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Ecology of nonnative Siberian prawn (*Palaemon modestus*) in the lower Snake River, Washington, USA

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Abstract We assessed the abundance, distribution, and ecology of the nonnative Siberian prawn *Palaemon modestus* in the lower Snake River, Washington, USA. Analysis of prawn passage abundance at three Snake River dams showed that populations are growing at exponential rates, especially at Little Goose Dam where over 464,000 prawns were collected in 2015. Monthly beam trawling during 2011–2013 provided information on prawn abundance and distribution in Lower Granite and Little Goose Reservoirs. Zero-inflated regression predicted that the probability of prawn presence increased with decreasing water velocity and increasing depth. Negative binomial models predicted higher catch rates of prawns in deeper water and in closer proximity to dams. Temporally, prawn densities decreased slightly in the summer, likely due to the mortality of older individuals, and then increased in autumn and winter with the emergence and recruitment of young of the year. Seasonal length frequencies showed that distinct juvenile and adult size classes exist throughout the year, suggesting prawns live from 1 to 2 years and may be able to reproduce multiple times during their life. Most juvenile prawns become reproductive adults in 1 year, and peak reproduction occurs from late July through October. Mean fecundity (189 eggs) and reproductive output (11.9 %) are similar to that in their native range. The current use of deep habitats by prawns likely makes them unavailable to most predators in the reservoirs. The distribution and role of Siberian prawns in the lower Snake River food web will probably continue to change as the population grows and warrants continued monitoring and investigation.

Keywords Invasive species · Abundance · Distribution · Freshwater shrimp · Zero-inflation modeling · Reproduction

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Introduction

Nonnative species pose a threat to the health and biodiversity of native plant and animal communities worldwide, and have been linked to the decline and endangerment of many species (Vitousek et al. 1996; Czech and Krausman 1997; Wilcove et al. 1998; Simberloff et al. 2005). Within aquatic systems, this threat is often manifested in altered food webs and competition for resources between native and nonnative species. For example, the introduction of the

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opossum shrimp *Mysis diluviana* Audzijonyte and Vainola, 2005 into many coldwater reservoirs and lakes in the USA has often resulted in a drastic reduction in cladoceran zooplankton populations and subsequent declines in planktivorous fish populations (Martinez and Bergersen 1991; Spencer et al. 1999). Similarly, the establishment of zebra mussels *Dreissena polymorpha* (Pallas, 1771) in the North American Great Lakes and elsewhere has reduced phytoplankton densities that in turn affects higher trophic levels (Holland 1993; Strayer et al. 1999). The invasion and establishment of nonnative species often result in hybrid food webs, which are typically poorly understood, yet are critically important to the conservation of native populations of aquatic organisms (Naiman et al. 2012).

The Siberian prawn *Palaemon modestus* (Heller, 1862; hereafter, prawns) is a relatively recent invader of the Columbia River and has rapidly expanded its range within the basin (Emmett et al. 2002; Haskell et al. 2006). In its native range, this species occurs in estuarine and freshwater habitats from Siberia south to China, Korea, and Taiwan (Holthius 1980). After their initial discovery in the lower Columbia River in 1995 (Emmett et al. 2002), prawns were next documented more than 575 km upstream at the fish collection facilities at Lower Granite and Little Goose dams (Fig. 1) in 1998, and were thought to have expanded their range upstream via transport in ballast water associated with barge traffic (Haskell et al. 2006). It was not until 2005 that prawns were observed in appreciable numbers (e.g., >50) at Lower Granite and other Snake River dams, and since that time their numbers have greatly increased with over 464,000 prawns being collected at Little Goose Dam in 2015 (Oregon Department of Fish and Wildlife, unpublished data). However, practically nothing is known about this species' distribution, abundance, and ecology in lower Snake River Reservoirs and their potential impact to the food web.

The establishment of prawns in the lower Snake River Reservoirs is important because most juvenile anadromous salmonids (many of which are federally listed species) produced in the Snake River basin pass through these reservoirs on their seaward migration. Additionally, many juvenile Snake River fall Chinook salmon *Oncorhynchus tshawytscha* (Walbaum, 1792) rear for extended periods in reservoir habitats (Connor et al. 2013; Tiffan et al. 2015). The role of prawns in the food web that supports juvenile salmon in Snake River Reservoirs is unknown but should be cause for concern given the limited data on their current impacts. In 2011, we began sampling Lower Granite and Little Goose Reservoirs to collect basic ecological information on Siberian prawns. Specifically, our objectives were to describe (1) the status and trends of the prawn population, (2) the spatiotemporal distribution of prawns, and (3) the seasonal changes in prawn population size structure and reproduction.

Study area

Prawns were collected mainly in Lower Granite and Little Goose Reservoirs, but dam passage data were also collected at Lower Granite, Little Goose, and Lower Monumental dams (Fig. 1). Lower Granite Reservoir is located on the lower Snake River in southeastern Washington and is impounded by Lower Granite Dam, which is located 173.0 river kilometers (rkm) upstream of the confluence of the Snake and Columbia Rivers. The reservoir extends 61.0 km upstream to Asotin, Washington. At rkm 224.0, the Clearwater River enters the reservoir at Lewiston, Idaho. Little Goose Reservoir is located downstream of Lower Granite Dam and is impounded by Little Goose Dam (rkm 113.1). Both reservoirs are run-of-the-river reservoirs and are operated primarily for hydropower and navigation. Flows can range from >4248 $m^3\ s^{-1}$ in the spring to 453 $m^3\ s^{-1}$ during winter. The average channel width in both reservoirs is about 630 m, and water depths average 17 m and range from less than 1 m in shallow shoreline areas to a maximum of 42 m. Normal pool elevations only fluctuate about 1.5 m. Lower Monumental Dam is located at rkm 66.9 and is downstream from Little Goose Dam.

