

Research Article

Habitat and co-occurrence of native and invasive crayfish in the Pacific Northwest, USA

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Abstract

Biological invasions can have dramatic effects on freshwater ecosystems and introduced crayfish can be particularly impacting. We document crayfish distribution in three large hydrographic basins (Rogue, Umpqua, Willamette/Columbia) in the Pacific Northwest USA. We used occupancy analyses to investigate habitat relationships and evidence for displacement of native *Pacifastacus leniusculus* (Dana, 1852) by two invaders. We found invasive *Procambarus clarkii* (Girard, 1852), in 51 of 283 sites and in all three hydrographic basins. We found invasive *Orconectes n. neglectus* (Faxon, 1885) at 68% of sites in the Rogue basin and provide first documentation of their broad distribution in the Umpqua basin. We found *P. clarkii* in both lentic and lotic habitats, and it was positively associated with manmade sites. *P. leniusculus* was positively associated with lotic habitats and negatively related to manmade sites. In the Rogue and Umpqua basins, *O. n. neglectus* and *P. leniusculus* were similar in their habitat associations. We did not find a negative relationship in site occupancy between *O. n. neglectus* and *P. leniusculus*. Our data suggest that *P. clarkii* has potential to locally displace *P. leniusculus*. There is still time for preventative measures to limit the spread of the invasive crayfish in this region.

Key words: crayfish; invasion; occupancy; *Orconectes*; *Procambarus*; *Pacifastacus*

Introduction

Biological invasions and habitat loss constitute the foremost threats to native species in freshwater ecosystems (Richter et al. 1997; Taylor et al. 2007). Invasive crayfish are expanding and can affect fundamental aspects of aquatic systems like water quality, physical habitat attributes, and trophic structure (Lodge et al. 2000; Creed and Reed 2005; Geiger et al. 2005). In Europe, invasive crayfish are thought to impact native crayfish via competition, predation, and disease introduction (Gherardi 2006, 2007). The USA is the center of crayfish diversity worldwide (Lodge et al. 2012). Invasive crayfish have received attention in the upper Midwestern USA (e.g., Olden et al. 2011), but effects on native crayfish in most other regions remain poorly known (Taylor et al. 2007; Lodge et al. 2012).

The Pacific Northwestern USA is rich in aquatic systems and hosts unique lineages of native fauna that may be at risk from invasive species (Smith et al. 1998; Hulse et al. 2002,

Sanderson et al. 2009). Invasive crayfish are known to be present in the Northwest, but their introduction history, distribution, and ecological effects are poorly understood (Larson and Olden 2011). For example, red swamp crayfish (*Procambarus clarkii*) (Girard, 1852) have been reported from a few sites in Oregon and western Washington (Pearl et al. 2005; Larson and Olden 2011). Ringed crayfish (*Orconectes n. neglectus*) (Faxon, 1885) are known from the Rogue River basin in southwestern Oregon (Fitzpatrick 1966, Bouchard 1977). Invasive *Orconectes virilis* (Hagen, 1870) and *Orconectes rusticus* (Girard, 1852) have recently been confirmed at scattered sites in Washington and Oregon, mostly east of the Cascade Range (Larson and Olden 2011). Given the effects of invasive crayfish elsewhere, it is important to improve our understanding of their ranges and effects in the northwest.

Our study had two main objectives: 1) to describe distributions and habitat associations of crayfish in the region; and 2) to assess evidence of native crayfish displacement by invasive crayfish.

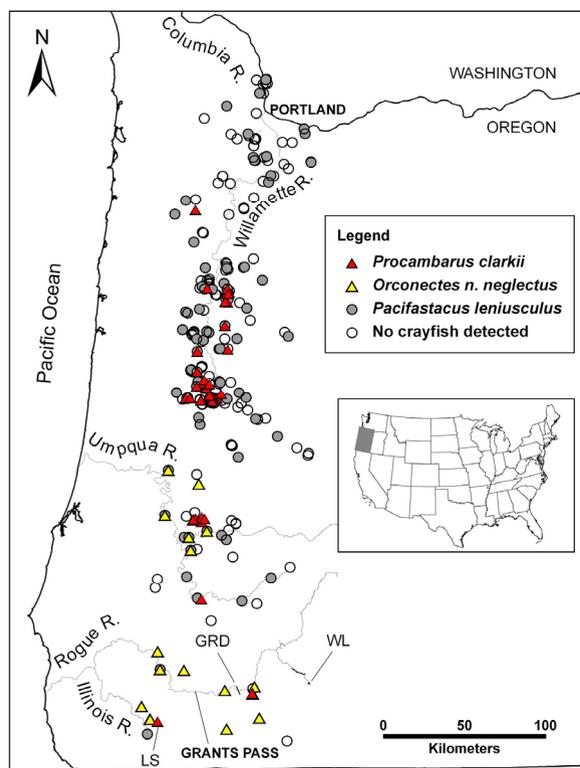


Figure 1. Crayfish sampling locations and detections in western Oregon and Washington, USA. LS=Lake Selmac; GRD=Gold Ray Dam; WL=Willow Lake. See also Appendix 1 for details.

We also searched museum records for historical information on invasive crayfish in the region. We used field surveys and occupancy models to evaluate co-occurrence of a widespread native species [signal crayfish, *Pacifastacus leniusculus* (Dana, 1852)] and two invaders (*P. clarkii* and *O. n. neglectus*) that differ in their habitat use and life histories. Occupancy models allowed us to account for imperfect detection and evaluate habitat associations of all species. We hypothesized that *P. clarkii* had greater potential to displace native *P. leniusculus* than *O. n. neglectus*. *Procambarus clarkii* is a large, fecund, aggressive species that uses a variety of habitat types (Gil-Sanchez et al. 2002; Gherardi 2006; Cruz and Rebelo 2007). These traits have been associated with invasion success among crayfish (Larson and Olden 2010), and *P. clarkii* has been implicated in local displacement of several native crayfish (Gil-Sanchez and Alba-Tercedor 2002; Hanshaw and Garcia 2012). Relatively little is known on invasion ecology of *O. n. neglectus*.

However, co-occurrence at the site scale might be more likely between native *P. leniusculus* and invasive *O. n. neglectus* because *O. n. neglectus* is smaller sized, less fecund, and less versatile in habitat use than *P. clarkii* (Gore and Bryant 1990; Larson and Olden 2010).

Methods

Study area

We sampled aquatic habitats in western Oregon and southwestern Washington State, USA (Figure 1). Sample sites were in three large hydrographic basins: the Willamette/Columbia (hereafter, ‘Willamette’), Umpqua, and Rogue river drainages. These drainages roughly correspond to 3rd or 4th field Hydrologic Unit Codes (HUC; Seaber et al. 1987). Sample sites were in lower elevation valleys and surrounding foothills (average elevation 140 m; range 2–1032 m above sea level). Climate in the study area is characterized by moderate, dry summers and cool, wet winters. Precipitation increases with elevation. Land uses in these lower elevations are predominately agriculture and forestry with lesser amounts of urban development (Loy et al. 2001).

