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Invasion success and population characteristics of the opossum shrimp, *Mysis diluviana*, in Wyoming, USA

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Abstract

Studying the colonization, distribution, demographics, and abundance of invasive species is important for understanding their invasion biology, including the conditions required for establishment. This information can also be used to reduce their risk of spread. Opossum shrimp *Mysis diluviana* Audzijonyte and Väinölä, 2005, is an invasive species in lakes and reservoirs of the western United States and Canada. Four lakes in western Wyoming, USA, were stocked with this nonnative crustacean in 1971, but no *Mysis* surveys have been conducted in Wyoming since 1981. We determined presence/absence, demographics, and abundance of *Mysis* in these and six nearby lakes that could have been invaded using vertical net tows and environmental DNA analysis. Environmental conditions were compared in lakes with and without *Mysis*, and we evaluated the potential for *Mysis* to disperse downstream. *Mysis* (> 500 individuals/m^2) persisted in two of the four stocked lakes and nowhere else. Both of the lakes with established populations had daytime light levels on the bottom below the visual feeding threshold for fish, and the hypolimnia were oxygenated. Hierarchical cluster analysis of lake physicochemical conditions grouped these two lakes with four others, all of which were deep (46–185 m), with high oxygen concentrations (> 3 mg/L) on the bottom, and relatively low light intensities (< 0.2 lx) near the bottom. A second cluster of lakes that all lacked *Mysis*, and appeared to be less suitable, were shallow (< 20 m), had severe hypolimnetic hypoxia, and higher light levels (≥ 590 lx) near the bottom. The interaction of strong light penetration with lake depth, compounded by strong clinograde oxygen profiles, would prevent the formation of a daytime predation refuge from fish in these lakes, reducing the likelihood of *Mysis* invasion. Given that only half of the purposeful introductions in Wyoming were successful, and that there have been no new invasions in nearly 50 years, future range expansion by the species in the region is unlikely without human facilitation.

Key words: Mysidacea, crustacean, dispersal, lakes

Introduction

Humans have intentionally introduced thousands of species to the United States and extended the range of many more (Pimental et al. 2005). Some of these species are invasive, meaning capable of spreading and establishing new self-sustaining populations outside their native range (Kolar and Lodge 2001). Some invasive species may also become a threat to human health, industry or local biodiversity (Pejchar and Mooney 2009). Monitoring the current distribution and abundance of harmful invasive species is important for understanding habitat requirements, dispersal pathways, identifying sites that are vulnerable to secondary spread of the species, and implementing management actions to minimize this risk (Vander Zanden and Olden 2008; Stohlgren and Jarnevich 2009).

The opossum shrimp *Mysis diluviana,* Audzijonyte and Väinölä, 2005 (formerly *M. relicta* Lóven, 1862, herein *Mysis*), was introduced into many lakes and reservoirs of western North America during the 1950s–1980s to improve the forage base for salmonid sport fishes (Lasenby et al. 1986). *Mysis* are small

(< 25 mm in body length) shrimp-like crustaceans native to deep, oligotrophic lakes in parts of the American Great Lakes region and Canada that were glaciated during the Pleistocene (Dadswell 1974; Audzijonyte and Väinölä 2005). They are coldwater stenotherms with a preferred temperature of about 9 °C (Boscarino et al. 2010) and an upper lethal temperature of 20 °C (Dadswell 1974; Degraeve and Reynolds 1975). *Mysis* are omnivorous, feeding on organic matter in the profundal zone during the day and migrating into the water column at night to feed on phytoplankton and zooplankton (Grossnickle 1982; Beeton and Bowers 1982).