Methods

To evaluate the status and trends of prawn populations (objective 1), we obtained daily prawn counts from juvenile fish bypass facilities at Lower Granite, Little Goose, and Lower Monumental dams (Fig. 1). Fish collection systems use screens to divert downstream migrating juvenile salmon and other incidental species away from turbines and into bypass channels and

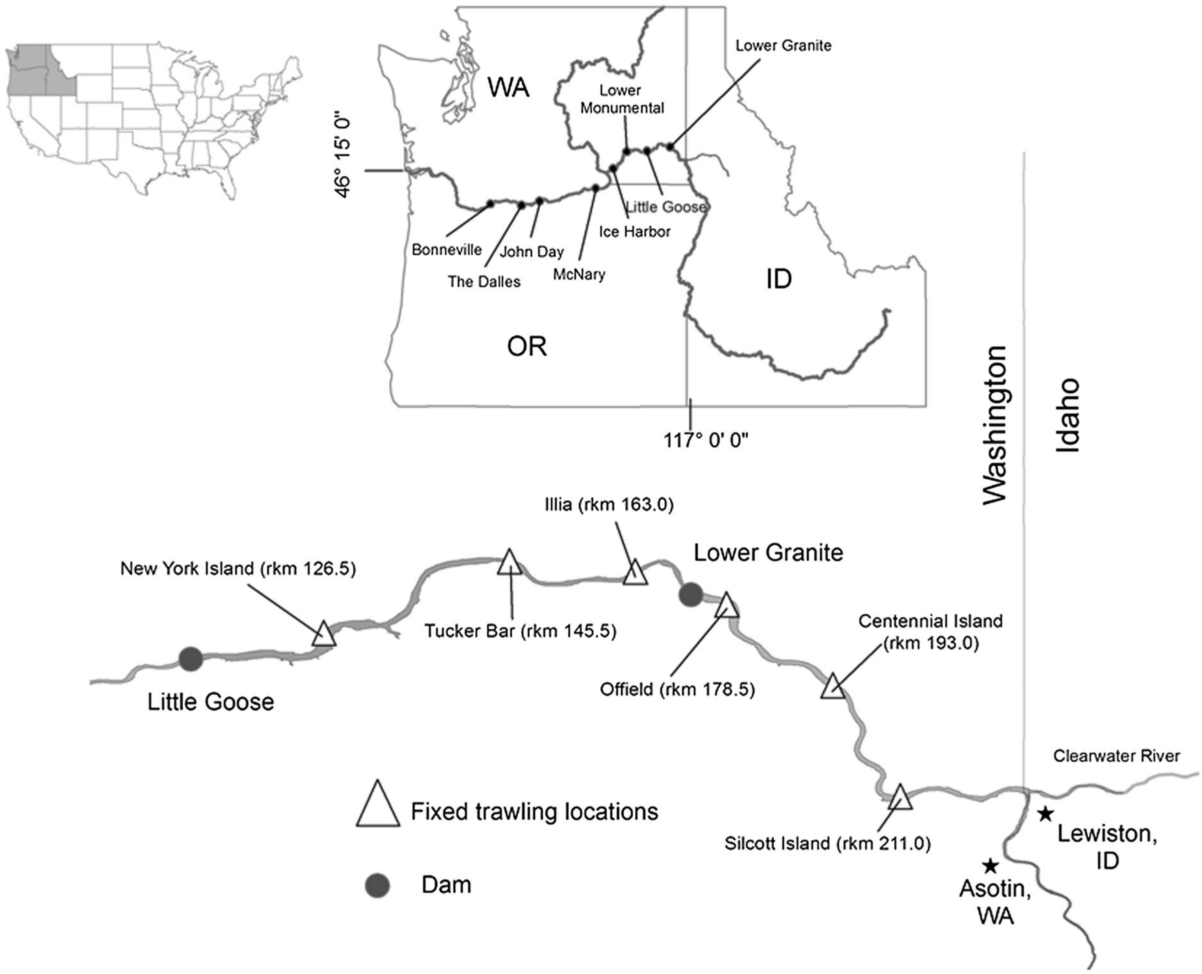

Fig. 1 A map showing the fixed sampling locations (*triangles*) within Lower Granite and Little Goose Reservoirs on the Snake River where Siberian prawns were collected during 2011–2013

holding tanks (Matthews et al. 1977). The daily catch is sorted, enumerated, and expanded by the system subsampling rate to derive a daily index of passage through the collection system for each species. We summed the daily passage of prawns to estimate the season-wide passage for the years 2004–2015. Prawn passage data for Lower Granite and Lower Monumental dams were obtained from the Washington Department of Fish and Wildlife, and data for Little Goose Dam were obtained from the Oregon Department of Fish and Wildlife.

To address remaining objectives, we collected prawns in monthly beam trawls from May 2011 to March 2013 in Lower Granite and Little Goose Reservoirs (Fig. 1). Each reservoir was divided into upper, middle, and lower reaches to ensure that samples were collected over a broad spatial area to incorporate longitudinal changes in depth, water velocity, and substrate. We then randomly selected up to seven 100-m transects (parallel to the current) at various locations in each reach, which were then fixed for the duration of the study. To sample a range of depths, four transects were in shallow water (<12 m) and three transects were in deep water (≥12 m), at each location, except at Illia where only shallow depths were available. Fixed sampling locations in Lower Granite Reservoir included Silcott Island (rkm 211.0), Centennial Island (rkm 193.0), and Offield (rkm 178.5). Fixed sampling locations in Little Goose Reservoir included Illia (rkm 163.0), Tucker Bar (rkm 145.5), and New York Island (rkm 126.5). We sampled an additional seven fixed locations (2–3 trawl transects per location) during the first year of sampling (May 2011–May 2012) at rkm 114.3, 118.3, 133.6, 152.1, 207.6, 213.2, and 216.5. During the second year of sampling, we replaced these seven fixed locations with transects sampled at random locations (three transects/reach/month). Once sampled, these locations were not sampled again, but new sites were selected that were at least 0.5 km distant from any previously sample location. These new random locations provided more variability to better assess the spatial distribution of prawns throughout the reservoirs. At each random location, three transects were spaced equally across the cross section, regardless of depth.

Sample collection

We used a beam trawl to collect benthic fauna at each 100-m transect. The trawl had a rectangular opening that measured 2 m wide × 0.5 m high and a 3.7-m-long net that tapered to a cod end. The trawl was constructed of 6.3-mm nylon delta mesh. The last 1.2 m of the cod end contained an internal liner constructed of 1.6-mm nylon delta mesh. Heavy nylon mesh was attached around the outside of the cod end to reduce chafing. A tickle chain was attached across the inside of the bottom of the trawl frame in front of the lead line to move benthic organisms off the bottom during trawling. Trawl samples were poured through a 600-μm sieve to remove silt and debris and then preserved in 90 % ethanol. When a large trawl sample was collected, a random subsample was preserved. In most instances, prawns were removed, enumerated, and preserved separately from the total sample before a subsample was taken to minimize the effect of subsample error on prawn estimates.

