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Rapid Communication

Poleward range expansion of invasive bopyrid isopod, *Orthione griffenis* Markham, 2004, confirmed by establishment in Central British Columbia, Canada

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Abstract

Dispersal of parasites into novel host populations is often initiated by human activities at global scales, but largely determined by parasite and host life history traits at local scales. In summer 2017, we discovered the parasitic bopyrid isopod, *Orthione griffenis* Markham, 2004, in a population of mud shrimp, *Upogebia pugettensis* (Dana, 1852), in Central British Columbia, Canada. This parasite has infested most host populations along the Pacific coast of North America to the south. We estimated that 25% of susceptible hosts on Calvert Island were parasitized during summer 2018 and winter 2019. Steady infestation of mud shrimp on Calvert Island confirmed that the invasive bopyrid has successfully established itself in a novel host population 300 km further north than previously recorded, but with lower parasite prevalence than in the known invasive range, where heavy infestations have been implicated in host population declines. Prevalence rates increased with host size as previously documented, with a minimum infestation size of 10.6 mm carapace length. The parasite has a planktonic larval phase, suggesting that its spread along the coast is not limited to transport via boat traffic. The prognosis for the persistence of *Upogebia* in Canada and further north is unclear, but population declines further south in the presence of *O. griffenis* provide a troubling outlook. As biodiversity monitoring efforts continue in this region, tracking the spread of parasites like *O. griffenis* and their impacts on host populations will yield new insights into the traits that make invasive species successful and the ecosystem consequences of invasions in changing environments.

Key words: Bopyridae, Upogebiidae, invasive parasites, marine life histories

Introduction

As human populations have become increasingly connected through ship-based transportation, so too have marine communities (Sax et al. 2007; Carlton 2009). Species moved through human intervention often take on important roles in recipient communities if they are able to invade (invasibility criterion; e.g., Grainger et al. 2019), yet invasions and their impacts are often overlooked. Parasites make particularly interesting invaders because they tend to have specialized niches and complex life histories, they are often cryptic, and they can occupy novel hosts (Gehman et al. 2019). Furthermore, interactions with novel hosts can lead to unpredictable dynamics, including population collapse of the host, and, as a consequence, the invader (Boots and Sasaki 2002). Host population declines can occur rapidly, leading to uncertainty in the cause of declines even in well-studied areas, such as the recent declines of mud shrimp in the Eastern North Pacific (Dumbauld et al. 2011; Chapman et al. 2012).

Orthione griffenis Markham, 2004, is a bopyrid isopod that parasitizes and functionally castrates gebiid shrimp, an ecologically important group of soft sediment burrowers (Smith et al. 2008; Repetto and Griffen 2012; Asson et al. 2017). The parasite is native to the Western North Pacific (Williams and An 2009; Chapman et al. 2012; Hong et al. 2015), although it was described from samples collected in Oregon (Markham 2004). The first records of *O. griffensis* on the coast of North America are from Washington and Oregon in the late 1980s and California in 1992. In the non-native range, it primarily infests the mud shrimp *Upogebia pugettensis* (Dana, 1852), which ranges from Valdez, Alaska, USA, to Point Conception, California, USA (Wicksten 2012), although the parasite has been documented with other *Upogebia* species in Mexico (Williams and An 2009). Shrimp hosts become susceptible to infestation above 12–15 mm carapace length (Dumbauld et al. 2011). The first bopyrid to enter a gill chamber of the shrimp becomes the female, and and a subsequent arrival becomes the male (O'Brien and Van Wyk 1985; Baeza et al. 2018).

