collection records indicate they are spreading away from San Francisco Bay (Figure 1). We did not find *Upogebia* in searches of the extreme north end of Tomales Bay or in Bolinas Lagoon in 2008 (Chapman et al. 2012) or in three searches of Elkhorn Slough between 2008 and 2014. We found *U. pugettensis* in Tomales Bay at a new, location in 9/16/2019 and 2/23/2020, that we did not search in 2008 and have not reexamined the 2008 Tomales Bay search location. Excluding Tomales Bay and Bolinas Lagoon, the sequence of *U. major* discoveries away from San Francisco Bay since ~ 2009 is therefore: Drakes Estero, 2014, Bodega Harbor, 2016 and Elkhorn Slough, 2020 (Figure 1). The increasing abundances of *U. major* in Bodega Harbor and the expanding collection records since 2016 indicate a building and expanding invasion.

The present 3,000 km East Pacific (Ensenada, Baja California Norte, Mexico) (Chapman et al. 2012) to Ketchikan, Alaska (herein) range of *O. griffenis* is likely to have established via larval dispersal in coastal currents. The 2,000 km Morro Bay, California to Haida Gwaii, British Columbia (BC) range of the invading green crab, *Carcinus maenas*, is also likely to have established by larval dispersal in coastal currents. These two invasions may thus be harbingers of an expanding *U. major* invasion by larval dispersal and consequent collapses of *U. pugettensis* based ecosystems as the invasion progresses.

Climate diversity within the Asian range of *U. major* and *O. griffenis* (southern Japan and central China to Vladivostok, Russia) (Sakai 2006; Sato et al. 2013; Hong et al. 2015; Golubinskaya et al. 2016) exceeds the Morro Bay to Prince William Sound climate range (McGowan et al. 1998; Chapman 2000) of *U. pugettensis*. *Orthione griffenis* have been in southern California for more than a decade (Chapman et al. 2012) and were established on Calvert Island, BC by 2017 (Whalen et al. 2020) and Ketchikan, Alaska by 2018 (herein). The *C. maenas* reproductive season and life history (Yamada et al. 2017) are similar to those of *Upogebia*

species (Dumbauld et al. 1996). *Carcinus maenas* was initially introduced to San Francisco Bay in the 1980s (Cohen et al. 1995), reached Morro Bay before 2010 (Hall 2010), the Salish Sea by 2016 (Yamada et al. 2017) and the Haida Gwaii Islands by 2020 (Strait of Georgia Data Center 2020). Without intervention, the range of *U. major* could equal those of *O. griffenis* and *C. maenas* within the next 30 years.

Ecosystem shifts

Vectors were necessary but were unlikely to have been the only mechanisms that determined the *U. major* and *O. griffenis* invasions. Both species arrived decades or a century after their likely and unregulated ballast traffic and/or the seafood trade dispersal vectors were in place. Both invasions are consistent with increasing vulnerabilities of northeastern Pacific nearshore ecosystems since the 19th century. *Orthione griffenis* are most likely to have established initially in an international port, such as San Francisco Bay or in the Salish Sea, years before its 1988 discovery in Willapa Bay, Washington. Willapa Bay receives little or no international ballast water traffic (Chapman et al. 2012). *Orthione griffenis* prevalence increased exponentially in Willapa Bay after 1997 (Dumbauld et al. 2011), a decade long invasion lag (Crooks 2005) after they were present. The 1998 and later population explosion of *O. griffenis* in Willapa Bay coincided with northeast Pacific ocean warming events after 1998 (Cloern et al. 2007; Cloern and Jassby 2012). The European green crab, *Carcinus maenas*, similarly established in Oregon and Washington estuaries by 1997 (Behrens-Yamada et al. 2005) and thrived in inlets of the west coast of British Columbia since 1998 (Yamada et al. 2017). The major but irregular expansions of *C. maenas* coincided with ocean warming events (1998, 2005–2006, 2010, 2014–2017) (Behrens-Yamada et al. 2005; Yamada et al. 2017; Schooler et al. 2020) and their expansions are consistent with 20th and 21st century disturbances in San Francisco Bay and northeastern Pacific estuaries.