Laboratory methods

All prawns were blotted to remove excess ethanol and weighed individually (±0.001 g, wet). A random subsample of prawns, encompassing a broad size range, was selected to develop a carapace length (CL)–weight relationship. Initially, prawns were measured (±0.001 mm) from the tip of the rostrum to the medial posterior margin of the carapace using an ocular micrometer ($CL_{rostrum}$). However, the rostrum was often broken, so we switched to measuring from the posterior margin of the eye orbit to the medial posterior margin of the carapace (CL). We converted the original measurements to the new measurement using the relationship $CL = 0.5271 \times CL_{rostrum} - 0.1091$ ($n = 555$, $r^2 = 0.98$). Remaining individual prawns were weighed, and their CL was estimated with the relationship $\text{Weight} = 0.0006 \times CL^{3.03}$ ($r^2 = 0.97$, $n = 1664$). The weights of all individual prawns in a sample were summed to determine their total weight. If the processed sample was a subsample, then its weight was multiplied by the subsampling rate to estimate a total sample weight, which was then used to estimate the total number of prawns in the sample.

Data analysis

Population status and trends

To assess the population status and annual trends in prawn abundance in the lower Snake River, we used linear regression to describe the relationship between $\log_e$-transformed annual prawn estimates collected at the juvenile fish facilities and year. We determined that the population was increasing if the relationship was significant ($P < 0.05$) and the slope positive. The slope of the regression, which is the instantaneous per capita growth rate (r), was assumed to be representative of the population within the reservoirs. Dam-specific regressions incorporated data from the first year that prawns were collected through 2015.

Spatiotemporal distribution

We examined temporal trends in prawn densities at fixed locations graphically and by calculating descriptive statistics. The total number of prawns collected in individual trawls were converted to densities (# m^{-2}) based on the distance trawled (~100 m). Data were pooled within each reach (i.e., upper, middle, or lower), depth strata (i.e., deep or shallow), season (i.e., spring, summer, autumn, and winter), and reservoir. Each season comprised 3 months (e.g., spring: March, April, and May). We calculated and plotted mean seasonal prawn density (# m^{-2}) and biomass (wet; g m^{-2}); however, for the sake of brevity, we only present statistical analyses of density because biomass analyses yielded similar results.

Owing to the preponderance of zero-prawn catches in many trawls, we used data from the random trawls in each reservoir and zero-inflated negative binomial regression (ZINB) to identify the variables that most influenced the spatial distribution of prawns. We standardized prawn catches to # 100 m^{-2} for use in regression. Zero-inflated models, which are applicable when excess zero observations in the data cause overdispersion, assume that some of the zero observations are caused by an alternative stochastic process (Lambert 1992). The ZINB model consists of two parts: a degenerate component that models the probability of a trawl containing zero prawns (logistic model), and a negative binomial model (including zero and positive catch values) whose estimations are modified based on the zero-probability model (i.e., logistic model). We initially fitted a zero-inflated Poisson model (ZIP); however, overdispersion was still evident (Lower Granite Reservoir: scaled Pearson $\chi^2 = 2.12$, Little Goose Reservoir: scaled Pearson $\chi^2 = 12.456$), and the null hypothesis of no overdispersion was rejected (Lower Granite Reservoir: $P < 0.001$, Little Goose Reservoir: $P < 0.001$). We used a ZINB model in which both model parts were a function of three covariates: season (four levels), distance from dam (measured in rkm), and depth (m). Mean water column velocity (cm s^{-1}) was also included as a covariate in the Lower Granite Reservoir model because velocity data were available for that reservoir. Velocities were estimated for each trawl transect from a two-dimensional hydrodynamic model (Tiffan et al. 2015) as follows. First, at each transect, velocities were estimated at each of the five discharges (1388, 3342, 4050, 4361, and 5664 m^3 s^{-1}) modeled by Tiffan et al. (2015). These were then used to construct 96 transect-specific regressions to predict velocity from discharge (mean $r^2 = 0.97$, range 0.07–0.99). Discharge data from each sample date (CBR 2015) were then used in transect-specific regressions to estimate velocity for that day and transect. We selected the ZINB model with the lowest Bayesian information criterion (BIC) after fitting the full model and various reduced candidate models using Procedure GENMOD (SAS 2010). Model fit was assessed by comparing the likelihood ratio of the full model to the null model and using Vuong's test to determine whether the ZINB models were an improvement over negative binomial only models (Vuong 1989).

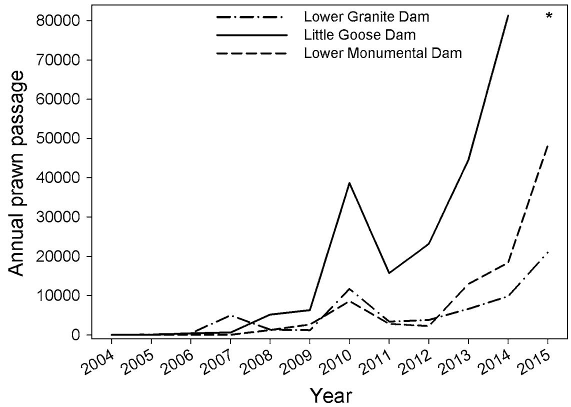

Fig. 2 Annual passage estimates of Siberian prawns at lower Snake River dams. The *asterisk* represents a passage of 464,586 prawns at Little Goose Dam in 2015

Size distribution and reproduction

We grouped prawn CL data into 1-mm bins for both reservoirs and constructed monthly CL–frequency histograms to graphically examine temporal patterns in size distributions. We also randomly selected 128 ovigerous prawns collected from July to December 2011 to estimate fecundity. Eggs from individual females were removed, counted, and weighed (g, wet). The percent reproductive output of each female prawn was calculated as the total egg mass divided by the mass of the female without eggs multiplied by 100 (Oh et al. 2002). We calculated and plotted the monthly percentage of ovigerous prawns >8 mm CL to determine reproduction timing and its peak. Only prawns >8 mm were examined because the smallest ovigerous prawn observed was 9 mm. The sex of non-ovigerous female prawns was distinguished from males by the lack of a ventral protuberance between the pleopods on the first two abdominal segments and the lack of a short, ridge-like ventral protuberance between the last pair of walking legs, which were widely spaced (St. John et al. 2014).

Results

Population status and trends

Estimates of annual prawn passage increased exponentially from 2004 to 2015 at all three dams (Fig. 2).