The initial introduction of *Mysis* in western North America occurred at Kootenay Lake, British Columbia, Canada in 1949. A dramatic increase in the growth of kokanee *Oncorhynchus nerka* Walbaum in Artedi, 1792, prompted well over 100 subsequent introductions across western North America (Lasenby et al. 1986). Most of these introductions proved harmful to fish populations, as studies showed that their diel vertical migrations allowed *Mysis* to avoid predation by planktivorous fish in many lakes, and that *Mysis* consumed the zooplankton preferred by these fishes (Nesler and Bergersen 1991). Thus, instead of becoming a new food resource, introduced *Mysis* often became strong competitors and the growth of sport fish such as kokanee and rainbow trout *O. mykiss* Walbaum, 1792, declined (Lasenby et al. 1986; Nesler and Bergersen 1991). *Mysis* introductions also stimulated reproduction of nonnative lake trout *Salvelinus namaycush* Walbaum in Artedi, 1792, which preyed on other sport fish and native species leading to fish population declines (Martinez et al. 2009; Schoen et al. 2015). Introduced *Mysis* have precipitated even broader food web changes. Selective predation by *Mysis* on large zooplankton favors smaller-bodied species (Martinez and Bergersen 1991) which are less efficient grazers of phytoplankton (Brooks and Dodson 1965). The diel vertical migrations of *Mysis* have affected contaminant and nutrient transport and recycling rates (Van Duyn-Henderson and Lasenby 1996; Devlin et al. 2016). *Mysis*-induced changes to the biomass and composition of the zooplankton community and disturbance of nutrient dynamics have altered primary production of recipient systems (Devlin et al. 2016). Thus, knowledge of *Mysis* distribution and abundance can help managers determine appropriate stocking and harvest policies for both planktivorous and piscivorous sport fish, evaluate lentic fish conservation strategies and interpret fish community and water quality dynamics (Ellis et al. 2011).

Once *Mysis* are established in a region, they can spread to nearby waters (Nesler 1986; Spencer et al. 1991). Because they are an obligate lacustrine species and they are relatively weak swimmers (Ricker 1959), *Mysis* dispersal is passive, via river connections to downstream lakes, or facilitated by interbasin water transfers. As with many other aquatic invasive species (AIS; Johnson et al. 2001; Wittmann and Ariani 2009), *Mysis* could also be transferred overland to unconnected waters by recreational boaters. Despite their limited dispersal capabilities, the history of *Mysis* introductions and subsequent invasions demonstrates the high vagility of this species. Establishing a population in Lake Tahoe, California-Nevada, was described as "surprisingly easy" (Fredrickson 2017). A single thermos containing 600–1,000 mysids collected from a lake in Minnesota was sufficient to establish a massive population in Twin Lakes, Colorado (Gregg 1976). Twin Lakes then became the source population for subsequent introductions in > 50 other waters in Colorado and Wyoming (Nesler 1986; Martinez and Bergersen 1989). Many of the introductions in Colorado were successful (DBS, unpublished data) and several other water bodies were subsequently invaded from upstream waters or facilitated by interbasin water transfers (Nesler 1986; DBS, unpublished data). Given the high vagility of *Mysis* and their potential to harm invaded systems, determining invasion success, monitoring population sizes and determining the extent of their range is important for assessing risk and preventing future *Mysis* invasions.

Although most *Mysis* introductions in this region occurred about 50 years ago, there have been very few studies to determine the outcome of many of these introductions, or surveys to investigate if there have been subsequent invasions. In Wyoming, there are a multitude of lakes and reservoirs with suitable *Mysis* habitat, but very few surveys of the species in the state. *Mysis* were introduced to four lakes in western Wyoming in 1971. Half Moon Lake, Middle Piney Lake, and Willow Lake near Pinedale, Wyoming were stocked with *Mysis* obtained from Twin Lakes, Colorado (Finnell 1977). Approximately 14,000 individuals were stocked in Half Moon Lake and Willow Lake in June, 1971 and an additional 50,000 were stocked in each lake in October (Grabowski and Ahern 1982). Approximately 20,000 mysids were stocked in Middle Piney Lake that year as well. Finnell (1972) stated that Brooks Lake, northwest of Dubois, Wyoming, was also stocked with *Mysis* but no details about numbers or dates stocked were provided. Surveys conducted by Wyoming Game and Fish Department (WGFD) in 1976 and 1977 and by the University of Wyoming in 1981 confirmed that *Mysis* had established self-sustaining populations in Half Moon and Willow lakes (Grabowski and Ahern 1982).

Table 1. Characteristics of the study lakes, near Pinedale, Wyoming, USA. All of the lakes are within the Green River Basin except Brooks Lake, which is in the Wind River Basin. "Stocked?" refers to whether *Mysis* were introduced by management agencies.

