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FEEDING ECOLOGY OF NON-NATIVE SIBERIAN PRAWNS, *PALAEMON MODESTUS* (HELLER, 1862) (DECAPODA, PALAEMONIDAE), IN THE LOWER SNAKE RIVER, WASHINGTON, U.S.A.

BY

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ABSTRACT

We used both stomach content and stable isotope analyses to describe the feeding ecology of Siberian prawns *Palaemon modestus* (Heller, 1862), a non-native caridean shrimp that is a relatively recent invader of the lower Snake River. Based on identifiable prey in stomachs, the opossum shrimp *Neomysis mercedis* Holmes, 1896 comprised up to 34-55% (by weight) of diets of juvenile to adult *P. modestus*, which showed little seasonal variation. Other predominant items/taxa consumed included detritus, amphipods, dipteran larvae, and oligochaetes. Stable isotope analysis supported diet results and also suggested that much of the food consumed by *P. modestus* that was not identifiable came from benthic sources — predominantly invertebrates of lower trophic levels and detritus. *Palaemon modestus* consumption of *N. mercedis* may pose a competitive threat to juvenile salmon and resident fishes which also rely heavily on that prey.

RÉSUMÉ

Nous avons utilisé à la fois les contenus stomacaux et les analyses par isotope stable pour décrire l'écologie de l'alimentation de la crevette de Sibérie *Palaemon modestus* (Heller, 1862), une crevette non indigène qui est un envahisseur relativement récent du bas de la rivière Snake. Sur la base des proies identifiables dans l'estomac, la mysidacé *Neomysis mercedis* Holmes, 1896, représente jusqu'à 34-55% (en poids) du régime des juvéniles aux adultes de *P. modestus*, avec peu de variations saisonnières. Les autres items/taxa consommés incluent des détritus, amphipodes, larves de diptères et oligochètes. Les analyses par isotopes stables supportent les résultats du régime et suggèrent aussi que l'essentiel de la nourriture consommée par *P. modestus*, qui n'était pas identifiable, provient de sources benthiques — de façon prédominante des invertébrés de niveau trophique bas et des détritus. La consommation de *N. mercedis* par *Palaemon modestus* représente une menace compétitive pour les juvéniles de saumons et les poissons résidants qui dépendent massivement de cette proie.

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INTRODUCTION

The Siberian prawn *Palaemon modestus* (Heller, 1862) 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 (Holthuis, 1980). After their initial discovery in the lower Columbia River in 1995 (Emmett et al., 2002), *P. modestus* 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 barge traffic (Haskell et al., 2006). It was not until 2005 that *P. modestus* 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 individuals being collected at Little Goose Dam in 2015 (Oregon Department of Fish and Wildlife, unpublished data). However, virtually nothing is known about this species' feeding ecology in lower Snake River reservoirs and their potential impact to the food web.

The establishment of *P. modestus* in the lower Snake River reservoirs is important because most juvenile anadromous salmonids — many of which are listed under the U.S. Endangered Species Act — produced in the Snake River basin pass through them 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). Recently, Tiffan et al. (2014) found that juvenile fall Chinook salmon growth in Lower Granite Reservoir was lower than in riverine habitats located upstream, and hypothesized that it could be due to increased competition with other species for food in the reservoir. Given that shrimps are generally omnivorous (Bell & Coull, 1978; Sitts & Knight, 1979), it is possible they could exert additional consumptive demand on the prey base if they share similar prey resources with salmon and other resident fishes.

Studies of *P. modestus* feeding ecology are challenging because shrimps typically masticate their prey making traditional stomach analyses difficult and uncertain (Siegfried, 1982). Additionally, stomach analyses only represent a snapshot in time and do not yield information on diet shifts over longer time intervals. In this study, we used a combination of traditional stomach content and stable isotope analyses to more completely understand *P. modestus* feeding ecology in Lower Granite Reservoir. Stable isotope analysis has the advantage of reflecting an animal's diet assimilated over time (Vander Zanden et al., 1999; Post, 2002). In addition, the stable isotope ratio of nitrogen ($\delta^{15}N$) is enriched by about 3-4‰ relative to prey for each level of trophic transfer and thus can be used as an indicator of