Prawn passage was highest at Little Goose Dam and displayed the highest exponential growth rate of 0.68 ($F_{1,8} = 69.03$, $r^2 = 0.90$, $P < 0.0001$). Passage estimates increased from 399 in 2006 to a high of 464,586 in 2015. Passage showed a marked increase in 2010 when an estimated 38,675 prawns passed the dam. Prawn passage at Lower Granite Dam showed a lower exponential growth rate of 0.56 ($F_{1,10} = 23.63$, $r^2 = 0.67$, $P = 0.0007$). Passage increased from a low of five prawns in 2004 to a high of 20,979 prawns in 2015. The estimates showed peaks in 2007 (5008 prawns) and 2010 (11,711 prawns), but strong $\log_e$-linear growth thereafter. Prawn passage at Lower Monumental Dam had the lowest exponential growth rate of 0.43 ($F_{1,6} = 14.84$, $r^2 = 0.66$, $P = 0.0084$). Passage estimates increased from 1,233 in 2008 to 48,243 in 2015 with a small peak in 2010. During most years, over 90 % of the prawns were collected in juvenile fish facilities from mid-July to mid-October at Lower Granite Dam and from mid-July to the end of October (also the end of seasonal facility operations) at Little Goose Dam. Peak daily passage generally occurred during either August or September and steadily declined thereafter. Interestingly, over 80 % of the prawns collected at Lower Granite and Little Goose dams in 2013 were females, which was true for prawns collected at Little Goose Dam in 2014, but not at Lower Granite Dam where the sex ratio was closer to 50:50 in 2014.

Spatiotemporal distribution

We collected an estimated 17,170 Siberian prawns during our study in both fixed and random trawls in Lower Granite and Little Goose Reservoirs. Surface temperatures at trawl locations ranged from 2.3 (January) to 23.5 °C (August) in Lower Granite Reservoir and 3.1 (February) to 23.5 °C (August) in Little Goose Reservoir. Water velocities ranged from 0 to 113 cm s^{-1} in Lower Granite Reservoir. Prawns were present in 45 % (597/1,335 trawls) of all trawls and were collected in all three reaches of both reservoirs. They were more frequently collected in trawls from Little Goose Reservoir (55 %; 377/682) than Lower Granite Reservoir (34 %; 220/653). For both reservoirs, prawns were more frequently collected from lower reaches (63 %; 273/435) than middle (50 %; 236/470) or upper (20 %; 88/430) reaches, and from deep sites (64 %; 400/626) than shallow sites (28 %; 197/710). Prawns were collected in depths ranging from 1.8 to 37.8 m and in velocities up to 55 cm s^{-1}. In Lower Granite Reservoir, prawn presence was associated with mean velocities of 8 cm s^{-1} in the lower reach, 12 cm s^{-1} in the middle reach, and 11 cm s^{-1} in the upper reach. The highest density of prawns (5.1 prawns m^{-2}) was observed near the Little Goose Dam forebay (rkm 114.3). Prawn densities were generally lowest in upper reservoir reaches and were collected as far upriver in Lower Granite Reservoir as the Port of Wilma (rkm 216.5) near Clarkston, Washington. The highest density of prawns in an upper reach (0.26 prawns m^{-2}) occurred in a shallow site at Illia (Little Goose Reservoir) in January.

Trends in prawn density and biomass were similar to frequencies of capture. Seasonal differences in mean prawn densities were most obvious in Little Goose Reservoir (Fig. 3). Mean prawn densities in deep trawls in the lower reach decreased slightly from spring (0.36 m^{-2}) to summer (0.29 m^{-2}) and then increased in autumn (0.52 m^{-2}) and winter (0.58 m^{-2}). Mean prawn densities in deep trawls in the middle reach also decreased slightly from spring (0.08 m^{-2}) to summer (0.06 m^{-2}) and then increased in autumn (0.15 m^{-2}) and winter (0.13 m^{-2}). Densities in shallow trawls were always low compared to deep trawls, the highest being 0.07 m^{-2} in the lower reach of Little Goose Reservoir, and no seasonal trends between shallow and deep trawls were apparent. In Lower Granite Reservoir, seasonal differences in prawn densities followed the same trend as those from deep trawls in lower and middle reaches in Little Goose Reservoir, but changes were minimal (lower reach: spring = 0.10 m^{-2}, summer = 0.07 m^{-2}, autumn = 0.09 m^{-2}, winter = 0.11 m^{-2}; Fig. 3). The highest prawn density in shallow trawls in Lower Granite Reservoir was observed during the summer in the lower reach (0.07 m^{-2}). Trends in prawn biomass generally followed those of prawn densities for both reservoirs (Supplement Fig. S1). However, an increase in biomass in the fall and winter was not apparent, despite an apparent increase in density.

Results from the ZINB regressions support findings from descriptive statistics and figures. Fully parameterized models for both reservoirs significantly fit the data over the null models (Lower Granite Reservoir: $\chi^2_{10} = 168.7$, $P < 0.001$; Little Goose Reservoir: $\chi^2_6 = 4{,}213$, $P < 0.001$), showed no

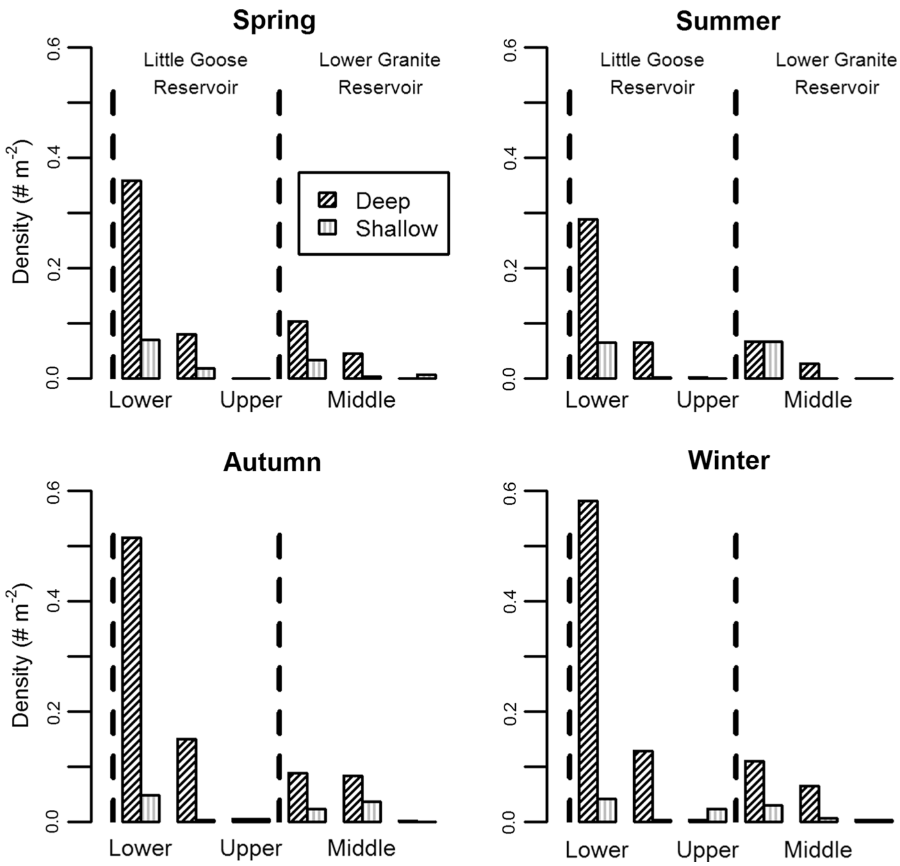

Fig. 3 Seasonal densities of Siberian prawns collected at *shallow* (<12 m) and deep (≥12 m) fixed locations in three reaches (*lower, middle, upper*) of Little Goose and Lower Granite Reservoirs on the Snake River, 2011–2013. *Vertical dashed lines* represent dams