Field sampling

We opportunistically sampled to: 1) spread sites across the study area such that we included at least one site in most 5th field HUC’s within the study area; 2) include lentic and lotic sites; and 3) include sites where any crayfish had been reported. This latter group of sites was drawn from regional reports and databases of past agency surveys, as well as historical museum collections. Most of our sampling was in 2008–2010 (Appendix 1). We also used data we collected using the same methods in 1999–2001 that were part of other studies (Appendix 1). For our *P. clarkii* – *P. leniusculus* analysis (see below), we ascribed a binomial variable, ‘Year’, to indicate whether the site was sampled in 1999–2001 group or 2008–2010 (Table 1). In instances where we sampled more than one site on a stream, we separated sampling locations by at least 1 km.

We used collapsible rectangular funnel traps deployed flat on the bottom and left overnight (Huner and Barr 1991). Traps were approximately 43 cm × 25 cm × 25 cm outer dimensions, with a circular funnel aperture about 6-cm diameter. We left traps for one night (18–28 hr). All traps in a site were set on the same day and retrieved on

Table 1. Covariates of occupancy (ψ) and detection probability (p) for analysis of invasive– native crayfish pairs in western Oregon and Washington, USA. All variables are categorical except for Date.

Variable	Use	Yes (=1)	No (=0)	Description
Species Pair 1: <i>Procambarus clarkii</i> - <i>Pacifastacus leniusculus</i> (283 sites)				
Date (D)	p			Ordinal date of sampling; Range of values was 130-285 (10 May – 12 October)
Bait (B)	p	698	1724	=1 if individual trap is baited
Year (Yr)	p	198	85	=1 if site sampled in 2007-2010; =0 if sampled 1999-2001
Silt (S)	ψ , p	186	97	=1 if site dominated by Silt substrate
Manmade (M)	ψ , p	176	107	=1 if site is anthropogenic or heavily modified
Lotic (L)	ψ , p	113	170	=1 if site is flowing water
ConnPerm (C)	ψ , p	151	132	=1 if site is linked to other sites by permanent water
Long Tom (LT)	ψ , p	84	199	=1 if site is in Long Tom basin
Species Pair 2: <i>Orconectes n. neglectus</i> - <i>Pacifastacus leniusculus</i> (51 sites)				
Date (D)	p			Ordinal date of sampling; Range of values was 180-264 (29 June – 21 September)
Bait (B)	p	247	247	=1 if individual trap is baited
Silt (S)	ψ , p	19	32	=1 if site dominated by Silt substrate
Manmade (M)	ψ , p	18	33	=1 if site is anthropogenic or heavily modified
Lotic (L)	ψ , p	32	19	=1 if site is flowing water
ConnPerm (C)	ψ , p	44	7	=1 if site is linked to other sites by permanent water

the same day. We set 3 to 16 (average 8.6 ± 3.0 SD) traps per site, generally according to surface area. Wherever possible, we separated traps by at least 25 m to reduce chances that one trap would affect capture success in others. All sampling was during crayfish active season (May–October) after most snow melt had dissipated and before autumn rains. In 2010, we baited every other trap with 3–5 cm³ of dry cat food (Purina Fancy Feast™). Each trap was scored yes/no for Bait. We identified all crayfish to species and recorded gender of adults.

We categorized sites as Lentic (marshes, ponds, lakes, reservoirs) or Lotic (small streams, irrigation canals, rivers) (Table 1). We scored whether or not sites were: Manmade (=1 if anthropogenic or heavily altered, e.g., reservoirs, stock or ornamental excavations, ditches); dominated by Silt (=1 if visual inspection showed majority of site in fine substrate rather than pebble, cobble or boulder); or connected to other water bodies via permanent surface water (ConnPerm=1 if visual inspection found a connecting water body with evidence of persistent water and vegetation types requiring persistent water). We took Universal Transverse Mercator (UTM) coordinates for each sampling site. We use ArcMap (Version 9.3.1) and UTM to identify 4th, 5th and 6th field HUC's for sample sites. From large to small, these can be considered at scale of Basin, Sub-basin, and Watershed, respectively. We

present that information as another index of breadth of distribution.

Historical data

To gather information on invasion history, we queried biologists, databases, and museum collections for crayfish records. We focused on regional museums and those with sizeable crayfish collections. We did not inspect specimens, but communicated with museum staff to attempt to confirm species identification. We queried the US Geological Survey's Nonindigenous Aquatic Species database (NAS), which is a compilation of records for invasive aquatic species in North America (<http://nas.er.usgs.gov>).

Analysis

We examined crayfish habitat associations and whether the distribution of native *P. leniusculus* was related to the distribution of either invader (*O. n. neglectus* or *P. clarkii*). We used 2-species, single season occupancy models (PRESENCE 3.1; Hines 2006, <http://www.mbr-pwrc.usgs.gov/software/presence.html>) to separately evaluate each invasive – native species pair. These models enable an estimate of the proportion of sites occupied, accounting for variation among sites and traps in the probability of detecting a species that is present. *Procambarus clarkii* and *P. leniusculus* were found in all three of the major basins we

sampled (Willamette, Umpqua, Rogue), so we used our whole pool of sites (n=283) in the analysis for that species pair. Neither our sampling nor museum collections identify *O. n. neglectus* as present in the Willamette basin portion of our study area. We thus used data from sites in the Rogue and Umpqua basins (n=51) for our analysis of the *O. n. neglectus* – *P. leniusculus* species pair. In the results, tables and figures in this paper, we refer to our crayfish taxa with 2-letter abbreviations: *Pc* (*P. clarkii*), *Pl* (*Pacifastacus leniusculus*), *On* (*Orconectes n. neglectus*).

For each species pair, we started by comparing simple models representing *a priori* hypotheses. Occupancy models use repeat observations to estimate detectability (p), which can be incorporated into estimates of a site occupancy parameter (ψ), where Ψ_A =proportion occupied by species A; Ψ_B =proportion occupied by species B). Each trap was an observation. A trap that contained crayfish was scored ‘present’ (=1) for that respective species. We used the phi/delta parameterization option, which allows estimation of detectability of each species in the absence of the 2nd species (p_A or p_B). This parameterization can also estimate detectability for either species independent of the presence of the 2nd species (r_A and r_B), which can provide insight on whether presence of one species affects detection of the other. Because of limited species overlap, we did not have sufficient data to model some parameters. We thus set $r_A = p_A$ and fixed delta to 1, which means that the models did not allow the detection of one species to influence the detectability of the other. The phi/delta parameterization includes a ‘species interaction factor’ (phi, Φ ; MacKenzie et al. 2004). Phi quantifies the strength of association between distributions of two species. A phi value of 1 indicates species distributions are independent; values < 1 suggest the two species co-occur less frequently than should occur by chance and are consistent with displacement or avoidance. Phi values > 1 suggest a positive relationship in occupancy patterns of the two species.