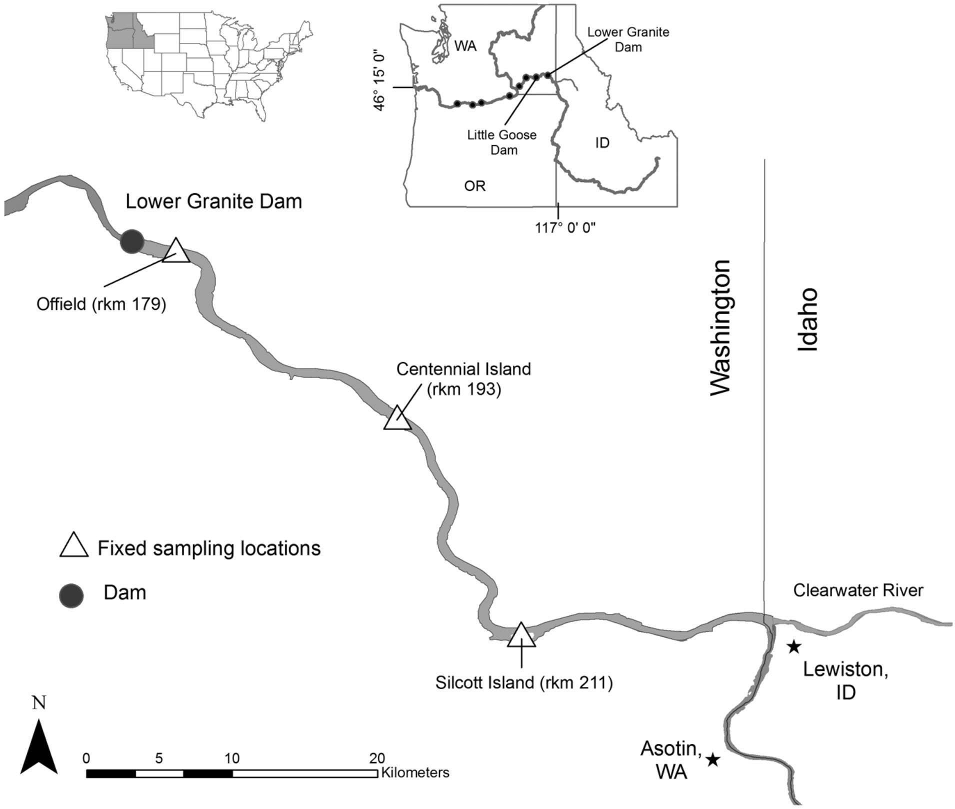

Fig. 1. A map showing sampling sites in Lower Granite Reservoir on the Snake River where *Palaemon modestus* (Heller, 1862) were collected during 2011-2013.

trophic position (Vander Zanden & Rasmussen, 1996; Vander Zanden et al., 1997). For example, a predator with a δ^{15}N signature 3.5‰ higher than that of a prey organism has a greater likelihood of feeding on that prey than one with a similar δ^{15}N signature. Carbon isotope signature (δ^{13}C) is typically only enriched by about 1‰ during trophic transfer from prey to predator, and is often used as a dietary tracer to show whether prey are from benthic (enriched) or pelagic (depleted) sources (France, 1995; Hecky & Hesslein, 1995). For example, a predator with a δ^{13}C signature similar to that of a prey organism reflects a greater likelihood of preying on it compared to a prey with a more dissimilar δ^{13}C signature. The disadvantage of stable isotopes is that they lack the specificity of prey selection that analysis of stomach contents provide.

Currently, the role of *P. modestus* in lower Snake River reservoir food webs is unknown. *Palaemon modestus* were sampled in Lower Granite Reservoir during 2011-2013 to study their diet and feeding as part of a larger study of their ecology in the lower Snake River. The objective of this study was to describe the seasonal and ontogenetic changes in *P. modestus* diets to better understand their trophic relation to other invertebrate and fish species.

MATERIAL AND METHODS

Palaemon modestus were collected in Lower Granite Reservoir on the lower Snake River in southeastern Washington (fig. 1). It is the first reservoir encountered by emigrating juvenile salmon. The reservoir 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. The reservoir is operated as run-of-the-river primarily for hydropower and navigation. Flows can range from >4248 m^3/s in the spring to 453 m^3/s during winter. The average channel width is 634 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.