evidence of overdispersion at $\alpha = 0.05$ (Lower Granite Reservoir: scaled Pearson $\chi^2 = 1.086$, $P = 0.2151$; Little Goose Reservoir: scaled Pearson $\chi^2 = 1.147$, $P = 0.0704$), and better captured the shape of the distribution of the relative frequencies. Vuong tests indicated a significant improvement in model fit using ZINB models over standard negative binomial models (Lower Granite Reservoir: $Z = 2.3946$, $P = 0.0166$; Little Goose Reservoir: $Z = 2.4113$, $P = 0.0159$), and Wald 95 % confidence intervals of the dispersion parameter estimate were greater than zero. For Lower Granite Reservoir, the model with the lowest BIC (432.53, Table 1) indicated that distance (km from dam) positively influenced the probability of collecting zero prawns in a trawl (100-m-long trawl), and that distance and velocity (cm s^{-1}) negatively influenced the count (# $trawl^{-1}$) of prawns collected (Table 2). Zero-model results predicted that for every 1 km upriver from Lower Granite Dam, the probability of a true zero-prawn catch in a 100-m trawl transect increased by a factor of 1.09 (Supplement Fig. S2). The negative binomial model predicted that the count of prawns decreased by a factor of 0.97 for every 1 km upriver from Lower Granite Dam a trawl was made (while velocity was kept constant) and by a factor of 0.96 for every 1-cm s^{-1} increase in velocity (while distance was kept constant; Fig. 4). For Little Goose Reservoir, the model with the lowest BIC (1307.65, Table 1) only included depth and distance. Zero-model results predicted that for every 1-m decrease in depth, the probability of collecting zero prawns in a trawl increased by a factor of 0.44 (Supplement Fig. S2). The negative binomial model predicted that the count of prawns increased by a factor of 1.09 for every 1-m increase in depth while distance was held constant. Conversely, the model predicted that the number of prawns increased by a factor of 0.93 for every 1-km closer to Little Goose Dam while depth was held constant (Fig. 4).

Table 1 Comparison of zero-inflated negative binomial models (full and reduced) of Siberian prawn counts (# 100-m trawl^{-1}) regressed on season, distance from dam (km), depth (m), and water velocity (cm s^{-1}) for Lower Granite and Little Goose Reservoirs in the Snake River, 2012–2013

Model	Deviance	BIC	ΔBIC
Lower Granite Reservoir			
Count = distance + velocity; Zero model = distance	401.6	432.5	0.0
Count = distance + depth + velocity; Zero model = distance	401.6	437.7	5.2
Count = season + distance + depth + velocity; Zero model = distance	400.1	451.5	19.0
Full model: Count = season + distance + depth + velocity + distance × depth + distance × velocity + depth × velocity; zero model = season + distance + depth + velocity + distance × depth + distance × velocity + depth × velocity	381.7	489.7	57.2
Little Goose Reservoir			
Count = distance + depth; Zero model = depth	1275.2	1307.6	0.0
Count = season + distance + depth; Zero model = depth	1267.3	1316.0	8.4
Count = distance + depth; Zero model = distance	1290.1	1322.5	14.9
Full model: Count = season + distance + depth + distance × depth; zero model = season + distance + depth + distance × depth	1247.8	1328.9	21.3

Not all model results are shown

Size distribution and reproduction

Monthly carapace length–frequency distributions showed two distinct size classes of prawns progressing through time (Fig. 5). The largest prawn observed was 17 mm CL. Growth of prawns, as seen in the rightward shift in the size-class modes, was greatest in the spring and early summer for both years (Fig. 5). These two size classes, which we classified as juveniles and adults, merged by late summer (August–September), coinciding with the emergence of a new juvenile size class. The new adult size distribution then stabilized for the next few months, followed by a slight decrease in the modes, which we attributed to mortality of the largest individuals. Adult prawn densities also declined during this same time, suggesting many adults die after a year of life, but some survive as evidenced by the presence of the larger size-class mode throughout the year. New juveniles continued to appear from August to October during which growth modestly increased before slowing through winter. During the autumn and winter, prawn densities increased more dramatically than biomass because the population was largely composed of smaller juveniles. During the first winter of sampling, modes of the adult and juvenile size classes remained separate, suggesting that no juveniles born the previous summer were able to grow to adulthood before the following summer (Fig. 5). During the second winter, modes of adult and juvenile size classes were still separate, but the distinction was not as evident compared to the first winter. These results suggest the life span of most prawns in the Snake River is probably around 1 year, but could range from 1.6 to 2.1 years for some individuals.

Ovigerous female prawns were collected from May to January in 2011–2012 and from July to October in 2012, but most of the reproduction occurred from late July to early October (Fig. 6). Peak reproduction (peak in percent ovigerous prawns) in Lower Granite Reservoir occurred about a month earlier than in Little Goose Reservoir for both years. Ovigerous females had a mean carapace length of 12.7 mm (SD = 1.5 mm, range 9–16.3 mm) and a mean total weight of 1.4 g (SD = 0.4 g, range 0.7–2.4 g; Table 3). The mean number of eggs per female was 189 (SD = 55, range 66–332) and reproductive output averaged 11.9 % (range 1.7–23.5 %; Table 3). We found ovigerous females from the largest adult size

Table 2 Maximum likelihood parameter estimates for best fitting (lowest BIC) zero-inflated negative binomial regressions of Siberian prawn counts (# 100-m trawl^{-1}) and covariates in Lower Granite and Little Goose Reservoirs on the Snake River, 2012–2013

Parameter	*DF*	Estimate	SE	Wald 95 % confidence limits		X^2	$P > X^2$
				Lower	Upper		
Lower Granite Reservoir: negative binomial model							
Intercept	1	2.300	0.365	1.581	3.011	39.61	<0.001
Distance to dam	1	−0.038	0.016	−0.070	−0.006	5.50	0.019
Velocity	1	−0.046	0.0191	−0.830	−0.008	5.66	0.017
Dispersion	1	2.296	0.958	1.013	5.202		
Lower Granite Reservoir: zero model							
Intercept	1	−2.929	1.800	−6.457	0.560	2.65	0.104
Distance to dam	1	0.091	0.043	0.043	0.174	4.46	0.034
Little Goose Reservoir: negative binomial model							
Intercept	1	2.272	0.390	1.508	3.036	34.00	<0.001
Distance to dam	1	−0.073	0.010	−0.092	−0.0546	59.30	<0.001
Depth	1	0.090	0.017	0.058	0.123	29.54	<0.001
Dispersion	1	2.385	0.278	1.897	2.998		
Little Goose Reservoir: zero model							
Intercept	1	5.083	2.053	1.059	9.108	6.13	0.013
Depth	1	−0.082	0.315	−1.435	−0.202	6.76	0.009

class in May and June (12–14 mm CL), and from a wide range of size classes during August and September (9–17 mm CL). Incorporating these results with the CL–frequency histogram results (Fig. 5) suggests that prawns that live more than 1 year may be able to reproduce multiple times during their life.