Lake	Latitude N	Longitude E	Elevation (m)	Surface area (ha)	Maximum depth (m)	Stocked?
Boulder Lake	42.847	−109.664	2,222	700	79	N
Brooks Lake	43.757	−110.004	2,764	87	18	Y
Fremont Lake	42.946	−109.806	2,261	2,061	185	N
Half Moon Lake	42.925	−109.730	2,316	381	85	Y
Little Half Moon Lake	42.905	−109.710	2,315	24	17	N
Meadow Lake	42.888	−109.689	2,434	50	20	N
Middle Piney Lake	42.598	−110.574	2,699	67	46	Y
New Fork Lake	43.097	−109.947	2,383	497	62	N
Soda Lake	42.961	−109.844	2,302	129	14	N
Willow Lake	43.002	−109.869	2,346	726	85	Y

We are unaware of any other surveys of *Mysis* populations in Wyoming until the present study.

The objectives of this study were to determine the presence/absence, demographics, and abundance of *Mysis* in the four lakes where they were originally introduced, and evaluate invasion success. We also sampled six neighboring lakes that could have been colonized by the stocked populations. We compared environmental conditions in lakes with and without *Mysis* to better understand habitat requirements for this invasive species outside its native range. Finally, we evaluated the potential for *Mysis* to disperse to downstream waters.

Methods

The survey was conducted on 10 glacial lakes in the Bridger-Teton and Shoshone National forests, in northwestern Wyoming, USA (Figure 1). During July 17–20, 2017 we sampled the four lakes reported to have been the original *Mysis* introduction sites (Brooks, Half Moon, Middle Piney, and Willow lakes). We then sampled six neighboring lakes during August 28–31, 2017 (Boulder, Fremont, Little Half Moon, Meadow, New Fork, and Soda lakes) which were all within 10 km of a lake inhabited by *Mysis* because other crustaceans can disperse readily over this distance by a variety of mechanisms (Havel and Shurin 2004). These lakes were also > 10 m deep and therefore likely to stratify, providing cold hypolimnetic temperatures required by *Mysis*. Each of the lakes was also directly accessible by public roads that made overland transfer of *Mysis* via trailered boats more likely. The lakes were relatively small (mean: 477 ha, range: 24–2,061 ha), deep (mean: 61 m, range: 14–185 m), high elevation (≥ 2,222 m AMSL) waters (Table 1). Only Soda Lake did not have a surface outflow. All of the lakes are managed as coldwater fisheries with a variety of salmonid species including brown trout *Salmo trutta* Linnaeus, 1758, cutthroat

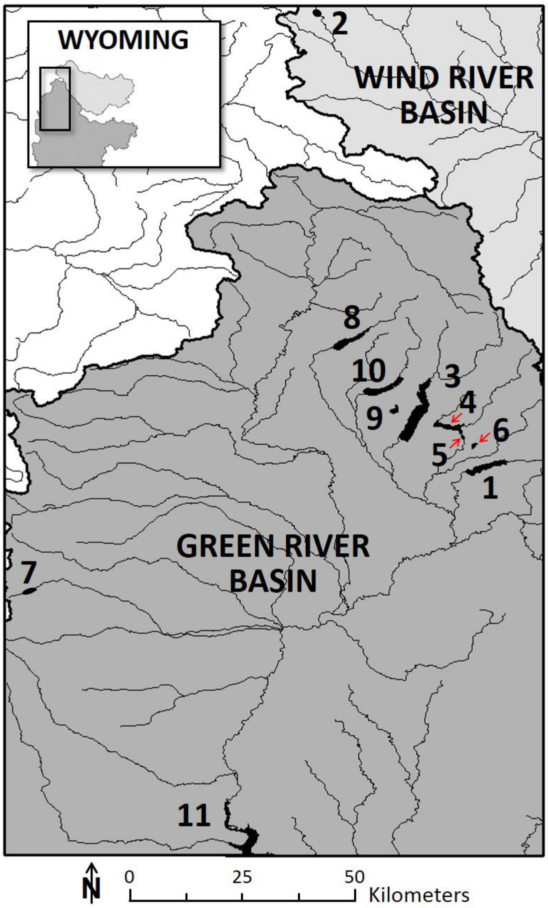

Figure 1. Locations of 10 Wyoming waters surveyed for *Mysis diluviana*: 1) Boulder, 2) Brooks, 3) Fremont, 4) Half Moon, 5) Little Half Moon, 6) Meadow, 7) Middle Piney, 8) New Fork, 9) Soda, and 10) Willow lakes. Location of Fontenelle Reservoir (11), which was not surveyed but is connected to study lakes, is also shown.

trout *O. clarkii* Richardson, 1836, lake trout, and rainbow trout. Native fishes include highly unusual lacustrine populations of two imperiled riverine species in some of the lakes, flannelmouth sucker *Catostomus latipinnis* Baird and Girard, 1853, and roundtail chub *Gila robusta* Baird and Girard, 1853 (Laske et al. 2011), as well as mountain sucker *Catostomus platyrhynchus* Cope, 1874, and speckled dace *Rhinichthys osculus* Girard, 1856.

