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Asian copepods on the move: recent invasions in the Columbia–Snake River system, USA

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Nine Asian copepod species have been introduced into the Northeast Pacific, seven of which are largely confined to the San Francisco estuary. However, several of these copepods recently invaded the Columbia–Snake River system in Washington state, USA. In addition to the calanoid copepod *Pseudodiaptomus inopinus*, which appeared in the 1980s, the Columbia River now has populations of the calanoids *Pseudodiaptomus forbesi* and *Sinocalanus doerrii*, and the cyclopoid copepod *Limnoithona tetraspina*. Sampling in the Columbia–Snake River system in 2005 and 2006 indicated that (i) newer invaders may have displaced the previously introduced *P. inopinus*; (ii) *P. forbesi* had moved upstream into the first five reservoirs in the system; (iii) the other species occurred only in the tidal regions of the lower river; (iv) *P. forbesi* dominates the late summer holoplankton in the lower river and estuary; and (v) *P. forbesi* is relatively rare, and the holoplankton is dominated by native species in upstream free-flowing segments of the Columbia River and in reservoirs of the Snake River. Zooplankton samples from ships in Puget Sound suggest that ballast water from California is a major source of the introduced copepods and that the Columbia River itself may be a new source of ballast-introduced copepods.

Keywords: ballast water, copepods, invasive species, plankton surveys.

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Introduction

Estuaries along the west coast of the US have experienced many introductions of planktonic copepods via ballast water discharges of commercial ships. All but one of these introductions first appeared in the San Francisco Bay–Sacramento/San Joaquin Delta area (referred to here as the San Francisco estuary). In all, three cyclopoid and six calanoid copepods have been introduced and have successfully established themselves in the region (Table 1). Subsequent to their original introductions in the San Francisco estuary, several of these copepod species became established elsewhere. For example, three were recently found in the Columbia River estuary, presumably introduced by ballast water from ships originating in the San Francisco estuary or Asia (Sytsma *et al.*, 2004). Following their introduction, most of these copepods became very abundant and radically changed the make-up of the planktonic communities in the invaded estuaries; for instance, much of the San Francisco estuary now has an East Asian copepod fauna (Orsi and Ohtsuka, 1999; Bollens *et al.*, 2002; SMB and JRC, unpublished data). One result is that, in invaded habitats, introduced copepods can affect native species as potential predators, by changing foodweb dynamics, or by displacing pre-existing species (Hooff and Bollens, 2004; Cordell *et al.*, 2007).

In at least two instances in Northeast Pacific estuaries, previously introduced non-indigenous copepods may have been displaced by new copepod invaders. The first case is that of the small cyclopoid copepod *Limnoithona sinensis*, which was abundant in the upper San Francisco estuary from first detection in 1979 until the introduction of *L. tetraspina* in 1993. Thereafter, *L. tetraspina* became the dominant copepod in low-salinity regions, and *L. sinensis* disappeared (Orsi and Ohtsuka, 1999; Bouley and Kimmerer, 2006). *Limnoithona sinensis* was also present in the Columbia River estuary in the early 1980s, but it has disappeared from that system (JRC, unpublished data). In the second case, the calanoid copepod *Pseudodiaptomus inopinus* was first found in the Columbia River estuary in 1990 and has been found since then in many other estuaries in Washington and Oregon (Cordell *et al.*, 1992; Cordell and Morrison, 1996). However, in Columbia River samples beginning in 2002, *P. inopinus* is rare and has been replaced by another species, *Pseudodiaptomus forbesi* (Sytsma *et al.*, 2004). *Pseudodiaptomus inopinus* remains abundant in smaller estuaries in Oregon and Washington that have not been invaded by *P. forbesi* (JRC, unpublished data).

In addition to *P. forbesi*, two other introduced copepods, *L. tetraspina*, and the calanoid *Sinocalanus doerrii*, recently appeared in the Columbia River. In plankton surveys in 2003, *S. doerrii* was abundant in tidal tributaries of the Columbia River estuary, but *L. tetraspina* was rare (Sytsma *et al.*, 2004). In addition, the surveys found that the previously introduced *P. inopinus* was rare. Except *P. inopinus*, these invasions are apparently recent, because they were not found in a summer

Table 1. Chronology of first appearance of introduced copepods in the San Francisco and Columbia River estuaries.