Subtidal *U. pugettensis* were vanishingly rare or absent in San Francisco Bay at the time of the 1912–13 *Albatross* survey (Schmitt 1921, Appendix 2), abundant or common before 1878 (Lockington 1878) and abundant or common again by the 1970s (herein). The low abundance or absence of subtidal *U. pugettensis* in 1912 coincided with massive alterations of the San Francisco Bay sediments due to hydraulic gold mining of the previous century in the Sierra Nevada that was outlawed in California in 1884 because the derived sediments were blocking navigation channels of the Sacramento-San Joaquin Rivers (Hedgepeth 1979). The greatest quantities of the eroding mine tailings migrating through San Francisco Bay in the early 1900s coincided with the *Albatross* survey (Hedgepeth 1979). Sediment disturbances of the early 1900s were thus likely to have affected sediment dependent benthic species.

Inverse, sediment dependent interactions of burrowing shrimp and commercially valuable bivalves are well documented (Dumbauld et al. 1996; Pillay et al. 2007; Takeuchi et al. 2013, 2015; Hong et al. 2015). The 1912–13 *Albatross* survey was initiated in response to declining intertidal bivalves (oysters) (Sumner et al. 1914; Nichols 1973) that are widely attributed to manifold human mediated alterations of the San Francisco Bay estuary (Nichols 1973; Cloern and Jassby 2012). Although direct connections between sediment disturbances and declines of oysters and subtidal burrowing shrimp in San Francisco Bay in the early 20th century were not resolved, later 20th century sediment disturbances are nevertheless associated with burrowing shrimp abundances and oyster declines.

Pesticide applications to Oregon and Washington estuary mudflats began in the 1950s to manage increased populations of *Neotrypaea californiensis* and *U. pugettensis* that were incidentally burying beds of the introduced oyster, *Crassostrea gigas* (Thunberg, 1795) (Dumbauld et al. 1996, 2008). The affected oyster beds had been successfully cultured for the previous 100 years (Dumbauld et al. 1996, 2008) on tide flats where oysters had not previously occurred. Those introduced oysters are likely to have altered sediment surface waterflow underlying sediment geochemistry and sediment microflora. Thus, presently unexplained, *U. major* and *O. griffenis* invasions followed anthropogenically influenced alterations of animal/sediment relationships. Resolution of the specific mechanisms for these interactions would be useful for oyster aquaculture production and for burrowing shrimp management and conservation.

Declines of bivalve biomass and record increases of crangonid shrimp, juvenile Dungeness crab and English sole abundances in San Francisco Bay coincided with abrupt inter-annual and decadal changes in phytoplankton abundances and coastal ocean warming after 1998 (Cloern et al. 2007; Cloern and Jassby 2012) and with the *O. griffenis* explosion in Willapa Bay (Dumbauld et al. 2011). In contrast to the declining native marine decapod species, the introduced catadromous mitten crab, *Eriocheir sinensis*, (Cohen and Carlton 1989) reached peak abundances in San Francisco Bay in 1998 and declined to near or absolute extinction by 2010 as native decapod populations recovered (Hieb 2011). Except possibly for *U. pugettensis* (infested by *O. griffenis* since the late 1980s), subtidal decapod species that have ocean or estuarine dependent larvae, increased in San Francisco Bay after 1998 while free living bivalves declined (i.e. Figure S4). Over the same period, *E. sinensis*, the only freshwater decapod in San Francisco Bay with estuary dependent larvae, declined. Widespread anthropogenically driven climate and ecosystem shifts that altered *U. pugettensis* population dynamics and the vulnerability of East Pacific estuaries to invasions have thus been ongoing since at least since the early 20th century.