There are few data that address habitat associations and detectability of crayfish in our region, so we developed models based on studies in other regions and our past field observations. For example, *P. clarkii* can be a burrowing species associated with fine substrates, standing or slow-moving water, and anthropogenic or altered habitats (Huner and Barr 1991; Gil-Sanchez and Alba-Tercedor 2002). We knew *a*

priori that *P. clarkii* was established in the Long Tom basin (tributary of Willamette River) for at least 20 years, so we included that basin as a covariate. *O. n. neglectus* is associated with cool, permanent streams with coarser substrates in its native range in the Ozark highlands and plains of the central USA (Williams 1954; Gore and Bryant 1990). *Pacifastacus leniusculus* has been associated with cool gravel and cobble streams in its native Pacific Northwestern range (Lewis 2002; Cole et al. 2003).

For both species-pairs, we compared simple models to investigate relationships between crayfish and a small set of habitat variables (Silt, Manmade, Lotic, ConnPerm). We started by considering covariates for crayfish detectability. We include Date, Silt, and Bait as covariates of p in all models – the combination of these three variables produced better performing models than single- or 2-variable combinations. Each of these variables was linked to crayfish activity or detection in other areas (Flint 1977, Somers and Stetchy 1986; Huner and Barr 1991). We considered Year as a potential detectability covariate for the *P. clarkii* – *P. leniusculus* analysis, but it was correlated with Date ($r^2 > 0.7$; S-Plus 8.0, Insightful Corp.) so we did not include Year in our model comparisons.

We then examined habitat associations by ranking models with and without variables hypothesized as influencing occupancy for each species. For example, to assess support for an effect of Silt on occupancy of Species A and B, we compared 3 models: a) a base model lacking an effect of Silt on occupancy by either species, b) a model with Silt as a covariate with both species but that does not vary between species (hypothesis that both species respond similarly to Silt), c) a model with Silt as a covariate of both species that allows for each species to relate differently to effects of Silt (hypothesis that the two species respond differently to Silt). Our notation depicts parameters with no covariates as followed by ‘(.)’. The aforementioned three models are written, respectively, as:

a) $\Psi_A(\cdot), \Psi_B(\cdot), \Phi(\cdot), p(\text{Date, Silt, Bait})$

b) $[\Psi_A, \Psi_B(\text{Silt})], \Phi(\cdot), p(\text{Date, Silt, Bait})$

c) $\Psi_A(\text{Silt}), \Psi_B(\text{Silt}), \Phi(\cdot), p(\text{Date, Silt, Bait})$

Where we found support for the model with species-specific response in occupancy, we ran a *post hoc* comparison model for each species individually (e.g., the model representing an hypothesis that Species A occupancy is related to Silt is $\Psi_A(\text{Silt}), \Psi_B(\cdot), \Phi(\cdot), p(\text{Date, Silt, Bait})$).

We ranked models with Akaike's Information Criterion (AIC). We considered a change in AIC of ≥ 2 units to indicate a difference between models (lower is better; Burnham and Anderson 2002). We plotted effect sizes for occupancy covariates based on estimates of Ψ from models with separate effects for each species (e.g., model c from the list above). We did not use ConnPerm in the *O. n. neglectus* – *P. leniusculus* analysis because our sample was too unbalanced (>86% of our sites had ConnPerm=1).

We evaluated a hypothesis that species distributions are independent by comparing a model where we set $\Phi = 1$ to a model where Φ was allowed to vary. We tested models where dependence of the two species (as represented by Φ) was associated with Silt and Lotic. Our test of Silt was based on a hypothesis that silt favors burrowing species, while greater interstitial complexity in coarse substrates might lessen competition for shelter and resources. Our test of Lotic represented a hypothesis that Northwestern streams (which have seasonal high flows and floods) might influence co-existence by flushing and reducing densities of invasive crayfish (e.g., Kerby et al. 2005). For these tests, we allowed Φ to vary as a function of Silt or Lotic, and compared that model with one with no covariates of Φ .

Our last step for each species pair was to examine a fuller model for more parameterized estimates of Φ and crayfish detectability. This model included covariates that were supported in our *a priori* and *post hoc* simple model comparisons. For the *O. n. neglectus*–*P. leniusculus* analysis, we report a final model that does not include Lotic because it was negatively correlated with both Silt and Manmade ($r^2 \geq 0.7$). We did not include ConnPerm in the final model in the *P. clarkii*–*P. leniusculus* analysis, because it was positively correlated with Lotic ($r^2 = 0.7$). For each parameter in the model, we report beta coefficients (\pm standard error). We report the effect on odds (95% CI) associated with covariates: exp(beta) is the effect of one unit change in the covariate on the parameter of interest (e.g., occupancy, detectability). We report detectability (95% CI) for each species from our final model, estimated for a baited trap in a common habitat type for respective species-pairs. For *P. clarkii* – *P. leniusculus*, we report detectability based on a site that was Silt, Manmade, Lotic, and not in the Long Tom basin. For *O. n. neglectus* – *P. leniusculus*, we report detectability based on a site that was Lotic, not Manmade, and not dominated by Silt.

Results

We sampled a total of 283 sites (Figure 1, Table 2). We detected *Pl* at 71 sites (25.1%), *Pc* at 51 sites (18.0%), and *On* at 18 sites (6.4%). We found *Pl* and *Pc* in all three large basins. We found *On* in the two southern basins (Rogue and Umpqua) and did not detect them in the Willamette Basin. We detected *Pl* and *Pc* together at 5 sites. We detected both *Pl* and *On* at 8 sites.

Among the fifty-eight 5th-field HUC units where we had sample sites, we detected *Pl* in 35 (60.3%), *Pc* in 9 (15.5%), and *On* in 12 (20.1%). We had sample sites in 119 different 6th-field HUC units (scale of watershed); we found *Pl* in 60 (50.4%), *Pc* in 17 (14.3%), and *On* in 17 (14.3%).

Occupancy analyses

Species pair 1: Invasive *Procambarus clarkii* – Native *Pacifastacus leniusculus* (*Pc-Pl*)

We found support for species-specific responses to the occupancy covariates Silt, Long Tom, Manmade, ConnPerm, and Lotic (Table 3, Figure 2). Parameter estimates and *post hoc* model comparisons indicated that occupancy of *Pc* was positively related to being in the Long Tom basin (model 2d; $\beta_{Pc} = 1.40 \pm 0.33$ SE) and to Manmade sites (model 3d; $\beta_{Pc} = 1.43 \pm 0.45$). Occupancy by *Pl* was negatively related to Silt (model 1e; $\beta_{Pl} = -1.54 \pm 0.30$) and Manmade sites (model 3e; $\beta_{Pl} = -2.10 \pm 0.36$). Occupancy by *Pl* was positively related to Lotic sites (model 4e, $\beta_{Pl} = 2.85 \pm 0.46$). Both species were positively related to ConnPerm (model 5d, $\beta_{Pc} = 1.16 \pm 0.36$; model 5e, $\beta_{Pl} = 2.98 \pm 0.50$). We found marginal support ($\Delta AIC \sim 2$) for an effect of Long Tom on *Pl* occupancy (model 2e).