Species	Year first recorded	Location	Reference
Oithona davisae (Ferrari and Orsi, 1984)	1963	San Francisco estuary	Ferrari and Orsi (1984)
Sinocalanus doerrii (Brehm, 1904)	1978	San Francisco estuary	Orsi *et al.* (1983)
Sinocalanus doerrii	2002	Columbia River	Sytsma *et al.* (2004)
Limnoithona sinensis (Burckhardt, 1912)	1979	San Francisco estuary	Ferrari and Orsi (1984)
Pseudodiaptomus marinus (Sato, 1913)	1986	San Francisco estuary	Orsi and Walter (1991)
Pseudodiaptomus forbesi (Poppe and Richard, 1890)	1987	San Francisco estuary	Orsi and Walter (1991)
Pseudodiaptomus forbesi	2002	Columbia River	Sytsma *et al.* (2004)
Pseudodiaptomus inopinus (Burckhardt, 1913)	1990	Columbia River	Cordell *et al.* (1992)
Acartiella sinensis (Shen and Lee, 1963)	1993	San Francisco estuary	Orsi and Ohtsuka (1999)
Tortanus dextrilobatus (Chen and Zhang, 1965)	1993	San Francisco estuary	Orsi and Ohtsuka (1999)
Limnoithona tetraspina (Zhang and Li, 1976)	1993	San Francisco estuary	Orsi and Ohtsuka (1999)
Limnoithona tetraspina	2003	Columbia River	Sytsma *et al.* (2004)

1992 plankton survey of the river's lower 350 km (Prahl *et al.*, 1998). Here, we present data on plankton sampling in the lower Columbia River and estuary in 2005, and the middle Columbia and lower Snake rivers in 2006, and document the expansion of introduced copepods in the system. We also include data on non-indigenous copepods from ship ballast obtained in the San Francisco estuary and Columbia River, and we discuss sources and implications of these planktonic invaders.

Methods

Zooplankton data from the Columbia and Snake rivers were taken from two studies. First, sampling was conducted from five docks on the lower Columbia River, spanning an area from near the mouth of the river to the city of Vancouver, Washington, ~160 km upstream (Figure 1). Sampling began in January 2005 and is ongoing. Once per month at each station, one vertical plankton tow was taken with a plankton net of 0.5 m diameter and 73 μm mesh. For our analyses, samples from all five sites taken on 25 May and 23 August 2005 were examined, and 12 consecutive samples (January–December 2005) were examined from Astoria, Oregon (Figure 1). The second study was part of a summer 2006 survey of the middle Columbia and lower Snake rivers to document non-indigenous plants and invertebrates. Zooplankton sampling was conducted between 13 July and 7 September 2005 in four reservoirs in the middle Columbia River, four reservoirs in the lower Snake River, and in one free-flowing segment of the middle Columbia River (Hanford Reach; Figure 1). Non-quantitative oblique plankton tows were taken from a small boat using a plankton net of 0.5 m diameter and 200 μm mesh lowered to near the bottom and retrieved by hand.

We also examined a subset of data from plankton samples taken from the ballast tanks of 386 ships entering Puget Sound, Washington, between February 2001 and March 2007. Specifically, ships that had obtained ballast water in either the San Francisco estuary or the Columbia River were analysed for the presence of non-indigenous copepods. Most of these samples were from ships at the ports of Seattle and Tacoma, Washington. Three replicate vertical tows were taken with a plankton net of 33 cm diameter and 73 μm mesh, from the tank bottom to the surface.

Samples were fixed in the field in 5% formalin solution. For the non-quantitative samples from the middle Columbia and lower Snake rivers, plankton was subsampled using a Hensen–Stempel pipette in a beaker agitated with compressed air to randomize the sample. Aliquots with the pipette were taken until ~100 holoplanktonic organisms were obtained, which were then enumerated under a dissecting microscope and assigned to the following categories: the non-indigenous copepod *P. forbesi*, native calanoid copepods, native cyclopoid copepods, native cladocerans of the genus *Daphnia*, and other native cladocerans. For lower Columbia River dock and Puget Sound ship samples, plankton was subsampled as previously described until ~200 of the most abundant taxa were obtained. Most adult organisms were identified to species, but some only to class or order level. However, for the purposes of this study, the following categories of holoplanktonic organisms were used for analysing the dock and ship samples: the non-indigenous copepod *P. forbesi*, native marine plankton, native brackish water plankton, and native fresh-water plankton.