Importantly, both the host and parasite molt through several dispersive planktonic stages; the shrimp through a series of planktonic zoeal and megalopa stages (Hart 1937), and the isopod through a free-swimming epicaridium stage that then parasitizes planktonic calanoid copepods as intermediate hosts (microniscus stage), then a dispersive cryptoniscus stage that parasitizes the definite host (Williams and Boyko 2012; Baeza et al. 2018). Infestation results in nearly complete castration of both male and female shrimp hosts as a result of the energetic burden of the parasite (Dumbauld et al. 2011). Therefore, the dynamics of these two populations are dependent on the ability of hosts and parasites to survive and reproduce, disperse in ocean currents, and settle in appropriate habitat, which in turn is dependent on the level of infestation of the host by the parasite, and host population size. Importantly, little is known about host specificity of pelagic life stages, although *O. griffenis* likely has a wider breadth of intermediate than adult hosts given its wide distribution across two coasts and host-use patterns in other bopyrids (e.g., Owens and Rothlisberg 1995). Impacts in this host-parasite system could intensify as infested hosts compete for space and other resources while contributing little or no genetic material to future generations, potentially modifying selection landscapes in ways that may limit adaptive host responses.

Since its arrival to the Eastern North Pacific, *O. griffenis* has spread rapidly and has been implicated in the collapse of several host populations, although some uncertainty remains surrounding the cause of mud shrimp declines because they are also harvested for bait and controlled because of their economic impact on oyster aquaculture (Dumbauld et al. 2006, 2011; Chapman et al. 2012). The bopyrid has been reported as far north as Barkley Sound, British Columbia, Canada (Williams and An 2009), but the potential to continue its poleward spread into novel host populations has been unclear for several reasons related to life history of the parasite and its hosts, oceanography and dominant thermal environments of the region, and anthropogenic factors (e.g., shipping and aquaculture throughout the region).

Here, we document the northward range extension of *O. griffenis* and its establishment in a population of *U. pugettensis* in the central coast of British Columbia, Canada. We further document the establishment of this parasite in populations of *U. pugettensis* on eastern Vancouver Island and relate infestation prevalence to host size and sex. The discovery of this range extension was made possible by a biodiversity survey organized by the Hakai Institute and Smithsonian's Marine Global Earth Observatory (MarineGEO), highlighting the value of combining expert taxonomy with molecular techniques in intensive biodiversity surveys (e.g., Cohen et al. 2005; Ashton 2006). The goal of this paper is to estimate parasite prevalence of *O. griffenis* and provide insight into its northward range expansion along the Pacific coast of North America. We hypothesized that parasite prevalence would be lower on Calvert Island than on Vancouver Island because of the remote location of Calvert Island and the presumable youth of the infestation.

Materials and methods

Study Sites and Sampling

This study focuses on the area around the Hakai Institute Calvert Island Ecological Observatory in British Columbia, Canada (51.6544°N; 128.1309°W), and includes comparisons with intertidal shellfish aquaculture sites further south within Baynes Sound, East Vancouver Island, British Columbia (49.5278°N; 124.8498°W) (Figure 1).

From July to August 2017, the Hakai Institute and MarineGEO jointly conducted a three-week inventory of biodiversity (hereafter "BioBlitz") on Calvert Island, combining taxonomic expertise, photography, voucher collection, and molecular barcoding to catalogue invertebrate species diversity in nearshore marine habitats. Sampling during the Hakai-MarineGEO BioBlitz combined targeted sampling to maximize species diversity, with ecological survey methods to rapidly characterize communities across habitats. Samples from soft sediments during the BioBlitz were collected as part of an ongoing soft sediment biodiversity monitoring program (Cox et al.