We used a stratified sampling design to establish *Mysis* sampling stations on each lake (Martinez et al. 2010). The number of stations chosen depended on lake area (area < 40 ha: 3 stations, 40 ≤ area < 400 ha: 5 stations, area ≥ 400 ha: 10 stations). Within each lake, stations were distributed across up to four depth contour strata: 10–20 m, 20–40 m, 40–60 m, and > 60 m, as lake depth (Z_{max}) allowed. Three sampling stations were established on Little Half Moon Lake, five on Brooks, Half Moon, Middle Piney, New Fork and Soda lakes, and 10 stations on the larger Boulder, Fremont and Willow lakes. A water sample from the hypolimnion of each lake was collected with a van Dorn bottle for *Mysis* environmental DNA (eDNA) analysis. We have used this eDNA method in conjunction with vertical net tows in at least 20 lakes with no discrepancies in presence/absence between the two sampling methods (BMJ, unpublished data). We could not sample Meadow or Soda lakes with the *Mysis* net due to time constraints, but these two lakes were shallow and had the most severe hypoxia which suggested that it was unlikely *Mysis* could persist there. We did collect eDNA samples at these two lakes to determine presence/absence.

Mysis sampling commenced at least 60 minutes after sundown and consisted of vertical tows with a 1-m diameter plankton net with 500-µm Nitex mesh (Silver et al. 2016). Boat lights were turned off during vertical net tows to avoid affecting *Mysis* distribution. The net was lowered until the cup was within 1 m of the bottom, as guided by a depth sounder. The net was allowed to rest for 60 s and then retrieved at a constant rate of 0.4 m/s with an electric winch. We collected one sample at each station. The catch from each haul was preserved in 70% ethanol. The water for the eDNA samples was collected with a Van Dorn sampler from within 1 m of the bottom and processed using the protocol provided by Carim and Wilcox (2014). Prior to collecting the lake water eDNA sample a distilled water control was processed to insure adequate decontamination of the sampling equipment. The eDNA samples were analyzed by the U.S.G.S. Molecular Ecology Laboratory in Fort Collins, Colorado, using methods described in Carim et al. (2016). Lakes were classified as "exposed" if they were known to have been stocked (Brooks, Half Moon, Middle Piney, and Willow lakes) or if *Mysis* were detected in our vertical net tows or eDNA sampling. The remaining lakes were classified as "exposure unknown" because we could not know if *Mysis* had ever been present in the past but did not persist.

We measured environmental conditions at one to five stations on each lake, depending on the parameter measured and lake area. A temperature-dissolved oxygen profile was measured at the deepest station in each lake. Other water quality parameters were measured at the surface at three stations (area < 400 ha) or five stations (area ≥ 400 ha) per lake. Surface conductivity, pH, salinity, and TDS were measured with an Oakton PCSTestr35 multimeter. Turbidity was measured at the surface with a Hach 2100Q turbidimeter. Water transparency was measured during daylight with a standard 20-cm Secchi disk on the shaded side of the boat without sunglasses. Temperature and dissolved oxygen profiles were measured with an YSI ProODO meter. We evaluated suitability of thermal and oxygen conditions assuming that *Mysis* would avoid temperatures ≥ 14 °C (Ricker 1959; Martinez and Bergersen 1991) if dissolved oxygen allowed (Dadswell 1974; Degraeve and Reynolds 1975), and that the avoidance threshold for hypoxia in *Mysis* was 3 mg/L (Sandeman and Lasenby 1980; Sherman et al. 1987). We used temperature and dissolved oxygen profile data and this oxygen threshold to determine the maximum habitable depth (Z_3), and the corresponding temperature at that depth (T_3), in each lake, because low dissolved oxygen in the hypolimnion has been shown to force a closely related species (*M. relicta*) into unfavorable water temperatures (Horppila et al. 2003).