Discussion

Since their initial detection in the late 1990s, Siberian prawns have become well established in the lower Snake River Reservoirs where their populations continue to grow exponentially. The high rate of unbounded population growth since the mid-2000s suggest that run-of-the-river reservoirs are a favorable environment, and population growth will likely continue in the lower Snake River. Similar growth was observed in the Siberian prawn population in the San Francisco Estuary, USA, after their initial introduction in the late 1990s (Brown and Hieb 2014). The population there grew rapidly in the first few years but then decreased and stabilized soon after (Brown and Hieb 2014). Predation by striped bass *Morone saxatilis* (Walbaum, 1792) and competition with a variety of other prawn species (e.g., *Crangon franciscorum* Stimpson, 1859, *Syncaris pacifica* [Holmes, 1895], *Palaemon macrodactylus* Rathbun, 1902; Nobriga and Feyrer 2008, Brown and Hieb 2014) may have curtailed the population growth of prawns in that system. However, in Lower Granite and Little Goose Reservoirs, predation by piscivorous smallmouth bass *Micropterus dolomieu* Lacepède, 1802 and northern pikeminnow *Ptychocheilus oregonensis* (Richardson, 1836) is probably nominal given differences in current habitat use between these species and prawns. Additionally, there are no other large prawn species to compete with in the Snake River. The only other larger-sized crustacean is the native signal crayfish *Pacifastacus leniusculus* (Dana, 1852). At this time, predation or competition may not be significant enough to curb prawn population growth.

Our inferences about prawn population growth are based on analyses of dam passage data. In order for dam passage to be a useful estimator of population growth rate, it must be a function of population size. For prawns to be entrained into the fish bypass system, they must swim up about 10 m into the water column to be guided by fish screens that extend down into the upper one-half of the turbine intakes (Matthews et al. 1977). Water velocities in the forebay are typically low ($\sim$7 cm s^{-1}) during late summer when peak prawn passage occurs, suggesting that prawns are entrained as a result of some kind of behavioral vertical migration

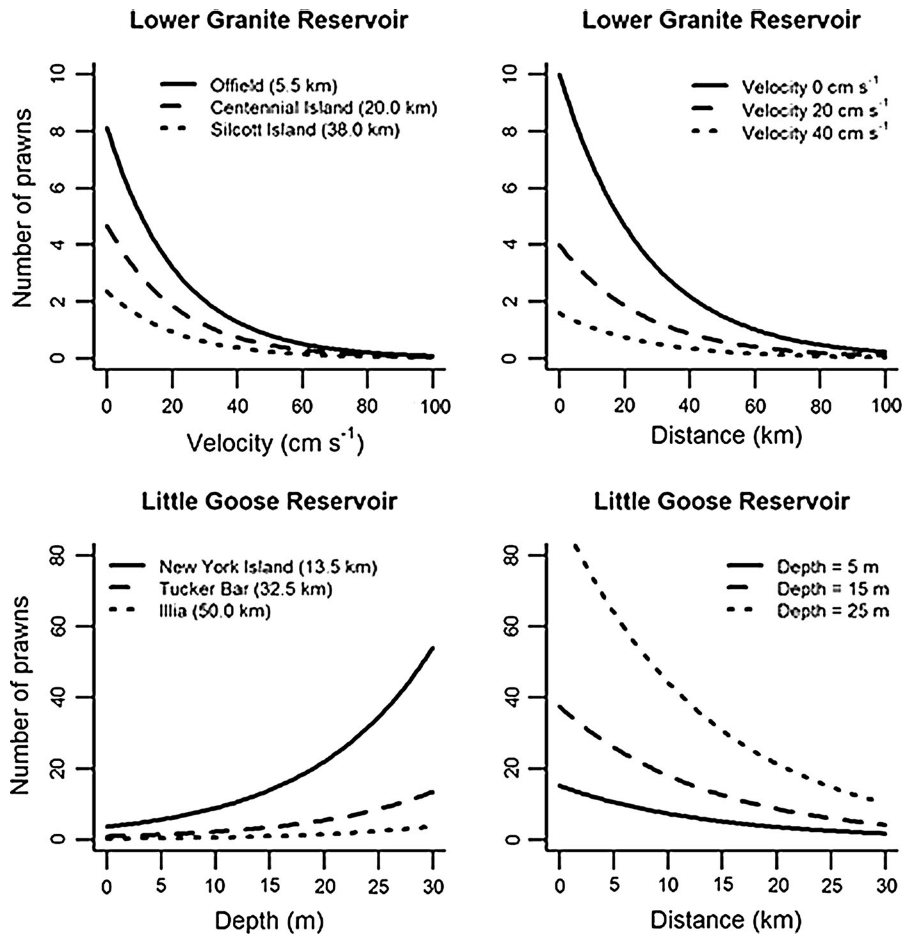

Fig. 4 Predicted number of prawns in 100-m beam trawls as a function of covariates from zero-inflated negative binomial regressions of prawn counts Lower Granite (*top*) and Little Goose (*bottom*) Reservoirs. *Top left*: Predicted number of prawns with changes in water velocity at three locations (distance held constant). *Top right*: Predicted number of prawns with changes in distance (km upstream of dam) at three constant velocities. *Bottom left*: Predicted number of prawns with changes in depth at three locations (distance held constant). *Bottom right*: Predicted number of prawns with changes in distance at three constant depths

as opposed to being dislodged by current. Given that most prawns collected at Lower Granite and Little Goose dams in 2013 were females (over 80 %), this passage may be linked to some sort of reproductive behavior. Sex ratios of prawns collected in beam trawls varied monthly but were also skewed toward females in September of 2012 and 2013 (St. John et al. 2014), similar to the dam ratios. Whether vertical migration of Siberian Prawns in the Snake River Reservoirs is related to reproduction or triggered by another behavioral response, the strength of the log-transformed regressions suggests that prawn passage is likely a good predictor of population growth at this time, especially since densities are highest near the dam forebays.