Results

In the middle Columbia–lower Snake River study, the non-indigenous copepod *P. forbesi* was found in all samples from the first four reservoirs in the Columbia River and dominated the zooplankton numbers at 7 of the 15 reservoir sampling locations (Figure 1, Table 2). It was present in one sample from the first reservoir in the Snake River, but otherwise was absent from that river. In the Snake River, native cyclopoid copepods dominated samples from the more upstream stations, and native *Daphnia* spp. dominated those from the more downstream stations (Table 2). *Pseudodiaptomus forbesi* was also absent from samples taken from the free-flowing part of the Columbia River at Hanford Reach, where native calanoid copepods dominated.

Except the station furthest downstream, holoplankton from the lower Columbia River docks was dominated by native fresh-water species in samples from 25 April 2005, and by *P. forbesi* in samples from 23 August 2005 (Table 3). At the station near the river's mouth, a combination of marine and brackish species dominated on 25 May 2005. At the same station on 23 August 2005, brackish species dominated, *P. forbesi* constituting 24% of the numbers. At the station in Astoria, Oregon, where samples were available for all 12 months of 2005, *P. forbesi* peaked distinctively in August and September, but was otherwise relatively scarce (Figure 2).

Two other non-indigenous copepods, *L. tetraspina* and *S. doerrii*, were found in small numbers in the dock samples. They were several orders of magnitude less abundant than