Palaemon modestus were collected in monthly daytime beam trawls from May 2011 to March 2013, and then every three months from July 2013 to April 2014. The reservoir was divided into upper, middle, and lower reaches to ensure that individuals were collected over a broad spatial area. Within each reach, seven 100 m transects (parallel to the current) were randomly selected, which were then fixed for the duration of the study. Transects were located in the vicinity of Silcott Island (rkm 211.0), Centennial Island (rkm 193.0), and Offield (rkm 179.0; fig. 1). To sample a range of depths, four transects were in shallow water (<12 m) and three transects were in deep water ($\geqslant 12$ m), in each reach.

Palaemon modestus were collected with a beam trawl that had a rectangular opening that measured 2 m wide $\times$ 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. The trawl was deployed and retrieved from an 8.3 m boat using hydraulic winches. Each trawl sample was 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. All samples were pooled by depth and reach within each month before individuals were removed for diet analyses.

All *P. modestus* were blotted to remove excess ethanol and weighed individually ($\pm$0.001 g, wet). Up to 15 individuals were then randomly selected per month from pooled samples in each of three size classes (juvenile: <4.3 mm carapace length (CL), sub-adult: 4.3-9.1 mm CL, adult: >9.1 mm CL) for diet analysis. CL was measured to the nearest 0.01 mm from the posterior margin of the eye orbit to the medial posterior margin of the carapace. Individuals had their stomach contents removed by dissection and individual taxa were identified under a dissecting microscope to the lowest practical level. Prey from different individuals were pooled by taxon within each sampling category (i.e., month and size class) to obtain sufficient mass for subsequent weighing. Each pooled taxon was dried at 60°C for 24 h and dry weights were recorded to the nearest 0.00001 g.

Individuals analyzed for stable isotopes were collected from July 2013 to April 2014 by trawling in winter (January), spring (April), summer (July), and autumn (October). During each season, 6-12 adults (9-12 mm CL) were collected and immediately frozen on solid CO_2 and then stored at −20°C until processing. Only adults were analyzed because smaller size classes were not present during all seasons. In addition, other invertebrates that *P. modestus* potentially prey on were saved from trawl samples when they were collected during trawling. These were held for at least 12 h in freshwater to allow their guts to evacuate before being frozen. Detritus was collected from the surface layer of soft substrates during summer from shoreline areas. Tube-dwelling amphipods, *Americorophium* spp., were collected during summer and autumn, oligochaetes were collected during autumn, and opossum shrimp *Neomysis mercedis* Holmes, 1896 were collected during all seasons. Bulk zooplankton was collected during summer and winter in horizontal tows made with 63 μm conical nets in the top 10 m of the water column.

Palaemon modestus abdominal muscle and whole invertebrates were dried at 60°C for 24 h and then ground to a fine powder with a mortar and pestle. A 1.0 ± 0.1 mg sample of tissue was encapsulated in tin and analyzed for δ^{13}C and δ^{15}N signatures with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Stable Isotope Facility, University of California, Davis, California). The quantity measured in stable isotope analysis, δ, is the relative difference between isotope ratios of the sample and a standard, and is expressed in parts per thousand (‰) as $\delta = ((R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}) \times 1000$, where R_{sample} is the isotopic ratio of the sample and R_{standard} is the isotopic ratio of the standard. Standard materials were Vienna Pee Dee Belemite for δ^{13}C and atmospheric air for δ^{15}N. Samples were considered "enriched" if they contained more of the heavy isotope relative to other collected samples and "depleted" if they contained less of the heavy isotope. Every twelfth sample analyzed was a replicate, and the mean ($N = 13$) difference between replicate samples was 0.05‰ for δ^{13}C and 0.06‰ for δ^{15}N.

Palaemon modestus diet data were pooled by the seasons described above. Diet composition was expressed in terms of percent frequency of occurrence and percent by weight of different prey taxa consumed, and examined graphically for general seasonal and ontogenetic patterns. The SIAR mixing model (R 3.2.4 software) was used to determine the seasonal, proportional contribution of different food sources to *P. modestus* diets. One-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) using Euclidean distance was used to test for differences in prawn isotopic signatures (δ^{13}C-δ^{15}N centroids) by season. Pairwise a posteriori comparisons with Bonferroni correction were made between seasons. Analysis was conducted using R 3.2.4 software. Finally, a bivariate plot of mean nitrogen and carbon isotope ratios was constructed to examine the trophic relationship between *P. modestus* and other prey taxa.