Our assessment of habitat suitability also depended on the presence of a daytime predation refuge. We used water transparency and surface illuminance to compute light availability at the bottom of each lake to determine if *Mysis* have a low-light refuge from visual predators (fish), in the manner of Hansen and Beauchamp (2015). A light extinction coefficient, k, was computed from water transparency (Idso and Gilbert 1974):

$$k = 1.7/Z_{SD}$$

where Z_{SD} is Secchi depth (m). The mean June–August surface illuminance, I_0 (lx), during midday was computed from an algorithm that used latitude, longitude, date, and time of day (Janiczek and DeYoung 1987). We estimated illuminance at depth from surface illuminance and the extinction coefficient using the Beer-Lambert equation (Horne and Goldman 1994):

$$I_Z = I_0 \cdot e^{-kZ}$$

where I_Z is illuminance (lx) at depth Z (m). We computed light intensity at the maximum habitable depth for *Mysis* (dissolved oxygen ≥ 3 mg/L), I_3, because low dissolved oxygen in the hypolimnion could have forced *Mysis* into shallower water where they would be visible to predators. A predation refuge was assumed to exist if $I_3 < 0.001$ lx, the minimum light intensity for visual feeding in salmonids (Ali 1959).

In the laboratory, the total catch from each net haul was enumerated directly, or the catch was subsampled with a Folsom plankton splitter (Sell and Evans 1982). Subsamples of approximately 150 mysids from each lake and station were examined under a stereomicroscope at 7^x magnification. Each individual was classified as 1) juvenile (< 10 mm), 2) male (extended pleopods), 3) female (brood pouch exposed), or 4) adult of undetermined sex (≥ 10 mm and lacking identifiable sexual characteristics). Each mysid was measured (nearest 0.1 mm) along a dorsal line from the tip of the rostrum to the tip of the telson using a calibrated micrometer. Lengths in the measured subsamples were weighted by total catch at each station to create an overall length-frequency distribution for the population. Total counts of the catch in each sample were normalized to individuals/m^2 based on the cross-sectional area of the net opening (0.785 m^2).

Areal densities of *Mysis* were compared with unpaired t-tests (equal variances) in the two lakes with established populations of *Mysis*. We also compared our estimated densities in these two lakes with those in a previous study (Grabowski and Ahern 1982) with two-sample t-tests as an indication of population stability. Physicochemical measures taken at multiple stations in each lake were averaged so that each lake had one observation. Correlations among physicochemical characteristics (area, conductivity, dissolved oxygen on the bottom, I_3, pH, salinity, T_3, total dissolved solids, turbidity, Z_3, Z_{max}, and Z_{SD}) across lakes were evaluated with the Pearson product-moment correlation coefficient, *r,* prior to selecting variables for the cluster analysis. A Bonferroni correction was used for multiple comparisons; a significance level of 0.0009 was used to judge significant correlations ($\alpha = 0.05$). A subset of uncorrelated variables (conductivity, DO, I_3, pH, turbidity, Z_3, and Z_{SD}) was used in a hierarchical cluster analysis to examine physicochemical characteristics among the 10 lakes, and associations of environmental conditions with presence/absence of *Mysis*. Ward's minimum variance method was used to form the clusters. Two clusters were selected. JMP Pro version 13 was used for correlation and cluster analyses.

Results

We captured *Mysis* in only three lakes: Half Moon, Little Half Moon, and Willow lakes. The eDNA samples yielded positive detections in these three waters and no others. Net and eDNA results suggest that *Mysis* have established only at Half Moon and Willow lakes. We captured a single juvenile (9.3 mm) mysid in our sampling at Little Half Moon Lake for an estimated density of 0.42 individuals/m^2. In contrast, we captured 3,080 mysids at Half Moon Lake, for an areal density of 784.7 individuals/m^2 ($SD = 533.5$) and 4,612 mysids at Willow Lake, for an areal density of 587.5 individuals/m^2 ($SD = 522.4$). *Mysis* density was not statistically different at Half Moon and Willow lakes ($t_{(13)} = 0.69$, $P = 0.49$), nor were these densities different from those reported by Grabowski and Ahern (1982) for Half Moon and Willow lakes ($t_{(6)} = -0.28$, $P = 0.78$; and $t_{(11)} = -0.06$, $P = 0.95$, respectively). Juveniles comprised 41.97% of the total population in Half Moon Lake, and 64.23% in Willow Lake (Figure 2). The modal lengths of juveniles and adults were larger in Willow Lake compared to Half Moon Lake, suggesting that growth may be faster in Willow Lake. The maximum size of adults was similar in the two lakes (20.63 mm in Half Moon Lake, 20.81 mm in Willow Lake). In both lakes, all of the males were immature and over 99% of females were immature, as expected for the time of year.