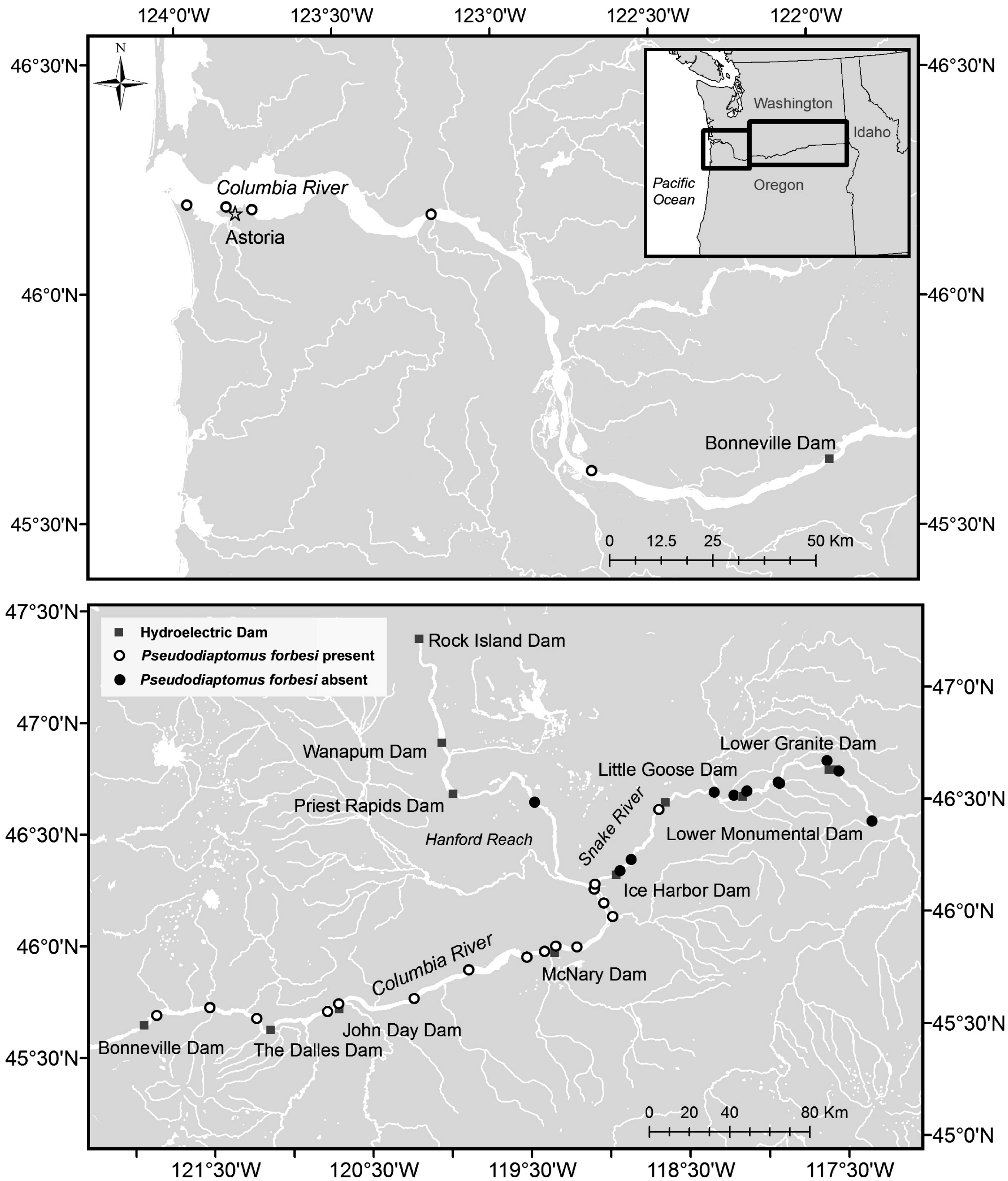

Figure 1. Station locations for monthly zooplankton sampling in 2005 in the lower Columbia River (top), for the summer 2006 zooplankton survey (bottom), and presence–absence of the introduced copepod *Pseudodiaptomus forbesi*. Hanford Reach is the only remaining free-flowing part of the middle Columbia River. See Tables 2 and 3 for station coordinates.

P. forbesi and were absent or rare upstream of river kilometre 75 (Figure 3). All three species are abundant in the San Francisco estuary and were also recently taken in surveys of the lower Columbia River, but they were absent from samples taken in the middle Columbia–Snake River survey.

Of the non-native copepod species in ballast tanks of ships entering Puget Sound that had recorded the San Francisco estuary as the ballast source, two species that prefer higher salinity—the cyclopoid *Oithona davisae* and the calanoid *Pseudodiaptomus marinus*—had relatively high densities and frequencies of occurrence (Table 3). Of the three low-salinity species introduced to the Columbia River system, *S. doerrii* and *P. forbesi* were found at low frequencies and densities, and *L. tetraspina* at relatively high frequencies and densities (Table 4). Three ballast tanks were sampled in December 2004 and October 2005 that contained water from Portland, Oregon, on the Columbia River. In these samples, the introduced copepod *P. forbesi* was abundant, constituting 51–69% of the identifiable holoplankton at densities of 53–4365 ind. m^{-3}.

Discussion

Although it has fewer non-native holoplanktonic species than the San Francisco estuary, the Columbia River system recently saw the successful establishment of at least three introduced copepod species. In both systems, the invasions are dynamic, with new species arriving and previously introduced species declining. We found that one recently introduced species to the Columbia River, the calanoid copepod *P. forbesi*, has spread upstream past

Table 2. Sampling station locations in the middle Columbia and lower Snake rivers, June–August 2006, and percentage composition by numbers of the non-indigenous copepod *Pseudodiaptomus forbesi* and native zooplankton groups.

		Native holoplankton			
Station location	***Pseudodiaptomus forbesi***	**Cyclopoida**	**Calanoida**	***Daphnia* spp.**	**Other Cladocera**
Snake River					
46°24′N 117°12′W	0	66	1	0	33
46°39′N 117°23′W	0	86	0	14	0
46°42′N 117°28′W	0	74	0	25	1
46°36′N 117°47′W	0	83	0	17	0
46°37′N 117°47′W	0	61	0	38	1
46°35′N 118°0′W	0	23	0	66	11
46°34′N 118°5′W	0	78	0	22	0
46°35′N 118°12′W	0	42	0	58	0
46°31′N 118°34′W	<1%	32	0	66	2
46°18′N 118°46′W	0	20	1	69	10
46°15′N 118°51′W	0	4	1	95	0
Hanford Reach					
46°41′N 119°26′W	0	35	60	0	5
46°35′N 119°22′W	0	6	81	0	13
Columbia River					
46°12′N 119°01′W	14	15	1	64	6
46°03′N 118°54′W	15	47	2	4	32
46°07′N 118°58′W	44	38	4	6	8
46°11′N 119°01′W	17	64	1	6	12
45°54′N 119°28′W	88	6	2	0	4
45°55′N 119°21′W	84	9	1	0	6
45°44′N 120°12′W	72	19	1	0	8
45°56′N 119°09′W	34	24	8	1	33
45°56′N 119°17′W	3	3	1	2	91
45°56′N 119°17′W	24	64	0	1	11
45°51′N 119°51′W	26	25	9	0	40
45°43′N 120°41′W	83	7	2	0	8
45°43′N 121°31′W	95	4	0	0	1
45°40′N 121°13′W	98	1	0	0	1
45°41′N 121°51′W	97	0	0	0	3

Table 3. Sampling station locations in 2005 in the lower Columbia River and percentage composition by numbers of the non-indigenous copepod *Pseudodiaptomus forbesi* and native zooplankton groups on two dates.