RESULTS

The stomach contents of 674 individual *Palaemon modestus* were examined to describe their diet in Lower Granite Reservoir (table I). The percentage of individuals with empty stomachs ranged from 13.9 to 73.9, and was generally highest for juveniles. Not surprisingly, unidentifiable material was often predominant both in terms of frequency of occurrence (table I) and by its percent weight (fig. 2) in stomachs. Of identifiable prey, *Neomysis mercedis* composed the majority of *P. modestus* diets by frequency of occurrence and by weight. *Neomysis mercedis* composed 31-55% of the diet (by weight) of adults, 5-44% of the diet of subadults, and 0-34% of the diet of juveniles (fig. 2). *Neomysis mercedis* contributed most to the diet of adults in autumn and least during summer by both frequency of occurrence and by percent weight. The frequency of occurrence of *N. mercedis* in the diet of subadults was greatest in autumn and winter but their contribution by weight during those seasons was intermediate to that found in *P. modestus* during spring and summer. The incidence of *N. mercedis* in the diet of juveniles was comparatively low during all seasons (fig. 2, table I). The maximum number of *N. mercedis* found in individual adult stomachs ranged from 4 in the winter to 10 in the spring, whereas subadults and juveniles typically only contained 1-2 *N. mercedis* during all seasons.

Other identifiable prey only comprised a mean of 8.5% of *P. modestus* diets by weight (range 0-27%) across all size classes and seasons (fig. 2). Other prey included amphipods (Gammaridae and *Americorophium* spp.), Asian clams (*Corbicula* spp.), cladocerans, dipterans (Chironomidae, Simuliidae), ephemeropterans, oligochaetes, ostracods, polychaetes (*Hediste* spp.), trichopterans, and detritus. Only the smallest *P. modestus* collected consumed cladoceran zooplankton, but the percentage in the diet was low (5.7% by weight). Detritus was mainly of plant origin, and generally occurred in stomachs with higher frequency than other

TABLE I

Seasonal diets of three size classes of *Palaemon modestus* (Heller, 1862) (adult, >9.1 mm CL; subadult, 4.3-9.1 mm CL; juvenile, <4.3 mm CL) collected in Lower Granite Reservoir on the Snake River during 2011-2013

Season	*N*	Stomach contents							
		Empty	Unidentifiable	*Neomysis mercedis*	Detritus	Amphipoda	Diptera	Oligochaeta	Other
Adult									
Spring	85	20	71.7	38.8	12.9	2.4	10.6	4.7	1.2
Summer	79	13.9	69.9	32.9	17.7	2.5	10.1	2.5	0
Autumn	61	18.0	75.4	47.5	9.8	1.6	3.3	1.6	3.3
Winter	70	27.1	65.7	40.0	10.0	2.9	1.4	5.7	1.4
Subadult									
Spring	70	57.1	31.4	8.6	5.7	2.9	1.4	1.4	1.4
Summer	69	15.9	75.4	7.2	11.6	1.4	8.7	1.4	1.4
Autumn	49	16.3	69.4	26.5	16.3	0	0	2.0	0
Winter	67	37.3	43.3	20.9	9.0	1.5	0	0	1.5
Juvenile									
Spring	23	73.9	8.7	4.3	17.4	0	0	0	0
Summer	5	20	60	20	0	0	0	0	0
Autumn	53	41.5	58.5	0	1.9	0	0	0	1.9
Winter	43	39.5	53.5	11.6	0	4.7	0	0	4.7

Shown are the number of stomachs examined (*N*) and the frequency of occurrence (%) of stomachs that were empty or contained at least one prey item shown. The "Other" category includes Ephemeroptera, Trichoptera, Polychaeta, Cladocera, Bivalvia and Ostracoda.

identifiable prey for all size classes and across all seasons (table I). Adults and subadults preyed more frequently on amphipods, dipterans, and oligochaetes than did juveniles (table I).

Based on stable isotope analysis, *N. mercedis* had the greatest proportional contribution to the diet of *P. modestus* during autumn (0.27) and winter (0.49; table II). *Americorophium* spp. were also prominent prey in all seasons except summer. Zooplankton was most important during summer coincident with peak production during that season. Oligochaetes composed about one quarter of *P. modestus* diets during fall and spring but were less important during other times of the year. Detritus composed relatively low proportions (0.06-0.14) of the diet during all seasons (table II).