All of the lakes were thermally stratified (Figure 3). Surface temperatures were lowest at Brooks (15.4 °C) and Middle Piney lakes (14.7 °C) in July; these lakes were 300–500 m higher in elevation than the others. Surface temperatures of the other two lakes sampled in July were 18.9 °C (Half Moon Lake) and 20.7 °C (Willow Lake). Surface temperatures were more similar across the six lakes sampled in August (17.3 °C–19.8 °C). The top of the thermocline was shallower in the lakes sampled in July (~ 4 m) than those sampled in August (5–9 m). The temperature of the hypolimnion was 4–6 °C in all of the lakes except one; Little Half Moon Lake, which is relatively shallow and receives inflow from the surface of Half Moon Lake, was relatively weakly stratified and had a bottom temperature of 15.2 °C.

Dissolved oxygen concentrations at the surface were high (≥ 7.5 mg/L) in all of the lakes (Figure 3). Dissolved oxygen concentration was above the *Mysis* avoidance threshold (3 mg/L) throughout the water column in all of the lakes except in the four shallowest lakes: Brooks, Little Half Moon, Meadow, and Soda lakes. In these four lakes the dissolved oxygen concentration decreased rapidly with depth below the thermocline, and the dissolved oxygen concentration at the bottom was < 0.6 mg/L. Based on the dissolved

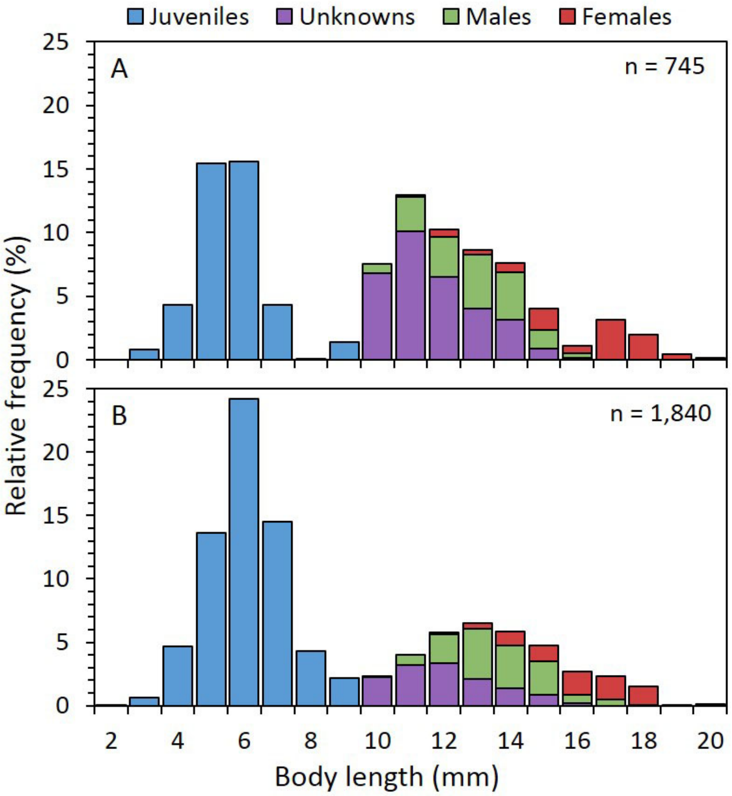

Figure 2. Size-frequency histograms of *Mysis diluviana* captured at A) Half Moon Lake on July 17, 2017, and B) Willow Lake on July 18, 2017, near Pinedale, Wyoming, USA.