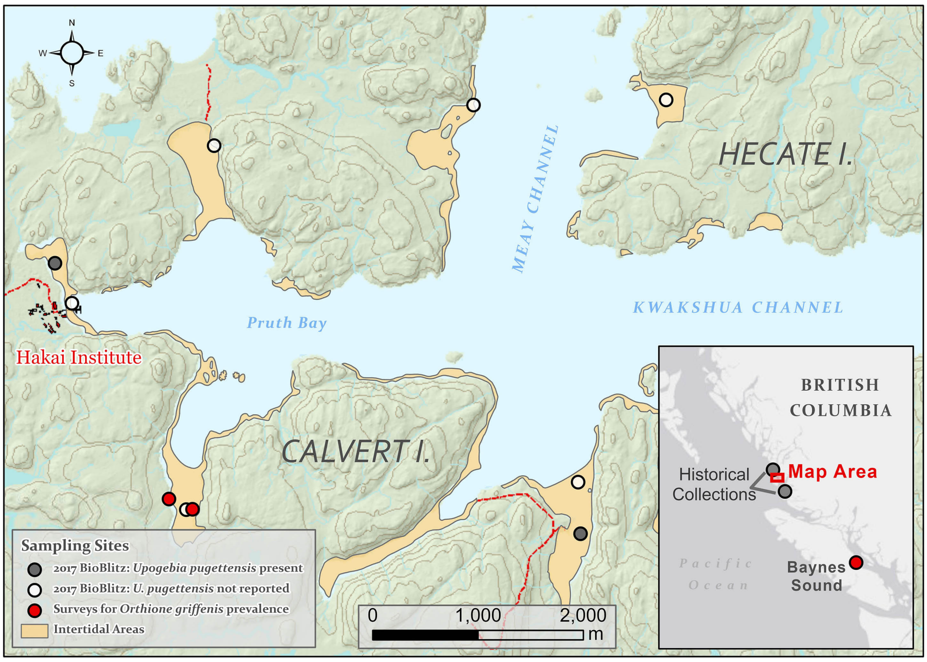

Figure 1. Map of study areas on Calvert Island and Vancouver Island (inset). Intertidal areas were identified using approximate tide heights from navigational charts.

2019). Surveys involved stratified random sampling of benthic infauna in 0.25 m^2 quadrats within high (3.0–2.2 m chart datum), middle (2.2–1.5 m), and low (1.5–0.8 m) intertidal zones. Fifteen community assessments occurred at each site, divided evenly among the three intertidal zones. Each community assessment involved surveying the epifaunal community present within a 0.5 × 0.5 m quadrat, and subsequently, excavating the quadrat to a depth of 0.25 m to quantify the infauna. Quadrat excavation was accomplished using a hand spade and 2 mm sieve. All *U. pugettensis* encountered were measured and visually assessed for the presence of *O. griffenis*. Two of six *U. pugettensis* collected during this survey in summer 2017 from two mudflats (Figure 1) each hosted a pair of *O. griffenis* (Figure 2). Morphological identification (Markham 2004; Hong et al. 2015) was confirmed by DNA barcoding (n = 3 *U. pugettensis*; n = 1 *O. griffenis* sequences; Supplementary material Table S1). Voucher specimens of both the host (UF 47784, 47786) and parasite (UF 47361, 47787) were accessioned at the Florida Museum of Natural History. These records provided the first observations of *O. griffenis* north of Vancouver Island.

Given our initial observation of *O. griffenis* on Calvert Island in 2017, additional sampling focused on the mud shrimp inhabiting Calvert Island was conducted in July–August 2018 and in January 2019 to estimate parasite prevalence and associate infestation status with host traits. The following four sampling events focused on mudflats located in Pruth Bay: July 29, 2018 at 51.6441°N; 128.1193°W, August 2 and 14, 2018 and January 19, 2019 at 51.6441°N; 128.1210°W. The southern arm of Pruth Bay is well protected with extensive intertidal soft sediment and eelgrass habitat at the mouth that tapers off towards the head of the bay. The sediment