The successful establishment and growth of the prawn population in Snake River Reservoirs, in addition to the lack of predators and competitors, is probably attributable to their broad habitat preferences and requirements, although such information is sparse. Prawn populations have been found in a broad range of depths and temperatures. Oh et al. (2002) reported that Siberian prawns in Young-am Lake, Korea, were found in depths ranging from 0.3 to 8.0 m and Wang et al. (2011) similarly collected prawns from a shallow lake in China averaging 8.4 m deep. We collected prawns in depths ranging from 1.8 to 37.8 m, but densities were higher in deeper habitats of both reservoirs. Prawns may prefer deeper habitats in the Snake River to escape predation or to exploit abundant food resources such as *Neomysis mercedis* Holmes, 1897, which are found there (St. John et al. 2014).

The temperatures that prawns were exposed to in the Snake River (2.3–23.5 °C) were similar to those experienced by Siberian prawns in Lake Chaohu, China (3.6–30.9 °C; Xu et al. 2008), and a closely related species (*P. paucidens* de Haan, 1844) in Sukdang Lake, Korea (4.2–25.0 °C, Kim et al. 2008);

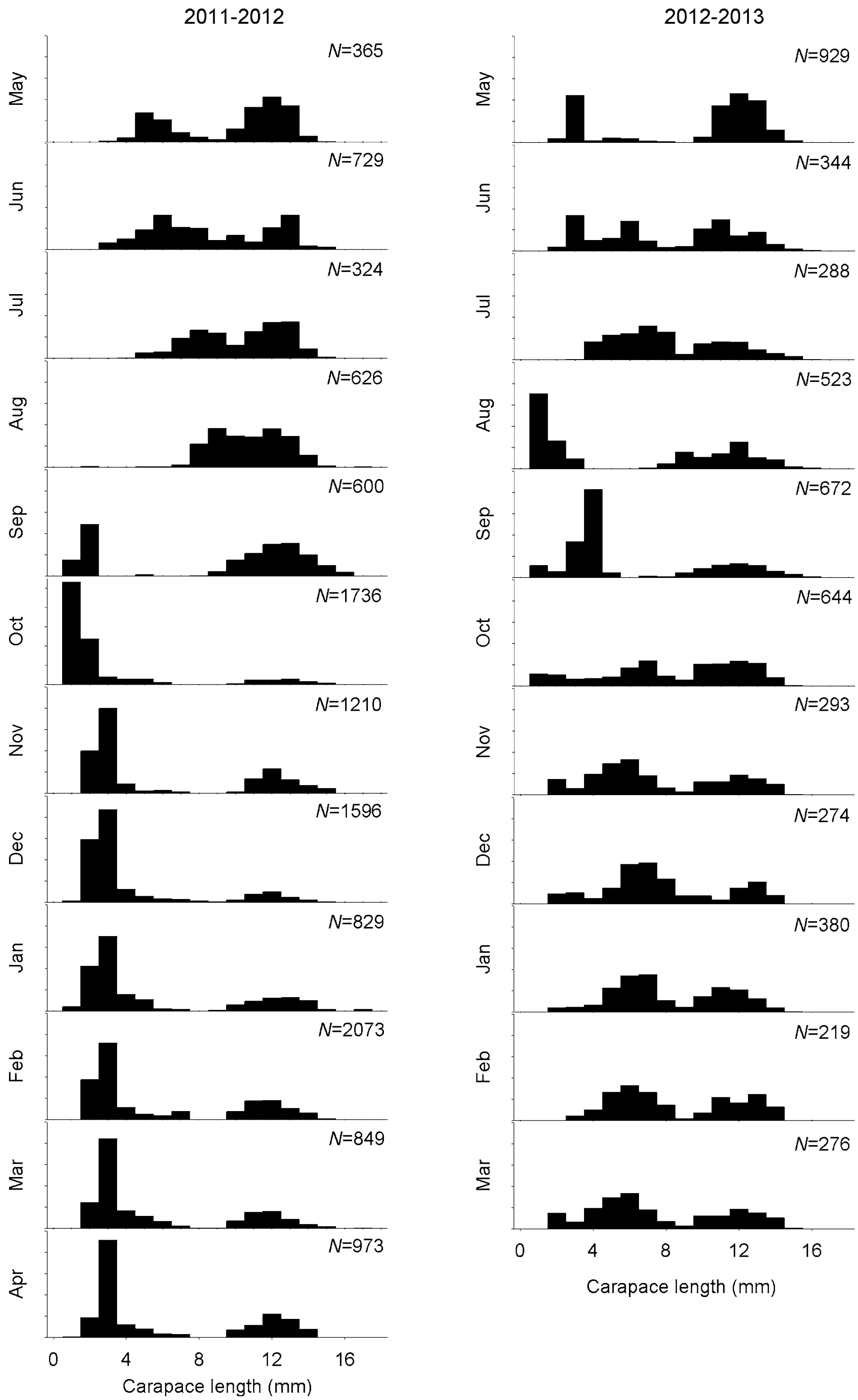

Fig. 5 Monthly relative carapace length–frequency distribution of Siberian prawns sampled from May 2011 to March 2013 in the Snake River. *N* in each panel is the number of prawns measured

however, they were lower than those experienced by Siberian prawns in other Asian lakes (11.5–29.5 °C, Oh et al. 2002; 19.7–32.1 °C, Wang et al. 2011). Prawns were able to survive the cold temperatures of the Snake River during winter, but length frequencies showed that growth was slow during this time. The

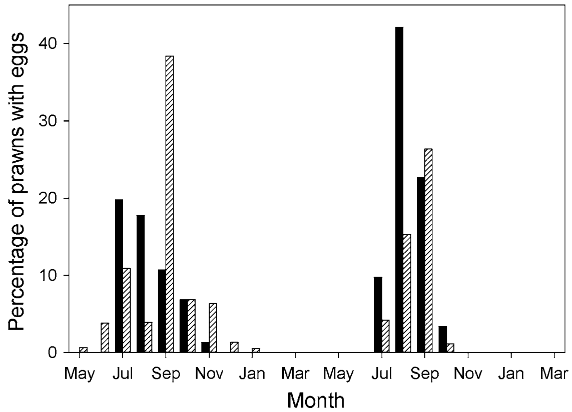

Fig. 6 Percentage of Siberian prawns (>8 mm CL) with eggs collected by month in Lower Granite Reservoir (*black bars*) and Little Goose Reservoir (*hatched bars*) on the Snake River, 2011–2013

Table 3 Summary of fecundity information from Siberian prawns collected in Lower Granite and Little Goose Reservoirs, 2011–2012