We did not find support for a hypothesis that *Pc* and *Pl* distributions are independent: the model with $\Phi = 1$ (6b) performed almost 10 units worse than a base model (6a) where Φ was allowed to vary. Including Silt (models 7a, 7b) or Lotic (8a, 8b) as covariates of Φ did not improve performance over a model lacking those covariates. Estimates of Φ across our simple models where it was allowed to vary ranged between 0.28 and 0.72 suggesting that these species occur together less often than would be expected by chance.

Our final model (Table 4) was consistent with results of the simple models. A version of the final model including Year as a covariate of *p*

Table 2. Crayfish detections in three large basins in western Oregon and Washington, USA. *Pacifastacus leniusculus* is native to the region; *Procambarus clarkii* and *Orconectes n. neglectus* are introduced.

Basin	Number of Sites Sampled	Number (%) of Sites Detected		
		<i>Pacifastacus leniusculus</i>	<i>Procambarus clarkii</i>	<i>Orconectes n. neglectus</i>
Willamette	232	55 (23.7%)	41 (17.7%)	0 (0)
Umpqua	35	13 (37.1%)	8 (22.8%)	7 (20.0%)
Rogue	16	3 (18.8%)	2 (12.5%)	11 (68.8%)

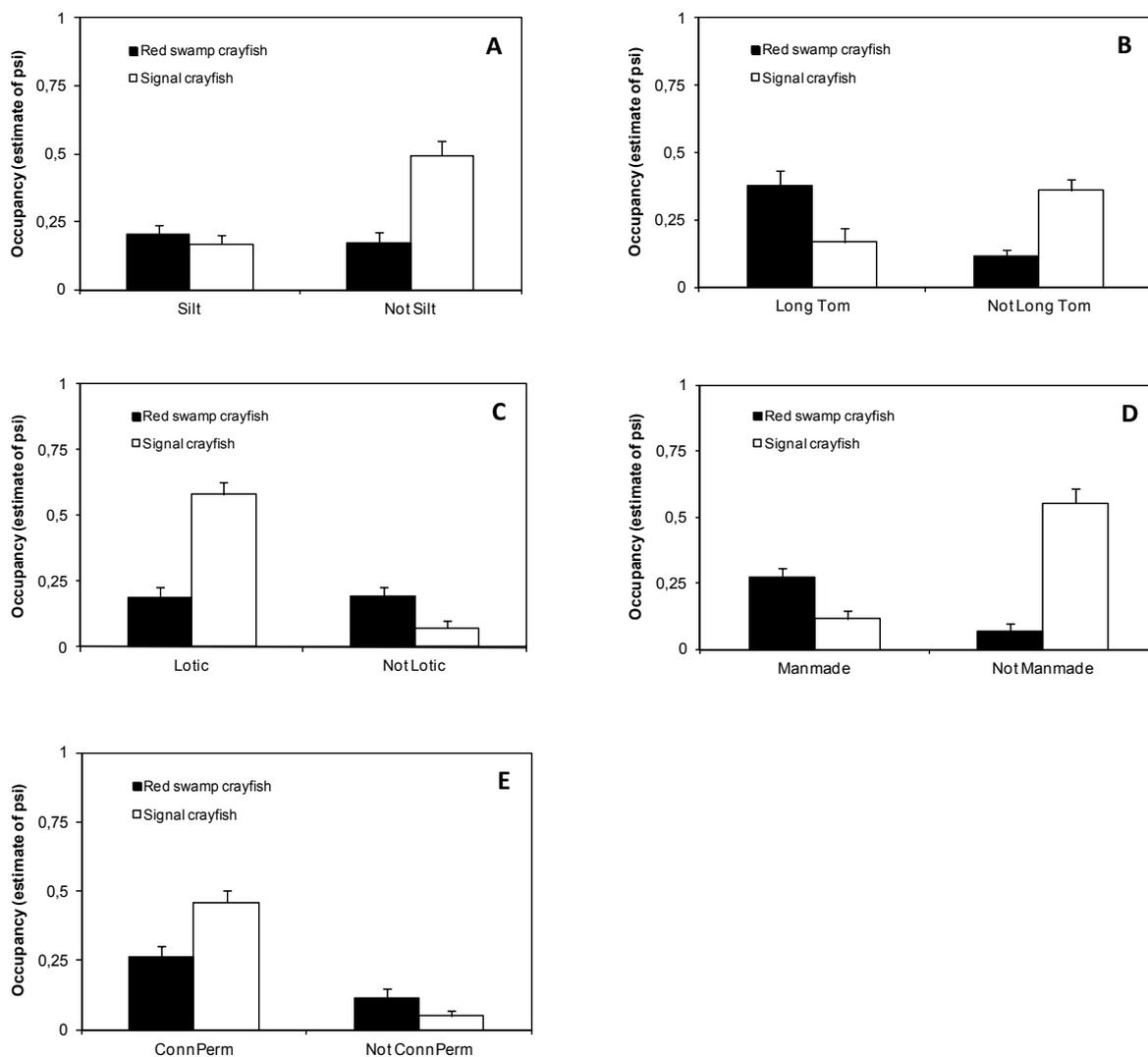


Figure 2. Estimates of proportion of sites occupied by invasive red swamp crayfish *Procambarus clarkii* and native signal crayfish *Pacifastacus leniusculus* at 283 sites in western Oregon and southwestern Washington, USA. Covariates are: Silt (A), Long Tom basin (B), Lotic (C), Manmade (D), and Connected by permanent water (E).

Table 3. Two-species occupancy models for invasive *Procambarus clarkii* (*Pc*) and native *Pacifastacus leniusculus* (*Pl*) in western Oregon and Washington, USA. Models are grouped by hypothesis and ordered by ascending AIC value. Model numbers with * are *post-hoc* comparisons. Covariates are Date (D), Silt (S), Bait (B), Manmade (M), Lotic (L), Connected by permanent water (C). Column headings are number of parameters in model (K), -2 times log-likelihood (-2l), Akaike's Information Criterion (AIC), difference in AIC value compared to base model (Δ AIC), Φ (species interaction factor) and its standard error (SE).