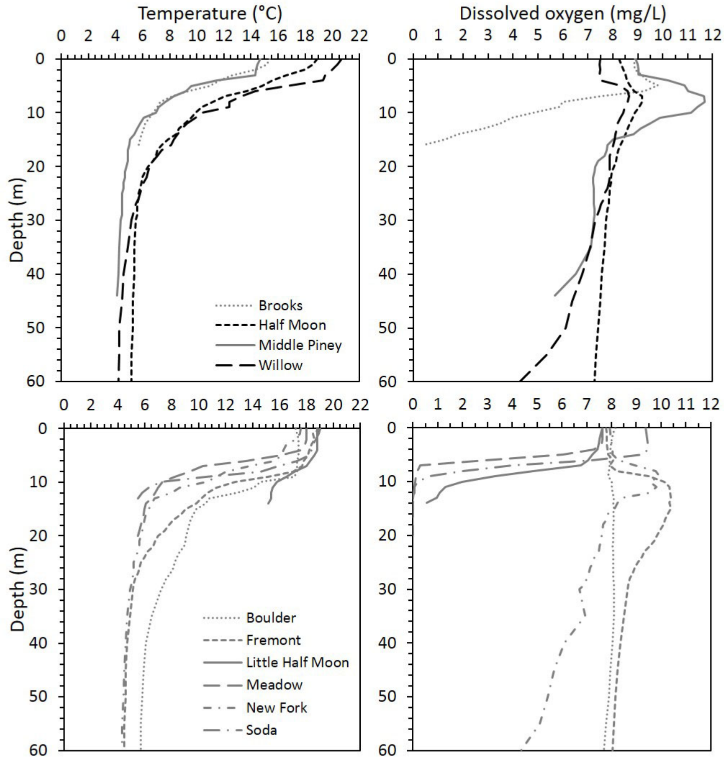

Figure 3. Temperature and dissolved oxygen profiles measured at a mid-lake station on four Wyoming lakes in July, 2017 (Upper panels), and six Wyoming lakes in August, 2017 (lower panels). *Mysis* were established in Half Moon and Willow lakes (black lines).

Table 2. Mean and standard deviation (SD) of physicochemical characteristics measured at the surface of 10 Wyoming lakes sampled in July and August, 2017.

Lake	Date sampled	Stations	Conductivity (µS/cm)		pH		Salinity (mg/L)		TDS (ppm)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
Boulder Lake	8/29/2017	5	17.90	0.07	7.80	0.08	15.00	0.20	12.70	0.07
Brooks Lake	7/20/2017	3	63.00	0.10	8.83	0.04	33.90	0.30	44.70	0.00
Fremont Lake	8/30/2017	5	18.76	0.46	7.45	0.13	15.70	0.23	13.44	0.38
Half Moon Lake	7/17/2017	3	18.00	0.10	8.27	0.12	15.13	0.12	12.80	0.10
Little Half Moon Lake	8/31/2017	3	17.80	0.10	7.49	0.03	15.37	0.06	12.67	0.06
Meadow Lake	8/31/2017	3	83.37	0.50	8.08	0.03	45.90	0.10	59.27	0.15
Middle Piney Lake	7/19/2017	3	309.33	0.58	8.71	0.01	154.67	1.15	218.33	0.58
New Fork Lake	8/28/2017	3	36.83	1.17	7.97	0.02	23.93	1.07	26.03	1.15
Soda Lake	8/29/2017	3	5.27	0.02	8.75	0.08	3.10	0.02	3.74	0.02
Willow Lake	7/18/2017	5	30.12	0.29	7.80	0.04	21.30	0.14	21.40	0.25

Table 3. Water transparency and light characteristics of the study lakes: Z_{SD} is Secchi depth, k Z_3 is the maximum depth habitable for *Mysis* (dissolved oxygen ≥ 3 mg/L), k is a light extinction coefficient (unitless), and I_3 is light intensity at the maximum habitable depth. A low-light predation refuge existed in lakes where $I_3 < 0.001$ lx, the minimum threshold for fish visual feeding.

Lake	Turbidity (NTU)	Z_{SD} (m)	Z_3	k	I_3 (lx)	Predation refuge?
Boulder Lake	0.76	8.83	79	0.192	2.63×10^{-2}	N
Brooks Lake	1.80	3.93	12	0.432	5.89×10^{2}	N
Fremont Lake	0.77	8.95	185	0.190	5.78×10^{-11}	Y
Half Moon Lake	1.16	5.30	85	0.321	1.52×10^{-7}	Y
Little Half Moon Lake	0.88	4.90	9	0.347	4.64×10^{3}	N
Meadow Lake	1.48	3.70	5	0.459	1.06×10^{4}	N
Middle Piney Lake	0.92	5.15	46	0.330	2.68×10^{-2}	N
New Fork Lake	0.71	8.05	62	0.211	2.17×10^{-1}	N
Soda Lake	2.19	4.41	7	0.386	7.09×10^{3}	N
Willow Lake	0.84	5.24	85	0.324	1.11×10^{-7}	Y

oxygen threshold, the maximum depths that *Mysis* would inhabit (Z_3) were 7 m in Meadow Lake, 8 m in Soda Lake, 10 m in Little Half Moon Lake, and 13 m in Brooks Lake. Temperatures at these lake depths (T_3) were: 12 °C, 14.5 °C, 16 °C and 6 °C, respectively. None of these temperatures exceeds the upper lethal temperature for *Mysis* but all were above their preferred temperature and two exceeded the avoidance threshold for *Mysis*.