	Native plankton							
	Pseudodiaptomus forbesi		**Marine**		**Brackish**		**Fresh water**	
Station location	**25 May**	**23 August**	**25 May**	**23 August**	**25 May**	**23 August**	**25 May**	**23 August**
46°11′N 123°57′W	<1	24	42	4	44	71	14	1
46°13′N 123°54′W	2	95	0	0	6	4	92	0
46°11′N 123°44′W	1	97	0	0	3	3	96	1
46°10′N 123°10′W	<1	99	0	0	0	0	99	1
45°37′N 122°40′W	<1	96	0	0	0	0	100	4

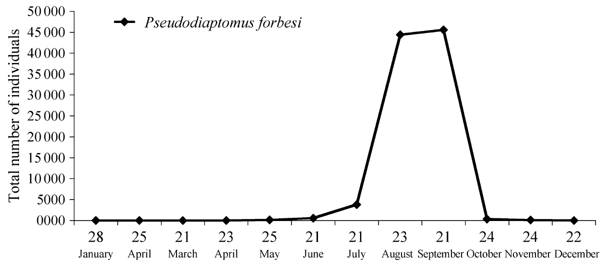

Figure 2. Total number of individuals of the non-indigenous copepod *Pseudodiaptomus forbesi* by month from plankton samples ($n = 3$ per date) collected from the Astoria, Oregon, city dock, January–December 2006.

five dams, and it dominated many of the plankton samples taken in late summer in the lower and middle Columbia River reservoirs. A previously introduced and abundant congener, *P. inopinus*, was not found, and is now rare or extinct (Sytsma *et al.*, 2004). Apparently, this is the first invasion of *P. forbesi* upstream of tidal influence; we could find no other records of it in North American lakes or reservoirs. Our and previous plankton survey findings suggest that, as in the San Francisco estuary, the copepod assemblage in parts of the Columbia–Snake River system may soon resemble an East Asian fauna.

Two other introduced species that were previously found in the lower Columbia River, *L. tetraspina* and *S. doerrii*, were mainly downstream and much less abundant than *P. forbesi*, particularly *L. tetraspina*, which makes up ~95% of copepod numbers in the low-salinity region of the San Francisco estuary (Bouley and Kimmerer, 2006). Also, results from our ballast-water sampling showed the species to be common in ships' ballast tanks. This suggests that inoculation rates for *L. tetraspina* in the Columbia

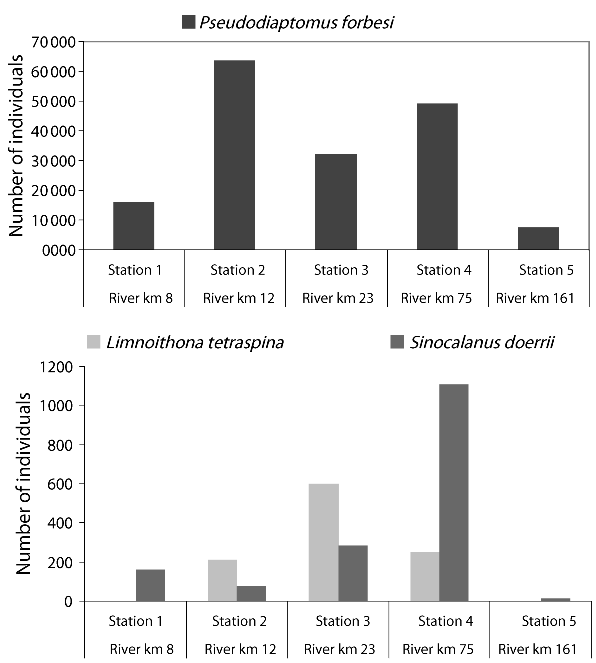

Figure 3. Total number of individuals of three non-indigenous copepod species by sampling station from plankton net samples collected from docks on the lower Columbia River, January–August 2005.