The attraction of *Upogebia* juveniles to adult populations (Dumbauld et al. 2011; Candisani et al. 2001) and the sharply defined borders of *U. pugettensis*

beds in otherwise seemingly homogenous mudflats (J. Chapman *personal observations*) indicate that *Upogebia* are closely dependent on particular sediment compositions and associated microbial communities (Li et al. 2020). Although occasionally found within rocky beaches, all *Austinogebia* and *Upogebia* species live in permanent mud lined burrows (Kinoshita 2002; Sakai 2006) constructed of fine sediments cemented together with polysaccharide compounds produced in a hind gut gland, which is the largest organ in the *Upogebia* body (Thompson 1972). The burrow lining appears to be a critical food source for *Upogebia* (Kinoshita et al. 2008; Pascal et al. 2019; Li et al. 2020).

The restriction of *U. pugettensis* within the present range of *U. major* to mudflats where they are surrounded by *U. major* (Bodega Harbor, Tomales Bay and San Francisco Bay) is consistent with overlapping sediment preferences and with high potentials for interspecific competition. Animal-sediment relationships in general and the burrowing shrimp-sediment interactions in particular, are thus increasingly in need of resolution for managing and conserving Northeastern Pacific estuary ecosystems.

Changes that exacerbate *O. griffenis* interactions with *U. pugettensis* benefit *U. major* where they co-occur. Additions of species are themselves alterations of the ecosystems they invade. The magnitudes of ecosystem change with species additions can be difficult to measure but default assumptions of the absence of change are false. The effects of *U. major* in northeast Pacific ecosystems are unlikely to be the same as those created by native *Upogebia* species that they displace or replace. The doubled down *U. major* and *O. griffenis* invasion thus contributes to expanding alterations of northeast Pacific estuary ecosystems (i.e., McGowan et al. 1998; Cloern and Jassby 2012) by presently unmeasured magnitudes and they may facilitate new invasions (i.e., Eriksson and Hillebrand 2019; Blowes et al. 2019; Pyšek et al. 2020). *Upogebia major* and *O. griffenis* are also, respectively, the first confirmed introduced gebiid crustacean and first confirmed bopyrid isopod in the world, but are unlikely to be the only burrowing shrimp or bopyrid isopod introductions that have occurred.

Conservation

Intervention is possible and warranted to conserve *U. pugettensis* and its ecosystems from ecological and absolute extinction. The genetic diversity among the remaining *U. pugettensis* populations over their North American range could reveal their connectivity, their evolutionarily significant units (ESUs), their populations at greatest risk, and potentially differential resistance to *O. griffenis*. Genetic information on North American *U. major* and *O. griffenis* populations could also indicate their initial North American population sizes and whether they are derived from single or multiple Asian populations. Environmental and bulk DNA samples of whole-communities, coupled with suitably designed primers and DNA metabarcode sequencing

(Thomsen and Willerslev 2015; Whalen et al. 2020) could serve to detect remaining or newly invading adult and larval *Upogebia* species and *O. griffenis* among estuaries and fjords. These data could be derived from new surveys and from existing DNA analyses and samples produced in ongoing surveys such as the Marine Invasive Species Program and the California Marine Habitats and Estuaries Program (Scianni et al. 2019).

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Funding Declaration

Author Contributions

JWC, RAB, JL, RA, KAH and CNP conceived the research. JWC, JL, RAB, MFM, KAH, CNP, LEE and RA designed sample methods and collected data. JWC, JL, KAH, CNP and RAB analyzed and interpreted data. JWC, JL, MFM, RAB, KAH, CNP, LEE and RA reviewed and edited the final MS.

Additional information

The data generated and specimens on deposit generated during and/or analyzed during the current study are available from the corresponding authors or collection repositories.