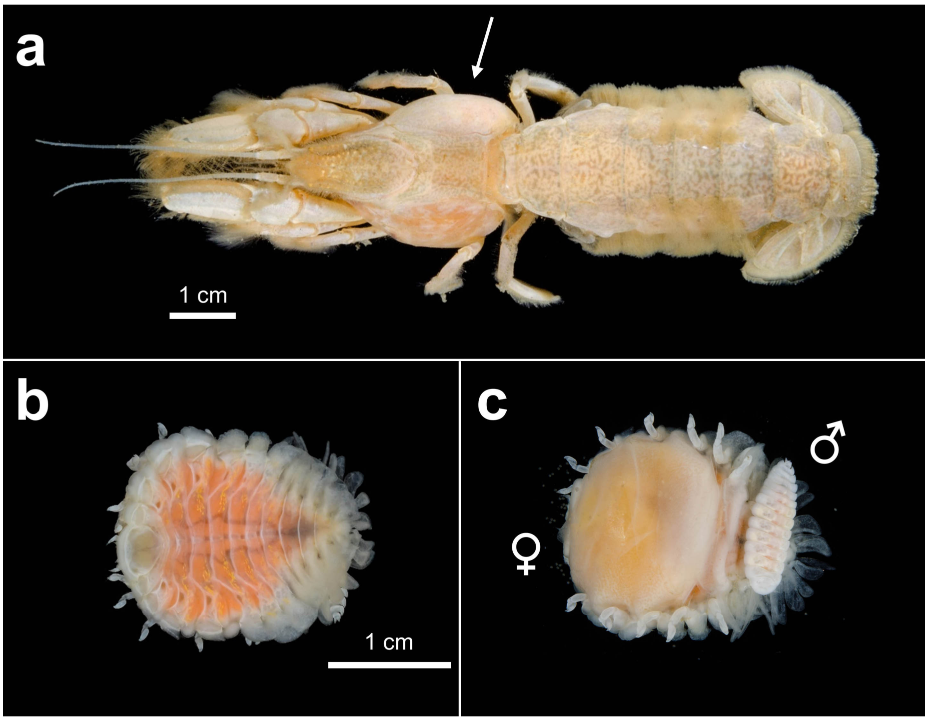

Figure 2. Photographs of (a) *Upogebia pugettensis* with (b, c) *Orthione griffenis* collected during the 2017 Hakai-MarineGEO BioBlitz. Note the swollen gill chamber on the right side of the host carapace (a; arrow) where the parasites reside. Panel (b) shows the dorsal view of an ovigerous female with male underneath, and (c) shows the ventral view of the same female with male attached to pleopods. Photo credits: Gustav Paulay, Amanda Bemis.

in the bay coarsens abruptly with tidal height from a composite of mud and silt in the center to gravel, cobble and boulder at the 2.5 m tideline. The four sampling events took place in the mid to upper intertidal zone (1.5 to 3.0 m chart datum) in both fine and coarse sediments where *U. pugettensis* appears to be most abundant in the Bay. During each sampling event, two to three 0.25 m^2 quadrats were haphazardly placed in areas with *U. pugettensis* burrows and excavated by shovel. During the first two sampling events, we only measured host total length, which we converted to carapace length (CL) using the conversion CL = 0.3 * total length (Dumbauld et al. 1996), and shrimp were visually assessed for *O. griffenis* infestation in the field. In the other two events, we brought shrimp to a laboratory where we measured host CL, determined host sex, and scored hosts for parasite presence and sex. Here, parasite presence and sex were assessed both visually and under a dissecting microscope. No additional *O. griffenis* females were detected by microscopy (n = 110 shrimp), indicating that visual assessment alone was accurate for estimation of prevalence. However, we found three additional parasites associated with female parasites through microscopic evaluation, indicating that males may have been overlooked in field assessments, which would lead to underestimation of parasite load. We therefore only provide estimates of parasite load from Calvert Island.

In Baynes Sound the prevalence of *O. griffenis* was assessed with opportunistic sampling of *U. pugettensis* in conjunction with ongoing monitoring of intertidal biodiversity responses to shellfish cultivation. Baynes Sound is British Columbia's premier shellfish growing region, with 50% of all shellfish produced in the province (British Columbia Ministry of Sustainable Resource Management 2002), and has been the focus of investigations into the ecological consequences of shellfish cultivation, with considerable attention to invasive species (Holden et al. 2018). In 2016, infaunal communities were surveyed in the middle intertidal zone (1.5–2.2 m chart datum) at six sites, including three intertidal shellfish aquaculture leases and three unmodified habitats. Surveys were conducted in a similar manner to Cox et al. (2017). Briefly, infauna were randomly sampled using 0.5 m × 0.5 m quadrats excavated to a depth of 0.25 m within an area stretching 40 m along the shore. When observed, *U. pugettensis* were measured for total length and visually assessed for the presence of *O. griffenis*.