Together, stable isotopic signatures of δ^{15}N and δ^{13}C varied significantly by season (pseudo $F = 9.83$, $P < 0.0001$), and all pair-wise comparisons between seasons were significantly different from each other except for autumn and winter, which were similar. Stable isotopes were useful in showing the relative trophic position of *P. modestus* adults to their food sources. The greatest difference between mean δ^{15}N signatures of *P. modestus* and *N. mercedis* was 2.1‰ during

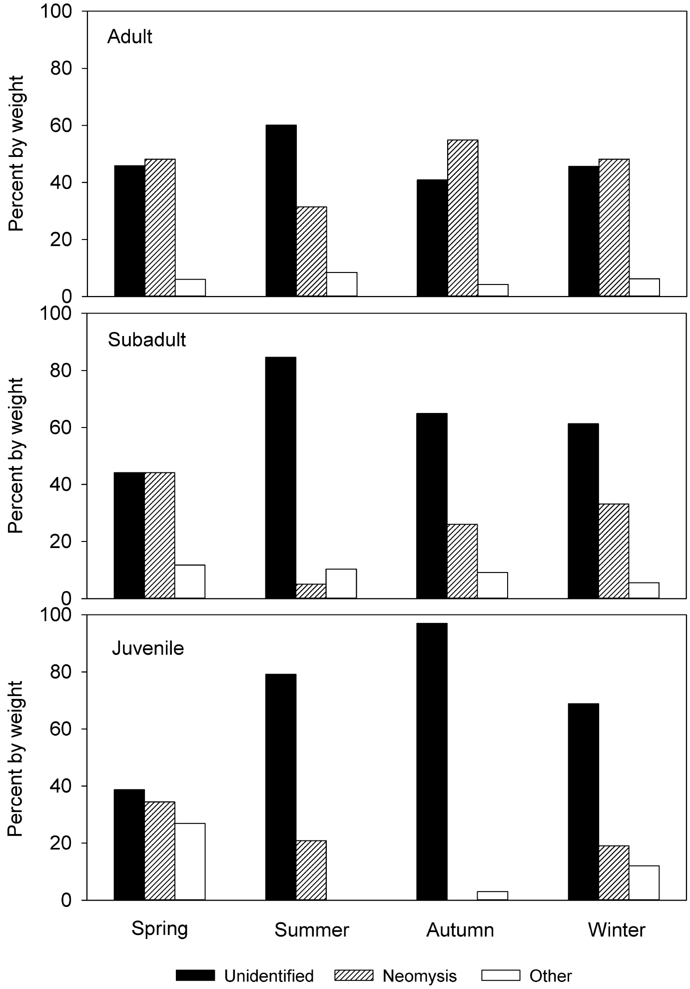

Fig. 2. Seasonal percentages (by weight) of different prey consumed by adult (>9.1 mm CL), subadult (4.3-9.1 mm CL), and juvenile (<4.3 mm CL) *Palaemon modestus* (Heller, 1862) in Lower Granite Reservoir during 2011-2013. The "Other" category included detritus, Amphipoda, Bivalvia, Cladocera, Diptera, Ephemeroptera, Oligochaeta, Trichoptera, Ostracoda, and Polychaeta.

spring, but otherwise only ranged from 0.2 to 0.9‰ (fig. 3, table III). Within corresponding seasons, the δ^{15}N signatures of *P. modestus* were >3.4‰ (one trophic level) higher than that of *Americorophium* spp., oligochaetes, and detritus, and 2.5‰ higher than *Americorophium* spp. during summer (table III).

Palaemon modestus showed relatively little seasonal variation in δ^{13}C signatures, which ranged from −26.1‰ in winter and spring to −25.2‰ in summer (fig. 3). *Palaemon modestus* δ^{13}C signatures during all seasons were most similar (approx. 1‰) to those of *Americorophium* spp. collected during summer, and to

TABLE II

Seasonal proportional contribution (95% credible intervals) of different food sources to adult (>9.1 mm CL) *Palaemon modestus* (Heller, 1862) in Lower Granite Reservoir on the Snake River during 2013-2014

Food source	Season			
	Autumn	Winter	Spring	Summer
Americorophium spp.	0.33 (0.29-0.82)	0.34 (0.20-0.65)	0.50 (0.27-0.73)	0.09 (−0.009-0.42)
Oligochaeta	0.27 (−0.004-0.35)	0.07 (−0.003-0.24)	0.26 (−0.004-0.40)	0.10 (−0.003-0.29)
Detritus	0.06 (−0.001-0.13)	0.08 (−0.001-0.10)	0.06 (−0.002-0.18)	0.14 (0.008-0.22)
Neomysis mercedis	0.23 (−0.005-0.45)	0.49 (0.13-0.69)	0.17 (0.004-0.38)	0.12 (−0.002-0.35)
Zooplankton	0.11 (−0.001-0.12)	0.02 (−0.001-0.13)	0.01 (−0.001-0.16)	0.55 (0.16-0.64)

Proportions were obtained with the SIAR mixing model using stable isotopes of nitrogen and carbon.