Model Number	Description	Notation	K	-2l	AIC	Δ AIC	Φ (SE)
Silt affects occupancy							
1e*	ψ, Pl	$\psi Pc(\cdot), \psi Pl(\text{Silt}), \Phi(\cdot), p(D,S,B,\cdot)$	13	1938.3	1964.3	-	0.40 (0.16)
1c	ψ, Pc, Pl different	$\psi Pc(\text{Silt}), \psi Pl(\text{Silt}), \Phi(\cdot), p(D,S,B,\cdot)$	14	1937.9	1965.9	1.6	0.39 (0.16)
1b	ψ, Pc, Pl same	$[(\psi Pc, \psi Pl)(\text{Silt})], \Phi(\cdot), p(D,S,B,\cdot)$	13	1950.7	1976.7	12.4	0.36 (0.14)
1a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B)$	12	1963.9	1987.9	23.6	0.38 (0.15)
1d*	ψ, Pc	$\psi Pc(\text{Silt}), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\cdot)$	13	1963.8	1989.8	25.5	0.37 (0.15)
Long Tom basin affects occupancy							
2c	ψ, Pc, Pl different	$\psi Pc(\text{LT}), \psi Pl(\text{LT}), \Phi(\cdot), p(D,S,B,\text{LT})$	16	1931.6	1963.6	-	0.46 (0.18)
2d*	ψ, Pc	$\psi Pc(\text{LT}), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{LT})$	15	1938.7	1968.7	5.0	0.45 (0.18)
2e*	ψ, Pl	$\psi Pc(\cdot), \psi Pl(\text{LT}), \Phi(\cdot), p(D,S,B,\text{LT})$	15	1952.9	1982.9	19.3	0.43 (0.17)
2b	ψ, Pc, Pl same	$[(\psi Pc, \psi Pl)(\text{LT})], \Phi(\cdot), p(D,S,B,\text{LT})$	15	1952.9	1982.9	19.3	0.38 (0.15)
2a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{LT})$	14	1956.9	1984.9	21.2	0.37 (0.15)
Manmade affects occupancy							
3c	ψ, Pc, Pl different	$\psi Pc(\text{M}), \psi Pl(\text{M}), \Phi(\cdot), p(D,S,B,\text{M})$	16	1895.7	1927.7	-	0.63 (0.24)
3e*	ψ, Pl	$\psi Pc(\cdot), \psi Pl(\text{M}), \Phi(\cdot), p(D,S,B,\text{M})$	15	1913.4	1943.4	15.7	0.64 (0.24)
3d*	ψ, Pc	$\psi Pc(\text{M}), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{M})$	15	1937.2	1967.2	39.6	0.62 (0.24)
3b	ψ, Pc, Pl same	$[(\psi Pc, \psi Pl)(\text{M})], \Phi(\cdot), p(D,S,B,\text{M})$	15	1947.2	1977.2	49.6	0.40 (0.16)
3a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{M})$	14	1949.8	1977.8	50.1	0.43 (0.17)
Lotic affects occupancy							
4e*	ψ, Pl	$\psi Pc(\cdot), \psi Pl(\text{L}), \Phi(\cdot), p(D,S,B,\text{L})$	15	1862.5	1892.5	-	0.40 (0.15)
4c	ψ, Pc, Pl different	$\psi Pc(\text{L}), \psi Pl(\text{L}), \Phi(\cdot), p(D,S,B,\text{L})$	16	1862.4	1894.4	2.0	0.40 (0.15)
4b	ψ, Pc, Pl same	$[\psi Pc, \psi Pl(\text{L})], \Phi(\cdot), p(D,S,B,\text{L})$	15	1882.9	1912.9	20.5	0.38 (0.15)
4a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{L})$	14	1885.6	1913.6	21.2	0.39 (0.15)
4d*	ψ, Pc	$\psi Pc(\text{L}), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{L})$	15	1885.6	1915.6	23.2	0.39 (0.15)
Permanent aquatic connections affect occupancy							
5c	ψ, Pc, Pl different	$\psi Pc(\text{C}), \psi Pl(\text{C}), \Phi(\cdot), p(D,S,B,\text{C})$	16	1876.3	1908.3	-	0.32 (0.12)
5b	ψ, Pc, Pl same	$[\psi Pc, \psi Pl(\text{C})], \Phi(\cdot), p(D,S,B,\text{C})$	15	1884.7	1914.7	6.4	0.31 (0.12)
5e*	ψ, Pl	$\psi Pc(\cdot), \psi Pl(\text{C}), \Phi(\cdot), p(D,S,B,\text{C})$	15	1884.7	1914.7	6.4	0.30 (0.12)
5d*	ψ, Pc	$\psi Pc(\text{C}), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{C})$	15	1908.3	1938.3	29.9	0.30 (0.12)
5a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B,\text{C})$	14	1919.7	1947.7	39.4	0.31 (0.13)
Species distributions are independent [Φ is 1]							
6a	Base model	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi(\cdot), p(D,S,B)$	12	1963.9	1987.9	-	0.38 (0.15)
6b	$\Phi=1$	$\psi Pc(\cdot), \psi Pl(\cdot), \Phi=1, p(D,S,B)$	12	1973.8	1997.8	9.9	1.00 (0)
Species distributions are related and co-occurrence is related to Silt							
7a	Base model	$\psi Pc(\text{S}), \psi Pl(\text{S}), \Phi(\cdot), p(D,S,B)$	14	1937.9	1965.9	-	0.39 (0.16)
7b	$\Phi[\text{Silt}]$	$\psi Pc(\text{S}), \psi Pl(\text{S}), \Phi(\text{S}), p(D,S,B)$	15	1937.2	1967.2	1.3	0.28 to 0.56
Species distributions are related and co-occurrence is related to Lotic							
8a	Base model	$\psi Pc(\text{L}), \psi Pl(\text{L}), \Phi(\cdot), p(D,S,B,\text{L})$	16	1862.4	1894.4	-	0.40 (0.15)
8b	$\Phi[\text{Lotic}]$	$\psi Pc(\text{L}), \psi Pl(\text{L}), \Phi(\text{L}), p(D,S,B,\text{L})$	17	1862.2	1896.2	1.8	0.38 to 0.65

Table 4. Parameter estimates and effects of covariates on odds of occupancy (ψ), species interaction factor (Φ), and detectability (p) from a final model for invasive *Procambarus clarkii* (*Pc*) and native *Pacifastacus leniusculus* (*Pl*).

Parameter	Beta (SE)	Covariate effect on Odds (95% CI)
ψ		
<i>Pc</i>	-2.87 (0.41)	
<i>Pl</i>	-1.68 (0.57)	
<i>Pc</i> Manmade	1.33 (0.45)	3.78 (1.57 – 9.09)
<i>Pl</i> Manmade	-0.88 (0.44)	0.41 (0.18 – 0.97)
<i>Pc</i> Long Tom	1.21 (0.35)	3.36 (1.70 – 6.65)
<i>Pl</i> Lotic	2.46 (0.52)	11.67 (4.23 – 32.19)
<i>Pl</i> Silt	-0.28 (0.40)	0.76 (0.34 – 1.66)
Φ	-0.74 (0.38)	
p		
<i>Pc</i>	-1.41 (0.49)	
<i>Pl</i>	-1.98 (0.42)	
<i>Pc</i> Long Tom	0.76 (0.37)	2.14 (1.04 – 4.39)
<i>Pl</i> Long Tom	0.17 (0.29)	1.19 (0.67 – 2.11)
<i>Pc</i> Lotic	-0.12 (0.31)	0.89 (0.48 – 1.64)
<i>Pl</i> Lotic	0.97 (0.37)	2.63 (1.26 – 5.48)
<i>Pc</i> Date	0.02 (0.13)	1.02 (0.79 – 1.32)
<i>Pl</i> Date	-0.14 (0.14)	0.87 (0.66 – 1.14)
<i>Pc</i> Manmade	-0.27 (0.42)	0.77 (0.34 – 1.74)
<i>Pl</i> Manmade	-0.28 (0.26)	0.76 (0.45 – 1.27)
<i>Pc</i> Silt	0.57 (0.31)	1.77 (0.95 – 3.28)
<i>Pl</i> Silt	0.11 (0.19)	1.12 (0.78 – 1.61)
<i>Pc</i> Bait	0.98 (0.34)	2.66 (1.37 – 5.15)
<i>Pl</i> Bait	0.91 (0.18)	2.48 (1.73 – 3.54)