Statistical analysis

We tested for an effect of parasite load (no parasite, female only, female + male) on CL of shrimp collected from Calvert Island using one-way ANOVA. We used generalized linear mixed effects models (GLMM) with a logit link function to estimate parasite prevalence and to test for effects of host body size on parasite presence while accounting for variation associated with different sampling events using random intercepts. We also provide empirical prevalence calculated from infested and uninfested hosts in each sampling event. Because we used different methods to measure hosts and parasites on Calvert Island and in Baynes Sound, we chose to estimate prevalence on Calvert Island alone in one model and then combine data from both locations in a second model to test differences based on location and the presence of aquaculture operations as fixed effects. Because *O. griffenis* infests larger, older hosts (Smith et al. 2008; Dumbauld et al. 2011), we present prevalence estimates for susceptible hosts that exceed the minimum infested size at each location. However, we included hosts of all sizes when analyzing the relationship between host size and parasite presence on Calvert Island. To evaluate the importance of host body size as an explanatory variable we used a chi-square test with one degree of freedom to compare models with and without this variable. All mixed models were fit in R 3.5.3 (R Core Team 2019) using the package "lme4" (Bates et al. 2015).

Results and discussion

Sampling of *U. pugettensis* on Calvert Island revealed sustained and high prevalence of *O. griffenis* within the host population across multiple time points (Table 1). Our estimates of prevalence on Calvert ranged from 20–36% on a given sampling date, averaging 24.8% (95% confidence intervals, 13.9–41.3%; binomial GLMM). Prevalence rates on Calvert Island were

Table 1. Summary of sampling events for bopyrid isopod *Orthione griffenis* on mud shrimp *Upogebia pugettensis*. The number and average size of host shrimp are provided for all hosts sampled and susceptible hosts (defined as hosts larger than the minimum infested size). We present the total number of infested hosts in each sampling event and the empirical prevalence as the percent of susceptible hosts containing at least one parasite.

Location	Date	Site Usage	Host Sample Size all (susceptible)	Mean Host Carapace Length (mm) all (susceptible)	Empirical Bopyrid Prevalence no. infested (%)
Baynes Sound	2016-07-18	No aquaculture	5 (2)	7.74 (11.9)	2 (100)
Baynes Sound	2016-07-19	Shellfish farm	10 (8)	9.75 (11.3)	3 (38)
Baynes Sound	2016-07-20	Shellfish farm	36 (6)	7.55 (15.8)	2 (33)
Baynes Sound	2016-07-21	No aquaculture	1 (0)	6 (N/A)	0 (N/A)
Baynes Sound	2016-07-22	No aquaculture	56 (22)	7.77 (11.6)	1 (5)
Baynes Sound	2018-07-17	Shellfish farm	7 (5)	12.7 (15.2)	4 (80)
Calvert Island	2018-07-29	No aquaculture	25 (22)	14.68 (15.6)	11 (50)
Calvert Island	2018-08-02	No aquaculture	95 (81)	13.88 (14.7)	19 (23)
Calvert Island	2018-08-14	No aquaculture	47 (45)	17.7 (18.1)	10 (22)
Calvert Island	2019-01-19	No aquaculture	63 (48)	14.4 (16.6)	8 (17)

comparable to those in both aquaculture (binomial GLMM, P = 0.45) and non-aquaculture (P = 0.12) settings in Baynes Sound (mean prevalence = 42%; range = 9–91%), counter to our hypothesis and suggesting that the parasite population on Calvert Island is well-established.