Ethics and Permits

Ethics approval was not required for this work. None of the target species, including, native *Upogebia* species are yet listed as "special status species" or "species at risk". This project however, was undertaken to document the invasions of *U. major* and *O. griffenis* and find at risk native *Upogebia* species that remain or are no longer present in protected areas. The parks, reserves, and protected areas that we sampled are in place largely to protect marine resources that include native species and are managed by overlapping private, city, military, county, state and federal agency stakeholders. We sampled only where we were able to contact managers to ensure compliance with regulations with appropriate sampling permission. The process of obtaining these permissions required more than 3 months of FTE.

Oregon collections were under the National Marine Fisheries Service and Oregon Department of Fish and Wildlife Scientific Taking Permits 20267, 22209 and 23775.

California Department of Fish and Wildlife (CDFW) does not require Scientific Collection Permits of CDFW staff. CDFW General Use Permit: GM-193610002-20002-001, issued by Melanie Huetter and Steve May both of CDFW, was issued for collection in all California locations in February 2020. Additional required permits, including the permitting organizations and permit numbers were issued to JWC, JL and LEE.

CDFW Specific Use Permit ID: S-193610002-20009-001 issued by Lara Slatoff, CDFW Marine Protected Areas Management Project. This permit approved collection in Marine Protected Areas: Morro Bay Estuary, Morrow Bay State Marine Reserve (SMR), Morro Bay State Park (SMP), Morro Bay State Marine Recreational Management Area (MRMA), Elkhorn Slough National Estuarine Research Reserve (NERR), Elkhorn Slough State Marine Conservation Area (SMCA), Elkhorn Slough SMR, Redwood Shores SMP, Albany Mudflats SMP, Corte Madera Marsh SMP. We thank Kerstin Wasson, Elkhorn Slough NERR, Lexie Bell, Executive Director Morro Bay National Estuary Program, Mike Walgren, California State Parks and Terris Kasteen, CDFW, Redwood Shores Ecological Reserve for their guidances.

California Department of Parks and Recreation (CDPR) permit number 20-820-10 issued by Nita Barve, CDPR. This permit permitted collection in regions under CDPR jurisdiction: Morro Bay State Park, Morro Estuary Natural Reserve, China Camp State Park and China Camp NERR, Moss Landing State Beach, Salinas River state Beach. Thanks to Matt Ferner, Research Coordinator China Camp; Amy Palkovic, and Bree Hardcastle both at CDPR.

United States Department of Interior National Park Service (NPS) Scientific Research and Collecting Permit PORE-2020-SCI-0001, for collection in Point Reyes National Seashore, Drakes Estero, Marin. Issued by Ben Becker, Point Reyes National Seashore.

Kendall-Frost Mission Bay Marsh Reserve, San Diego, research application 44612, managed by Isabelle Kay, reserve manager Kendall-Frost Mission Bay Marsh Reserve.

Research and Monitoring Special use Permit SDB TJS 20201 for collection in Tijuana Slough National Wildlife Refuge (NWR), San Diego Bay NWR, and Tijuana River NERR. Managed by Brian Collins and Jeff Crooks managers for San Diego Bay and Tijuana NWR respectively.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Records and material examined.
Appendix 2. *Upogebia pugettensis* in San Francisco Bay 1878 to 2020.
Table S1. Species, localities, collection dates, latitudes and longitudes, specimens, depths, collectors, archiving institutions and catalogue numbers.
Figure S1. *Albatross* specimen (USNM 213285) of *Upogebia affinis* (from Williams 1986) (USNM 213285).
Figure S2. Photographic records of *Orthione griffenis*, *Upogebia pugettensis* and *Upogebia major*.
Figure S3. Photographic records of *Upogebia pugettensis*.
Figure S4. Natural log clam abundances at IEP Stations 41A–C in San Pablo Bay, 1996 to 2015.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Chapman_etal_SupplementaryMaterial.pdf
http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Chapman_etal_SupplementaryTables.xlsx