and ψ would not converge. The final model estimated *Pc* was present at 19.5% and *Pl* was present at 28.1% of our study sites. This model estimated $\Phi = 0.48$ (95% CI 0.23 – 1.01; $\beta = -0.74 \pm 0.38$). Both species were more detectable with bait than without (βp_{Bait} for *Pc* = 0.98 ± 0.34 ; βp_{Bait} for *Pl* = 0.91 ± 0.18); the odds of detecting *Pc* increased by a factor of 2.66 ($=\exp(0.98)$) in baited traps relative to unbaited traps. Estimates of overall detectability were: 0.44 (95% CI 0.24–0.66) for *Pc*; and 0.24 (0.15–0.35) for *Pl*.

Species pair 2: Invasive *Orconectes n. neglectus* – Native *Pacifastacus leniusculus* (*On-Pl*)

Our model comparisons did not support species-specific responses to our hypothesized covariates (Silt, Manmade, Lotic) of occupancy by *On* and *Pl* in the Rogue and Umpqua basins (Table 5). For each of these covariates, a model with a common response by both crayfish (models 1b, 2b, 3b) outperformed a model with species-

specific responses (1c, 2c, 3c, respectively). Occupancy was negatively related to Silt (model 1b, $\beta_{\text{Both species}} = -1.73 \pm 0.66$) and Manmade (model 2b, $\beta_{\text{Both species}} = -2.08 \pm 0.76$), and positively related to Lotic (model 3b, $\beta_{\text{Both species}} = 3.01 \pm 0.85$). Estimates of Φ across models varied between 0.998 – 1.242.

A model with independent distributions of *On* and *Pl* (model 4b) was not supported (ΔAIC of 0.41 from base model). Models that tested Silt or Lotic as covariates of Φ would not converge (not included in Table 5).

We fit a final model with supported predictors that included Silt and Manmade as non-species specific covariates of occupancy (Table 6). We did not include Lotic because it was correlated ($r^2 \geq 0.7$) with both Silt and Manmade. This model suggests *On* ($\beta = 1.22 \pm 0.75$) is more widespread than *Pl* ($\beta = 0.18 \pm 0.40$) in our sample sites. This model estimated that *On* was present at 56.6% and *Pl* was present at 36.7% of our sample sites. Occupancy of both species was negatively related to Silt and Manmade habitats. This model estimated $\Phi = 1.00$ (95% CI 0.73 – 1.38). Both species were more detectable with bait than without (βp_{Bait} for *On* = 0.67 ± 0.34 ; βp_{Bait} for *Pl* = 0.68 ± 0.36). Model estimates of detectability were: 0.11 (0.05 – 0.22) for *On*; and 0.24 (0.15 – 0.36) for *Pl*.

Discussion

Biological invasions are one of many forces increasing stress on aquatic biodiversity (Richter et al. 1997; Gherardi 2007). Important components of invasion biology include understanding vulnerability of native species and systems, and factors that enhance or mediate invader effects (Parker et al. 1999; Gurevitch and Padilla 2004). Our study contrasts distribution and potential effects of two ecologically dissimilar invasive crayfish. We found that both invaders are substantially more common than previously known, confirming the ability of potentially damaging aquatic invaders to ‘fly under the radar.’ Occupancy models help accommodate imperfect detection, a common problem with aquatic invaders, and provide a tool for assessing patterns of co-occurrence between natives and exotics (MacKenzie et al. 2004). Accounting for low detection is important, as we estimated per-trap detection probabilities from 0.11 to 0.44 for our three crayfish species.

Table 5. Two-species occupancy models for invasive *Orconectes n. neglectus* (*On*) and native *Pacifastacus leniusculus* (*Pl*) in Rogue and Umpqua basins, southwestern Oregon, USA. Models are grouped by hypothesis and ordered by ascending AIC value. Model numbers with * are *post-hoc* comparisons. Covariates are Date (D), Silt (S), Bait (B), Manmade (M), Lotic (L). Column headings are number of parameters in model (*K*), -2 times log-likelihood (-2*l*), Akaike's Information Criterion (AIC), difference in AIC value compared to base model (Δ AIC), Φ (species interaction factor) and its standard error (SE).

Model Number	Description	Notation	<i>K</i>	-2 <i>l</i>	AIC	Δ AIC	Φ (SE)
Silt affects occupancy							
1b	ψ , <i>On</i> , <i>Pl</i> same	$[(\psi_{On}, \psi_{Pl})(\text{Silt})]$, $\Phi(\cdot)$, $p(\text{D,S,B,})$	13	505.52	531.52	-	1.08 (0.22)
1c	ψ , <i>On</i> , <i>Pl</i> different	$\psi_{On}(\text{Silt}), \psi_{Pl}(\text{Silt})$, $\Phi(\cdot)$, $p(\text{D,S,B,})$	14	504.96	532.96	1.44	1.06 (0.21)
1a	Base model	$\psi_{On}(\cdot), \psi_{Pl}(\cdot)$, $\Phi(\cdot)$, $p(\text{D,S,B,})$	12	512.27	536.27	4.75	1.24 (0.30)
Manmade affects occupancy							
2b	ψ , <i>On</i> , <i>Pl</i> same	$[(\psi_{On}, \psi_{Pl})(\text{M})]$, $\Phi(\cdot)$, $p(\text{D,S,B,M})$	15	487.91	517.91	-	1.01 (0.17)
2c	ψ , <i>On</i> , <i>Pl</i> different	$\psi_{On}(\text{M}), \psi_{Pl}(\text{M})$, $\Phi(\cdot)$, $p(\text{D,S,B,M})$	16	487.91	519.91	2.00	1.01 (0.17)
2a	Base model	$\psi_{On}(\cdot), \psi_{Pl}(\cdot)$, $\Phi(\cdot)$, $p(\text{D,S,B,M})$	14	496.35	524.35	6.44	1.21 (0.28)
Lotic affects occupancy							
3b	ψ , <i>On</i> , <i>Pl</i> same	$[\psi_{On}, \psi_{Pl}(\text{L})]$, $\Phi(\cdot)$, $p(\text{D,S,B,L})$	15	483.41	513.41	-	1.01 (0.18)
3c	ψ , <i>On</i> , <i>Pl</i> different	$\psi_{On}(\text{L}), \psi_{Pl}(\text{L})$, $\Phi(\cdot)$, $p(\text{D,S,B,L})$	16	482.73	514.73	1.32	1.00 (0.17)
3a	Base model	$\psi_{On}(\cdot), \psi_{Pl}(\cdot)$, $\Phi(\cdot)$, $p(\text{D,S,B,L})$	14	499.59	527.59	14.18	1.10 (0.27)
Species distributions are independent [Φ is 1]							
4a	Base model	$\psi_{On}(\cdot), \psi_{Pl}(\cdot)$, $\Phi(\cdot)$, $p(\text{D,S,B})$	12	512.27	536.27	-	1.24 (0.30)
4b	$\Phi=1$	$\psi_{On}(\cdot), \psi_{Pl}(\cdot)$, $\Phi=1$, $p(\text{D,S,B})$	12	512.68	536.68	0.41	1.00 (0)