As with other studies investigating this host-parasite relationship (e.g., Smith et al. 2008; Dumbauld et al. 2011; Chapman and Carter 2014; Asson et al. 2017), we found a strong relationship between host size and the probability of infestation on Calvert Island ($\chi^2_1 = 22.4$, $P < 0.001$; Figure 3). The smallest infested shrimp was 10.6 mm CL. Above this threshold, prevalence increased with host size consistently across sampling efforts (Figure S1). However, average prevalence varied over time on Calvert Island (GLMM random intercept SD = 0.7), likely due to a combination of variation in prevalence within the host population, differences in site characteristics, seasonal patterns of host demography and parasite recruitment, and error associated with our small-scale and opportunistic sampling. As with the relationship between host size and parasite presence, hosts with two parasites (female and male) tended to be larger than hosts with a single parasite. While this result was non-significant (Tukey posthoc test, P = 0.23; Figure 3b), it reflects the life cycle of the parasite requiring the sequential infestation of female and male parasites in the same host (Baeza et al. 2018). We found higher parasite prevalence among female (24%) than male (14%) hosts; however, these results were not significant (P = 0.23).

This study documents the establishment of *O. griffenis* on Calvert Island, 300 km north of known range in the literature. Prevalence on Calvert Island is comparable to sites further south on Vancouver Island, but low compared to many areas in the U.S. where high infestation rates have contributed to host population decline (Williams and An 2009; Dumbauld et al. 2011; Chapman et al. 2012). We found hosts infested down to 10.6 mm CL, smaller than previous studies (~ 12 mm) (Smith et al. 2008; Dumbauld et al. 2011; Chapman et al. 2012; Asson et al. 2017) and suggesting an unresolved aspect of this host-parasite system.