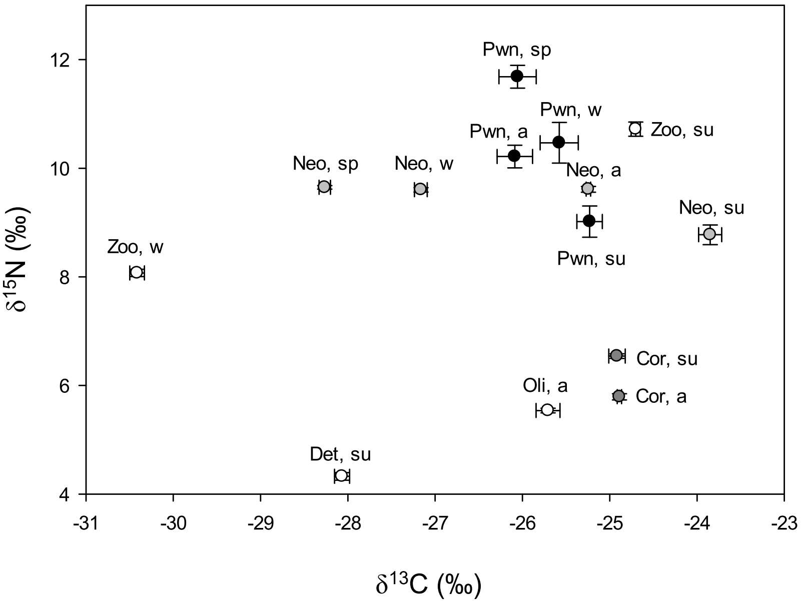

Fig. 3. Mean (± 1 SE bars) carbon and nitrogen isotope ratios of biota collected in Lower Granite Reservoir in 2013. Taxa are abbreviated as Pwn = *Palaemon modestus* (Heller, 1862), Neo = *Neomysis mercedis* Holmes, 1896, Zoo = zooplankton, Cor = *Americorophium* spp., Oli = oligochaete, and Det = detritus. Letters following each taxon denote the season each taxon was collected and are abbreviated as sp = spring, su = summer, a = autumn, and w = winter.

oligochaetes, *Americorophium* spp, zooplankton, and *N. mercedis* collected during autumn (fig. 3, table III). *Neomysis mercedis* δ^{13}C became increasingly depleted from summer (−23.8‰) to spring (−28.3‰). Zooplankton δ^{13}C signatures varied widely and were more enriched during summer (−24.7‰) than they were in winter (−30.4‰; fig. 3, table III).

DISCUSSION

Palaemon modestus in the lower Snake River preyed mainly on unidentifiable matter and invertebrates with *Neomysis mercedis* being the most common identifiable prey consumed by all size classes. *Neomysis mercedis* may have composed a large portion of *P. modestus* diets because they may have had a greater chance of being identified in the laboratory based on their relatively large size (approx. 12 mm total length), and they may not have been masticated to the same extent as smaller and softer prey such as oligochaetes (Siegfried, 1982). *Neomysis mercedis* was also the main prey consumed by oriental shrimp *Palaemon macrodactylus* Rathbun, 1902 (76% of diet) and Franciscan Bay shrimp *Crangon franciscorum* Stimpson, 1856 (67% of diet) in the Sacramento-San Joaquin River Delta where

TABLE III
Mean nitrogen ($\delta^{15}N$, ‰) and carbon ($\delta^{13}C$, ‰) signatures of taxa collected by season from Lower Granite Reservoir