Our results suggest that occurrence of native *P. leniusculus* in our sites may be more affected by invasive *P. clarkii* than by *O. n. neglectus*. Our raw detection data and occupancy models both show less co-occurrence between *P. clarkii* and *P. leniusculus* than between *O. n. neglectus* and *P. leniusculus*. We detected *P. clarkii* and *P. leniusculus* together at 1.8% of our whole pool of 283 sites; we found *O. n. neglectus* and *P. leniusculus* together at 15.7% of 51 sites in basins where *O. n. neglectus* is known to occur. The Long Tom was the only river basin where we had *a priori* information that *P. clarkii* was broadly established (more than two decades). We estimate *P. leniusculus* occupancy in the Long Tom is about half (16.7% of sites) as much as it is outside of the Long Tom drainage (36.0%). Much of the Long Tom basin is modified by agriculture and urban areas, and aquatic habitats are mainly low-gradient streams and ponds. These habitats are favored by *P. clarkii* in native and invaded ranges (Huner and Barr 1991; Cruz and Rebelo 2007) and are probably suboptimal for *P. leniusculus*. Our finding that *P. clarkii* and *P. leniusculus* co-occur less frequently than would be expected by chance is consistent with *P. clarkii* displacing *P. leniusculus*, *P. leniusculus* avoiding areas with *P. clarkii*, or both.

A negative effect of *P. leniusculus* on *P. clarkii* could also produce the pattern of occupancy we observed but is less likely for several reasons. Introduced *P. clarkii* are implicated in displacing native crayfish in multiple regions and habitat types. For example, *P. clarkii* appears to be displacing native crayfish in lowland streams in Spain (Gil-Sanchez and Alba-Tercedor 2002) and northern Mexico (Rodríguez-Almaraz and Campos 1994). *Pacifastacus leniusculus* is a successful invader in parts of Europe, Japan, and outside its native range in western North America (Lewis 2002; Nakata et al. 2005), so it might be hypothesized that they could better resist invasion by *P. clarkii* than some other crayfish. Higher abundance of *P. clarkii* than *P. leniusculus* in one Washington lake led Mueller (2007b) to suggest displacement of the native may be underway. Experiments from their invaded ranges in Spain showed that *P. clarkii* was more aggressive and tended to displace similarly-sized *P. leniusculus* from shelters (Alonso and Martinez 2006). Other factors that could favor *P. clarkii* over *P. leniusculus* are more rapid growth and sexual maturation, greater fecundity and breeding frequency, and tolerance of warmer or more degraded habitats (Mueller 2007a,b; Cruz and Rebelo 2007; Larson and Olden 2010).

Table 6. Parameter estimates and effects of covariates on odds of occupancy (ψ), species interaction factor (Φ), and detectability (p) from a final model for invasive *Orconectes n. neglectus* (*On*) and native *Pacifastacus leniusculus* (*Pl*).

Parameter	Beta (SE)	Covariate effect on Odds (95% CI)
Ψ		
<i>On</i>	1.22 (0.75)	
<i>Pl</i>	0.18 (0.40)	
Both Silt	-0.86 (0.84)	0.42 (0.08 – 2.18)
Both Manmade	-1.73 (0.82)	0.18 (0.04 – 0.88)
Φ	0.00 (0.16)	
p		
<i>On</i>	-3.56 (0.67)	
<i>Pl</i>	-0.57 (0.33)	
<i>On</i> Date	1.72 (0.54)	5.57 (1.92 – 16.17)
<i>Pl</i> Date	-1.23 (0.37)	0.29 (0.14 – 0.60)
<i>On</i> Manmade	2.03 (0.50)	7.61 (2.86 – 20.26)
<i>Pl</i> Manmade	-0.14 (0.68)	0.87 (0.23 – 3.26)
<i>On</i> Silt	-0.03 (0.53)	0.98 (0.34 – 2.77)
<i>Pl</i> Silt	-2.22 (1.13)	0.11 (0.01 – 0.99)
<i>On</i> Bait	0.67 (0.34)	1.96 (1.00 – 3.83)
<i>Pl</i> Bait	0.68 (0.36)	1.98 (0.98 – 3.99)

Habitat conditions influence success and effects of invasive crayfish and probably play a role in *P. clarkii* – *P. leniusculus* interactions (Light 2003; Magoulick and DiStefano 2007; Hanshew and Garcia 2012). We found *P. clarkii* at similar frequency in lotic and lentic sites, and silt or coarse substrates. Its ability to colonize a variety of waters is a factor in the species' success elsewhere (e.g., Cruz and Rebelo 2007). The association of *P. clarkii* with manmade habitats likely reflects more introductions and high establishment success in those sites (Riegel 1959; Riley et al. 2005). *Pacifastacus leniusculus* can occur in a variety of habitats and elevations around our region, but seems most common in streams or cool lakes with some coarse substrates (Lewis 2002). Co-occurrence of these species at the river basin scale is documented in systems with thermal, substrate, and flow characteristics favored by both species (Nakata et al. 2005; Bernardo et al. 2011). For example, *P. clarkii* appear most successful in lower elevations of invaded watersheds in Europe, Japan and California, while introduced *P. leniusculus* is established higher up in some of the same basins (Riegel 1959; Nakata et al. 2005; Bernardo et al. 2011). Low elevation constructed ponds and channelized or low-gradient ditches may be

particularly susceptible to *P. clarkii* invasion. Growth and reproduction in *P. clarkii* are higher in warmer waters (Oluoch 1990; Huner and Barr 1991). High flows can displace *P. clarkii* (Gil-Sanchez and Alba-Tercedor 2002; Kerby et al. 2005). The ability of *P. clarkii* to burrow allows them to use temporary waters and is facilitated by fine-grained substrates such as silts and clays (Huner and Barr 1991; Barbaresi et al. 2004). Fine substrates are common in lowlands in our study area. Our habitat variables were simplified, so further investigation of substrate and position in watershed could enhance understanding of crayfish distribution, co-occurrence, and patterns of invasion.