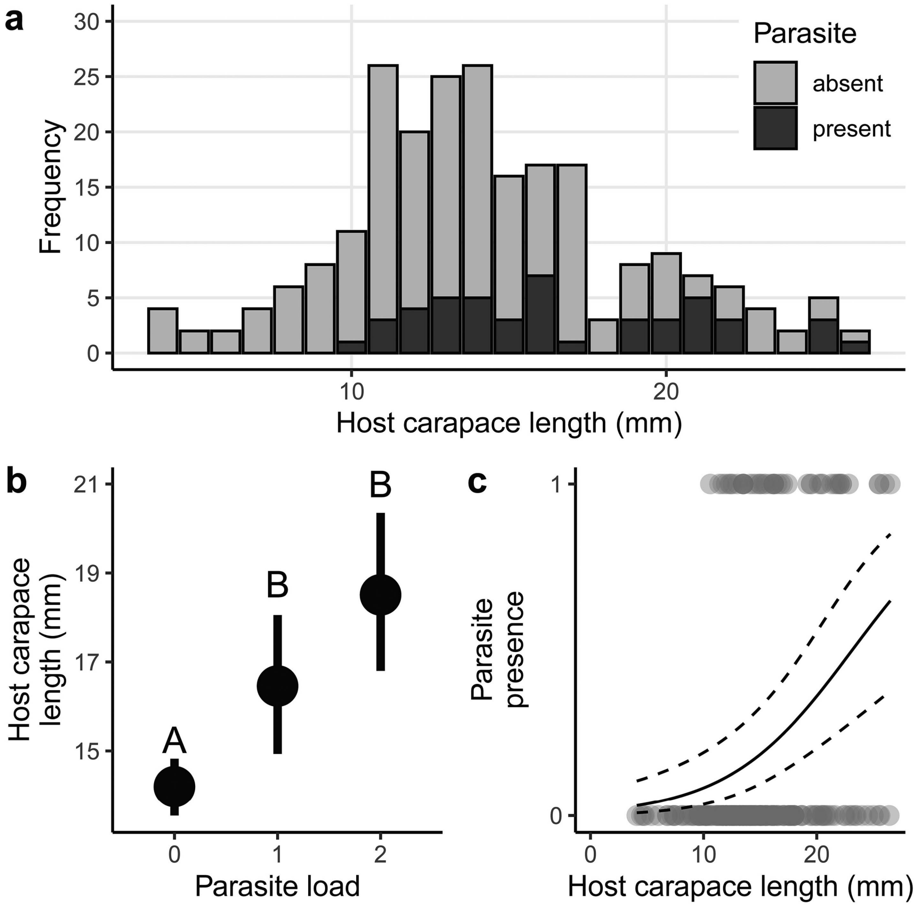

Figure 3. Host size and parasite presence relationships across all sampling events on Calvert Island. a) Size distribution of *Upogebia pugettensis* with and without *Orthione griffenis*. b) Observed host size as a function of parasite load (0 = no parasite, 1 = female parasite only, 2 = female and male parasite). Points and vertical lines show mean ± 95% confidence intervals, and letters show groups based on Tukey posthoc tests. c) Prevalence of *O. griffenis* modeled as a logistic function of host body size. The circles represent presence (0 = no, 1= yes) of at least one parasite in each sampled host. Solid and dashed lines show the mean prediction ± 95% confidence intervals that include variation associated with the different sampling events.

Calvert Island likely represents a relatively recently established population of *O. griffenis* given the trajectory of its spread from Oregon and Washington (Chapman et al. 2012), but we do not know when this bopyrid first arrived north of Vancouver Island. The most recent basis for comparison comes from 50 parasite-free *U. pugettensis* collected by Edward Bousfield and Lennox Marhue near Calvert Island in 1964 and 1966 (Canadian Museum of Nature collections; CMNC 2009-0006 from Hunter Island, CMNC 2004-4301 from Takush Harbor).

We suspect that the northward extension of *O. griffenis* is a result of natural spread through larval dispersal, including spread on copepod intermediate hosts, across generations, consistent with the general northerly flow of the Alaska Current in British Columbia (Sunday et al. 2014). Given these prevailing currents, it is highly likely that this invasion will continue to spread northward into the Gulf of Alaska, and could cover the entire range of *U. pugettensis*.

Many questions remain about the basic biology and ecology of the *O. griffenis* invasion, including the biotic and abiotic factors that influence the spread of the parasite and determine its impacts on mud shrimp populations. We do not know, for instance, the degree to which host populations are connected across space (but see Dumbauld and Bosley 2018), which would have implications for parasite-host coexistence and the scale of host persistence in the face of heavy infestation. We also do not know how host-parasite interaction is influenced by the environment, limiting our ability to assess and predict how the parasite affects host population dynamics. *Orthione griffenis* requires two hosts to complete its life cycle: its adult form appears specific to a few hosts (two reported genera; Williams and An 2009), but the breadth of intermediate copepod hosts is unknown and further complicated by the presence of multiple invasive calanoid copepods in the region that could serve as intermediate hosts (e.g., Cordell and Morrison 1996; Cordell et al. 2008).

Given the fossorial life habitat of the mud shrimp, the inability of adults to burrow once brought to the surface, the intimate association of the parasite within the host carapace, and pelagic life phases of both partners, studying this interaction in the lab and field is difficult. However, organisms like *O. griffenis* and its intermediate hosts could be good candidates for targeted monitoring by combining environmental DNA sampling with quantitative PCR, which would take advantage of the pelagic life phase of *O. griffenis* and allow scientists and managers to detect the presence and spread of the species using water samples or plankton tows collected in nearshore waters. Combining rigorous observations from intensive biodiversity surveys with molecular barcoding and environmental DNA monitoring will facilitate rapid tracking of population and community dynamics at broad geographic scales, potentially enabling more nimble decision-making surrounding risk assessment and management of non-native species.

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Data accessibility

All DNA sequence data has been deposited at NCBI (Accession numbers: *U. pugettensis*, MN701463, MN701464, MN701466; *O. griffenis*, MN701465)

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Ethics and Permits

This work was conducted under BC Parks Permit 107190, and under agreements with both the Wuikinuxv Nation and Heiltsuk First Nation. The authors have complied with all policies concerning collection and handling of invertebrate animals in Canada, and no ethics approval was required. Collections were permitted pursuant to Canada Department of Fisheries & Oceans license XR 317 2017.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Voucher information for host *Upogebia pugettensis* (Dana, 1852) and parasite *Orthione griffenis*, Markham, 2004, collections from the 2017 Hakai-MarineGEO BioBlitz.

Figure S1. Relationship between host (*Upogebia pugettensis*) body size and parasite (*Orthione griffenis*) prevalence on Calvert Island across sampling dates.

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