Taxon	Season	*N*	$\delta^{15}N$		$\delta^{13}C$	
			Mean	SE	Mean	SE
Palaemon modestus	Spring	12	11.7	0.21	−26.1	0.21
Palaemon modestus	Summer	6	9.0	0.29	−25.2	0.14
Palaemon modestus	Autumn	10	10.5	0.37	−25.6	0.22
Palaemon modestus	Winter	12	10.2	0.21	−26.1	0.21
Neomysis mercedis	Spring	6	9.6	0.03	−28.3	0.06
Neomysis mercedis	Summer	11	8.8	0.18	−23.8	0.13
Neomysis mercedis	Autumn	5	9.6	0.05	−25.2	0.03
Neomysis mercedis	Winter	6	9.6	0.04	−27.2	0.07
Zooplankton	Summer	15	10.7	0.13	−24.7	0.05
Zooplankton	Winter	5	8.1	0.07	−30.4	0.08
Americorophium spp.	Summer	7	6.5	0.04	−24.9	0.09
Americorophium spp.	Autumn	5	5.8	0.06	−24.9	0.03
Oligochaete	Autumn	6	5.5	0.04	−25.7	0.14
Detritus	Summer	5	4.3	0.07	−28.1	0.09

N is the number of individuals or samples composing each mean and SE is the standard error.

they are abundant (Sitts & Knight, 1979; Siegfried, 1982). Mysids were also the prey most frequently consumed by oriental shrimp and white shrimp *Palaemon longirostris* H. Milne Edwards, 1837 in separate studies in the Guadalquivir Estuary, Spain (González-Ortegón et al., 2010, 2015). *Neomysis mercedis*, which was absent in the Snake River before the 1990s, has expanded its range upstream from the Columbia River and is now very abundant in the reservoir. Benthic densities of *N. mercedis* approaching 400 mysids/m^2 have been reported in Lower Granite Reservoir (St. John et al., 2014). Thus, it is not surprising that this abundant prey constituted such a large percentage of *P. modestus* diets, and it is plausible that *N. mercedis* facilitated the successful establishment of *P. modestus* in the Snake River.

The percentage of *N. mercedis* in *P. modestus* diets increased with increasing *P. modestus* size, probably due to larger individuals becoming more efficient at capturing this mobile prey as well as being able to consume larger prey (Wahle, 1985). Indeed, single adults contained as many as 10 *N. mercedis* similar to the maximum of 13 *N. mercedis* observed for oriental shrimp (Siegfried, 1982), which were slightly smaller than the adult *P. modestus* examined here. It is probably more efficient for *P. modestus* to forage on fewer, larger prey than many, smaller organisms. *Palaemon modestus* consumption of mainly benthic prey agrees with the finding of Xu et al. (2008) who showed that *P. modestus* from two lakes in China obtained most of their energy from benthic pathways. Other studies have also documented the importance of benthic macroinvertebrates to shrimp diets (Bell & Coull, 1978; Collins & Paggi, 1998). The findings reported here may be influenced in part by the fact that *P. modestus* were only collected from benthic habitats during the daytime. Limited pelagic trawling during the daytime and nighttime was conducted but relatively few *P. modestus* were collected. In addition, very few *N. mercedis* were collected in monthly nighttime vertical tow-net sampling and virtually none during the day (USGS, unpublished). It is possible that some *P. modestus* ascend into the water column to feed at certain times (e.g., Wilcox & Jeffries, 1974; Wahle, 1985), but this aspect of *P. modestus* behavior or feeding ecology was not investigated.

Stable isotope analysis helped clarify the energy and trophic sources of prey beyond what could be inferred from stomach content analyses. Although *N. mercedis* was a significant identifiable prey in *P. modestus* stomachs, stable isotope analysis suggested that prey from lower trophic levels composed a significant portion of unidentifiable matter. It is acknowledged that only a few prey taxa that *P. modestus* consumed were sampled for stable isotope analysis, and that sufficient quantities of other taxa that were identified from *P. modestus* stomach contents could not be collected, such as ephemeropterans, dipterans, and trichopterans. Nonetheless, it is clear that *P. modestus* were not solely reliant on *N. mercedis* for prey since both species occupied a similar trophic position from summer through winter. During these seasons, *P. modestus* obtained some of their dietary energy from taxa with lower δ^{15}N signatures such as *Americorophium* spp., oligochaetes, detritus, and others that may not have been sampled. This is supported by the similarity in δ^{13}C signatures between *P. modestus* and oligochaetes and *Americorophium* spp., and to a lesser extent for detritus, indicating that *P. modestus* were deriving some of their energy from these sources. It is likely that much of the unidentifiable material in *P. modestus* stomachs were oligochaetes and chironomid larvae, both of which are abundant in the reservoir and comprise the majority of the benthic invertebrate biomass (Bennett & Nightengale, 1994). This is also consistent with the findings of Collins & Paggi (1998) who showed that oligochaetes and chironomids composed the greatest proportion of the diets of *Macrobrachium borellii* (Nobili, 1896) living in an Argentinian flood plain.