In contrast to the *P. clarkii* – *P. leniusculus* models, we found *O. n. neglectus* and *P. leniusculus* distributions were roughly independent of one another. We had expected some effect of *O. n. neglectus* on *P. leniusculus*, but less pronounced than that of *P. clarkii*. This occupancy analysis is focused on species presence, so we cannot make conclusions regarding effects on abundance. Both *O. n. neglectus* and *P. leniusculus* were associated with lotic waters and inversely related to manmade habitats. Bouchard (1977) surmised that *O. n. neglectus* may displace *P. leniusculus* in parts of the Rogue basin. In reaches where both species were found, *P. leniusculus* tended to be in faster and *O. n. neglectus* in slower water, and *P. leniusculus* was better able to hold position when exposed to current (Bouchard 1977). In the central USA, invading *O. neglectus chaenodactylus* Williams 1952 may be displacing two of four native crayfish (Magoulick and DiStefano 2007). There, *O. n. chaenodactylus* uses higher flow microhabitats. The two species that get displaced as *O. n. chaenodactylus* expands were those that share higher flow microhabitats; one is similar in body size to *O. n. chaenodactylus*, the other is smaller (Magoulick and DiStefano 2007). The two less-affected natives are habitat generalists and larger in size than *O. n. chaenodactylus* (Magoulick and DiStefano 2007).

Our data reveal a broad distribution of *O. n. neglectus* in low elevation streams in the Umpqua and Rogue basins, two large (>12,000 km²) and economically important watersheds in Oregon. Broad invasion of the Umpqua was not previously documented; our sampling suggests *O. n. neglectus* occurs or has direct access to >100 km on the lower North Umpqua and mainstem Umpqua rivers. *Orconectes n. neglectus* was present in the Rogue basin from at least 1960 (NMNH #178213) and occupied ≥ 2 km of river

by 1962 (Fitzpatrick 1966). It may have arrived significantly earlier: Rivers (1963) included reference to *O. n. neglectus* in his description of Rogue basin fisheries as of 1941. Historic data and our sampling suggest *O. n. neglectus* has continued to expand around the Rogue basin. Bouchard's (1977) sampling in the 1970's suggested *O. n. neglectus* had colonized at least 60 km of the middle Rogue River. They were also reported at three sites outside this contiguous range (one tributary and two reservoirs), but not found between those localities and the main river. We identified three areas that probably represent significant expansions:

1) *O. n. neglectus* is now established around Gold Ray Dam on the central Rogue River (Figure 1) where they were not found by Bouchard (1977). His searches around Gold Ray Dam found only *P. leniusculus*. During the draining of the Gold Ray impoundment in 2010, dozens of crayfish were collected (J. Doino, Oregon Department of Fish and Wildlife, pers. comm.), all of which we confirmed were *O. n. neglectus*. This extends the distribution into a reach of the river that Bouchard (1977) considered uninvaded. Sampling is needed to determine whether its distribution is continuous upstream to Willow Creek Reservoir, where a disjunct population was reported by Bouchard (1977).

2) *O. n. neglectus* is now established in the upper Applegate basin, a large tributary of the lower Rogue. We found *O. n. neglectus* in the upper Applegate River near Ruch, Oregon; 32 *O. n. neglectus* were collected in 1989 from Williams Creek (INHS #8211), a tributary of the upper Applegate River. Bouchard (1977) sampled these areas and did not find *O. n. neglectus*. These sites are >38 and >22 km, respectively, upstream of the Applegate – Rogue River confluence. It appears *O. n. neglectus* is adept at colonizing low gradient streams, particularly in the downstream direction (Bouchard 1977; our data), so are likely to occupy most of the mainstem Applegate River.

3) Bouchard (1977) sampled sites in the Illinois River basin, another large tributary, and found *O. n. neglectus* only near its confluence with the Rogue. Their sampling on the Illinois River upstream of the confluence did not detect *O. n. neglectus*. However, the species was reported from a reservoir far upstream in the Illinois basin (Lake Selmac; Bouchard 1977). Lake Selmac is drained by Deer Creek, a tributary of the Illinois River. We found *O. n. neglectus* in Deer Creek downstream of Lake Selmac and >60 km

upstream of its eventual confluence with the Rogue. It thus appears *O. n. neglectus* has expanded its range downstream of Lake Selmac and now occurs or has unobstructed access to Deer Creek and most of the lower Illinois River.

Our data, historic information, and observations of others show *O. n. neglectus* now occupies and has access to a large swath of southwestern Oregon from the foothills of Cascade Range to the Pacific Coast. Given this expanse, information on its ecological effects is needed, including relations with *P. leniusculus*. Our estimates of phi did not imply displacement of the native. However, the number of sites we sampled in the range of *O. n. neglectus* was relatively small. It is also possible that our study represents different stages of invasion in the Rogue and Umpqua basins, and effects of invaders take varying time to become evident (e.g., Westman et al. 2002). We tended not to find the two species together on the main stem Rogue River where *O. n. neglectus* has been established for at least 50 yr. If the streams listed above experienced more recent *O. n. neglectus* expansions, they have had less time to manifest negative effects on *P. leniusculus*. We know little about the timing of the Umpqua invasion and available data imply that *O. n. neglectus* can spread rapidly in these riverine systems. The oldest *O. n. neglectus* records we found in the Umpqua basin were from 1994 on the North Umpqua (a tributary of mainstem Umpqua River; INHS #4879) and 2001 in a reservoir on a tributary of the South Umpqua (the other major tributary; INHS #8400). If invasion is more recent in the Umpqua than Rogue, effects on *P. leniusculus* might not yet be evident, particularly at the level of complete displacement from a site.

Crayfish introductions occur via multiple pathways, including release from school classes, aquaculture and fishing bait (Hobbs et al. 1989, Peters and Lodge 2009, DiStefano et al. 2009). Lodge et al. (2000) consider bait releases to be the primary means of recent crayfish introductions. Observed crayfish distribution, vectors reported elsewhere, and the lack of evidence of local aquaculture suggest *O. n. neglectus* and *P. clarkii* invasions in our area are related to bait releases or stocking with game fish. Basins such as the Rogue and Umpqua are widely known for angling. All of our detections of *P. clarkii* in these basins were proximal with sites known for warm water fisheries. Bouchard (1977) concluded that *O. n. neglectus* in the Rogue basin arrived with stocked warm water fishes or

anglers, with the latter the likely mode at the disjunct sites found in the 1970's. Crayfish are a common food for largemouth (*Micropterus salmoides*) and smallmouth bass (*M. dolomieu*), for which they are raised and used as bait (Huner 1976). Largemouth bass and *P. clarkii* are co-introduced in parts of Europe, Japan, and Africa (Garcia-Berthou 2002; Maezono and Miyashita 2003; Foster and Harper 2007). Both bass are widely distributed and prized game fish in our study area (Scheerer 2002; Schade and Bonar 2005). Outreach with the angling community might offer potential to reduce at least the inter-basin spread of invasive crayfish.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Sampling sites, locations, dates, and crayfish detections in western Oregon and Washington, USA in 1999–2001 and 2008–2011.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Pearl_etal_Supplement.pdf