Table 4. Frequency of occurrence, density (based on samples in which each species was found), and salinity preference (from cited literature) of invasive copepods in the ballast tanks of ships entering Puget Sound, 2001–2007, that had recorded the San Francisco estuary as the ballast source ($n = 44$ ships).

Species	Frequency of occurrence (%)	Mean density (m^{-3})	Salinity preference (psu)	Reference
Sinocalanus doerrii	4.5	22	0	Orsi and Ohtsuka (1999)
Acartiella sinensis	9.1	4	3–9	Orsi and Ohtsuka (1999)
Pseudodiaptomus forbesi	9.1	6	<11	Orsi and Walter (1991)
Tortanus dextrilobatus	25.0	13	>14	Orsi and Ohtsuka (1999)
Limnoithona tetraspina	38.6	414	1–3	Orsi and Ohtsuka (1999)
Pseudodiaptomus marinus	38.6	61	>15	Orsi and Walter (1991)
Oithona davisae	81.8	5 285	>12	Ferrari and Orsi (1984)

River could be high, given that, from 2002 through 2005, 27% of high-risk ballast (that which has not been exchanged with ocean water) discharged into the Columbia River was from California (Simkanin and Sytsma, 2006). There are several possible reasons for the scarcity of *L. tetraspina* in the Columbia River, including (i) it is in the early stages of invading the system; (ii) the Columbia River may be inhospitable to relatively small copepods such as *L. tetraspina*, because it is a higher energy system than other estuaries on the US west coast (copepods residing there employ behaviours to help maintain their populations; Simenstad *et al.*, 1994; Morgan *et al.*, 1997); and (iii) it may be kept in check by native competitors or predators that either do not occur or have different effects in the San Francisco estuary. Further experimental and field data are required to determine which of these hypotheses is/are the controlling factors for the scarcity of *L. tetraspina* in the Columbia River.

In addition to *L. tetraspina*, the San Francisco estuary may also be the source of other introduced copepods. Two species found at higher salinities that occur frequently in ships' ballast water from California, *P. marinus* and *O. davisae*, have not been reported in the coastal ecosystems of Oregon and Washington. The Columbia River may also now be a vector for additional spread of non-indigenous species. This is suggested by our data from plankton samples taken from the ballast tanks of ships entering Puget Sound that had obtained ballast water in the Columbia River and had large proportions of *P. forbesi*.

Two of the areas sampled had few or no *P. forbesi*. Hanford Reach, a free-flowing course of the lower Columbia River, was the only area where native fresh-water copepods (family Diaptomidae) dominated, and the reservoirs on the Snake River were dominated by native cladocerans and cyclopoid copepods. *Pseudodiaptomus forbesi* was found in just one sample from the Snake River, at very small numbers, suggesting that *P. forbesi*, which was abundant in the Columbia River, may either be still expanding within the Snake River, or that it has experienced biological and/or physical factors limiting its spread there. Further sampling and experimental testing may help resolve this question.

The following questions arise from our findings and warrant further study. First, how will the dynamics of invasive copepods evolve in the Columbia–Snake River system? For example, will the rarer introduced copepods become more abundant and move upstream like *P. forbesi*, and will *P. forbesi* continue to move upstream in the Snake River and the mainstem Columbia River? Second, how do the invasive copepods interact with pre-existing species in the system? Elsewhere in the region, introduced copepods have been shown to have complex and sometimes important relationships with other native and introduced species, such as predator–prey and competition interactions (Kimmerer *et al*., 1994; Hooff and Bollens, 2004; Cordell *et al*., 2007). Third, are some habitats more susceptible to invasive copepods than others? We find it curious that samples from free-flowing sections of the river, the most upstream reservoirs sampled, and some locations in lower reservoirs were dominated by native species. The reasons for this are unknown, but they could be understood with additional collection of plankton, hydrological, and physical–chemical data. Finally, can invasive copepods be models for gauging the risk of arrival or spread of other non-indigenous species in the Columbia River? For example, movement of *P. forbesi* within the system might serve as a surrogate for predicting the spread of other highly destructive introduced species, such as quagga mussels (*Dreissena bugensis*), which have already been recorded in the western US, and which are probably already established by the time they are noticed (Stokstad, 2007).

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