The similarity in δ^{13}C signatures between *P. modestus* and *N. mercedis* during autumn suggest that *P. modestus* may actively feed on *N. mercedis* during this time. This is supported by the highest percentage by weight of *N. mercedis* in adult diets, and may be due to the presence of newly recruited juveniles to the *N. mercedis* population (St. John et al., 2014) that may be more easily captured by *P. modestus*. The differences between δ^{13}C signatures of *P. modestus* and *N. mercedis* during other seasons seem to indicate that *N. mercedis* contribute less to *P. modestus* diets, yet stomach content analysis suggests otherwise. *Neomysis mercedis* are mobile prey and thus the seasonal mismatch in δ^{13}C signatures between them and *P. modestus* might reflect changes in habitat use by *N. mercedis*. *Neomysis mercedis* move into littoral habitats in spring and early summer to reproduce (USGS, unpublished data). The progeny then move into offshore, benthic habitats by summer and thus probably still possess an enriched δ^{13}C signature from littoral habitats, which then become seasonally depleted as they remain there through the end of winter. In contrast, oligochaetes, *Americorophium* spp., and detritus are less mobile, and it was assumed their stable isotope signatures would show little seasonal variation due to movement. Although isotopic fractionation can vary with temperature (e.g., Power et al., 2003; Barnes et al., 2007), it was believed any seasonal variation in the isotope signatures due to temperature would be small compared to the relatively large differences observed between these prey and *P. modestus*, particularly for δ^{15}N. Thus, it was assumed that inferences about the contribution of these taxa to *P. modestus* diets could be made across the entire year. Finally, it is recognized that only adult *P. modestus* were analyzed for stable isotopes, and so inferences regarding smaller individuals should be made with caution.

Palaemon modestus consumption of invertebrates, and *N. mercedis* in particular, may pose a competitive threat to juvenile salmon and resident fishes in Lower Granite Reservoir. Juvenile salmon prey mainly on invertebrates in reservoir habitats (Rondorf et al., 1990; Muir & Coley, 1996). In Lower Granite Reservoir, Tiffan et al. (2014) found that subyearling fall Chinook salmon preyed predominantly on invertebrates with *N. mercedis* composing up to 80% of the diet (by weight) at times. Endemic sand rollers *Percopsis transmontana* (Eigenmann & Eigenmann, 1892), which also inhabit the same offshore, benthic habitats as *P. modestus*, prey mainly on *N. mercedis* and chironomids (USGS, unpublished data). Additionally, *P. modestus* may also compete with other invertebrates for resources. Native signal crayfish *Pacifastacus leniusculus* (Dana, 1852) probably occupy a similar ecological niche to that of *P. modestus* may also compete with them for prey. However, relatively few crayfish were collected in trawls compared to *P. modestus* which could be due to a negative interaction between the two species or that crayfish tend to prefer larger substrates (Wooster et al., 2012) that were not effectively sampled.

Currently, *P. modestus* mainly occupies deep, offshore habitats in Lower Granite Reservoir. There is anecdotal information that *P. modestus* is readily consumed by walleye *Sander vitreus* (Mitchell, 1818) in other Snake and Columbia River reservoirs. Some consumption of *P. modestus* by smallmouth bass *Micropterus dolomieu* Lacépède, 1802 has been documented but current habitat differences probably reduce the likelihood of *P. modestus* being an important food source for bass, which use shallower habitats. *Palaemon modestus* is probably not preyed upon by juvenile salmon given their relatively small size (60-140 mm) and gape for feeding on this large prey. An exception may be juvenile steelhead *Oncorhynchus* *mykiss* (Walbaum, 1792) that can attain sizes in excess of 200 mm. If, however, *P. modestus* expands its use of shallow habitats near shore as its population grows, then it may become an important prey for fish. The role of *P. modestus* in the lower Snake River food web will probably continue to change as the population grows, and their interactions with other species is an important area of future research.

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