Metric	*N*	Mean	SD	Range
Egg count	128	189	54.9	66–332
Reproductive output (%)[a]	122	11.9	4.6	2.6–20
Carapace length (mm)	127	12.7	1.5	9–16.3
Total prawn mass (g)	129	1.4	0.4	0.7–2.4

N is the number of prawns examined

[a] (egg mass/prawn mass without eggs) × 100

warmer temperatures during the rest of the year were adequate to support growth and reproduction. The maximum temperatures that Siberian prawns can tolerate in their native range (29.5 °C, Oh et al. 2002; 32.1 °C, Kim et al. 2008) indicate that prawns should not be limited by high temperatures in the Snake River, which generally do not typically exceed 20 °C (CBR 2015). Summer temperature differences between Lower Granite and Little Goose Reservoirs may explain differences in prawn abundance between the two reservoirs. Cool flows from the Clearwater River enter Lower Granite Reservoir during summer causing temperatures to vary from about 22 °C at the surface to about 15 °C at the bottom (Tiffan et al. 2009). The cooler summer temperatures in Lower Granite Reservoir may retard prawn growth and reproduction to some extent compared to Little Goose Reservoir where summer temperatures are generally homothermic and average about 20 °C (Tiffan et al. 2003).

Although water velocity was only analyzed in Lower Granite Reservoir, it appears to be a factor controlling prawn distribution. As the proximity to a dam increased, both the probabilities of collecting prawns and the number caught increased. This followed the trend of decreasing water velocity at lower reservoir locations where depths and cross-sectional areas were greatest and velocities lowest. The greater abundance of prawns in low-velocity habitats is consistent with caridean shrimp use of low current velocities where they are known to inhabit rivers (Conaway and Hrabik 1997; Bowles et al. 2000). Barko and Hrabik (2004) found both Ohio shrimp *Macrobrachium ohione* (Smith, 1874) and glass shrimp *Palaemonetes kadiakensis* Rathbun, 1902 in velocities averaging 10 cm s^{-1} in the Mississippi River, and Richardson and Cook (2006) observed the highest catch of *Paratya australiensis* Kemp, 1917 and *Caridina mccullochi* Roux, 1926 in velocities less than 22 cm s^{-1} in Australian rivers. We observed the highest densities of prawns in the lower reach of Lower Granite Reservoir where velocities averaged 8 cm s^{-1}, but considerably lower densities in the middle and upper reaches where average velocities exceeded 10 cm s^{-1}. It is likely that Siberian prawns have a relatively low velocity tolerance which may explain why relatively few prawns were collected in upper reservoir reaches where velocities were highest. Prawns were most frequently collected in upper reaches during autumn and winter when flows and velocities were lowest, which may allow them to move upstream during these times. Furthermore, the only places where prawn densities were higher in shallow sites than in deeper sites were in upper reaches (Fig. 3), suggesting prawns may use nearshore or slackwater areas for velocity refuge. Prawns collected in the upper reach of Lower Granite were typically large adults, suggesting they may have a higher velocity threshold than juveniles, which is similar to other freshwater prawns (Hancock and Bunn 1999, Lee and Fielder 1984). Low-velocity habitats may be important for sustaining up-reservoir prawn populations.

The successful establishment and growth of prawn populations in Snake River Reservoirs is also probably influenced by the fact that many of their reproductive attributes are similar to those in their native range (Oh et al. 2002). Ovigerous females averaged 12.7 mm CL and carried an average of 189 eggs (SD = 55, range

66–332). This compares favorably with Oh et al. (2002) who found that ovigerous females averaged 11.7 mm CL and carried and average of 182 eggs (SD = 68, range 60–353). The percent reproductive output we observed (11.9 ± 4.6), however, was lower than the 17.4 ± 4.6 reported by Oh et al. (2002) and was on the low end of the range for other Palaemonid shrimps (12–22 %; Anger and Moreira 1998). Peak reproduction timing of prawns in the Snake River is from July through October, which is similar to that reported by Oh et al. (2002), but more compressed than the March to December reproductive season in the San Francisco Estuary reported by Brown and Hieb (2014). We were unable to determine whether female prawns are able to reach maturity and reproduce before their first winter, but the few smaller (~9–10 mm CL) ovigerous females we collected each year in late summer suggest the possibility. The warmer temperatures in Little Goose Reservoir may facilitate rapid growth and maturation to adulthood in the first summer of life. This may result in a longer reproductive window that may explain the later peak in ovigerous female prawns that was observed in that reservoir. We suspect that the majority of reproductive females are 1-year-old adults produced from the previous year's brood, but females that live longer may be able to produce more than one brood during their lifetime and thus contribute to higher population growth rates.

Monthly prawn length frequencies confirmed the timing of summer reproduction with the emergence of the juvenile size class in late summer and autumn. This resulted in increased densities, but not biomass, during this time. The presence of only two size classes (juvenile and adult) is common in caridean shrimp populations (e.g., Guerao et al. 1994; Kim et al. 2008). The presence of the adult size-class mode throughout the year coupled with the continuous presence of two size classes suggests that prawns in the Snake River live longer than 1 year with some individuals living up to 2.1 years. This is longer than the 1.1–1.3-year life span reported by Oh et al. (2002). One reason for this is that cooler temperatures in the Snake River may slow growth and increase longevity. In Sweden, where temperatures are cold and the growing season short, up to 4-year classes of *P. adsperus* Rathke, 1837 were distinguished by Baden and Pihl (1984). While we acknowledge these authors examined a different prawn species from a different geographic area, the same could be true to some extent for prawns in the Snake River. The greater longevity of prawns in the Snake River compared to their native range is consistent with life history theory of caridean shrimp which suggests that prawns living at lower latitudes (thus warmer temperatures) have shorter longevity and earlier maturation (Bauer 1992; Guerao et al. 1994; Oh et al. 2002).

In conclusion, Siberian prawn populations are well established in the Snake River and are growing at exponential rates, although their effects on the food web are yet to be fully understood. Prawns could pose their greatest risk to biotic communities in littoral habitats by competing with Endangered Species Act-listed salmonids and resident fishes. They could also compete with salmon smolts for food in pelagic habitats if they make vertical migrations to feed, although we did not investigate the prevalence of this behavior. In deeper, benthic habitats, prawns may pose a competitive threat to native signal crayfish because they occupy similar habitats. Prawns are unlikely to be prey for migrating salmonids because of their large size, but they could become important prey for predators such as nonnative smallmouth bass, particularly if they expand their use of shallow-water habitats. Although little monitoring or research is being directed toward invasive species in the lower Snake River, such efforts could increase our understanding of prawn ecology, their impacts to other species, and may provide insights into their future control.

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