Conductivity, salinity and TDS were generally low (mean = 60 µS/cm, 34 mg/L, and 46 mg/L, respectively) and similar across lakes except for Middle Piney Lake where values of each were much higher (Table 2). With the exception of Little Half Moon Lake, Z_{SD} was lower and turbidity was higher in the shallowest lakes. Z_{SD} averaged 5.9 m across the lakes and was lowest in Brooks Lake (3.9 ± 0.6 m) and highest at Fremont Lake (8.9 ± 0.5 m) (Table 3). Turbidity was < 1.00 NTU in 6 of the 10 lakes, turbidity averaged 1.15 NTU and was highest in Soda Lake (2.19 ± 0.54 NTU), and lowest in New Fork Lake (0.71 ± 0.60 NTU). Differences in water transparency and lake depth resulted in 13 orders of magnitude differences in estimated light levels at the greatest depth habitable for *Mysis* (I_3) (Table 3). Only three lakes (Half Moon, Willow and Fremont) had daytime light levels at habitable depths that were below the minimum illuminance required for visual feeding by fishes, and thus provided a low-light predation refuge for *Mysis*. Both of the lakes with established *Mysis* populations (Half Moon, Willow) had a daytime predation refuge.

Conductivity, salinity and TDS were significantly correlated ($r > 0.99$, $P < 0.0001$) among lakes (Table 4). Surface area, Z_3, and Z_{max} were significantly correlated ($r > 0.95$, $P < 0.0001$). T_3 and I_3 were significantly correlated ($r = 0.90$, $P = 0.0004$). The physicochemical variables used in the hierarchical cluster analysis were conductivity, DO, I_3, pH, turbidity, Z_3, and Z_{SD}. Two clusters were selected from the hierarchical cluster analysis to characterize lakes (Figure 4). The first cluster consisted of six lakes (i.e., Boulder, New Fork, Half Moon, Willow, Fremont, and Middle Piney) and was characterized by higher conductivity, higher dissolved oxygen, lower I_3, lower pH, higher Z_{SD}, lower turbidity, and higher Z_3 than the four lakes in cluster two (Brooks, Soda, Little Half Moon, and Meadow) (Table 5).

Table 4. Pearson product-moment correlation coefficients among lake characteristics measured at 10 Wyoming lakes sampled for *Mysis diluviana*. Area = surface area, Cond = conductivity, DO = dissolved oxygen on the bottom, I_3 = light intensity at 3 mg/L of oxygen, Sal = salinity, T_3 = temperature at 3 mg/L of oxygen, TDS = total dissolved solids, Turb = turbidity, and Z_3 = depth at 3 mg/L of oxygen, Z_{max} = maximum depth, and Z_{SD} = Secchi depth. Significant correlations (Bonferroni adjusted significance level of 0.0009) denoted in bold text.

	Area	Cond	DO	I_3	pH	Sal	T_3	TDS	Turb	Z_3	Z_{max}	Z_{SD}
Area	1.000											
Cond	−0.308	1.000										
DO	0.672	0.076	1.000									
I_3	−0.437	−0.107	−0.738	1.000								
pH	−0.568	0.435	−0.342	0.110	1.000							
Sal	−0.292	**0.998**	0.100	−0.116	0.408	1.000						
T_3	−0.481	−0.238	−0.768	**0.902**	0.013	−0.245	1.000					
TDS	−0.308	**1.000**	0.075	−0.106	0.435	**0.998**	−0.238	1.000				
Turb	−0.464	−0.101	−0.685	0.570	0.734	−0.132	0.524	−0.101	1.000			
Z_3	**0.953**	−0.168	0.843	−0.606	−0.518	−0.150	−0.653	−0.168	−0.590	1.000		
Z_{max}	**0.965**	−0.187	0.816	−0.553	−0.538	−0.168	−0.611	−0.187	−0.570	**0.997**	1.000	
Z_{SD}	0.754	−0.230	0.763	−0.560	−0.565	−0.202	−0.528	−0.231	−0.676	0.762	0.747	1.000

Table 5. Hierarchical cluster analysis results (mean, standard deviation) using conductivity (µS/cm), dissolved oxygen on the bottom (DO, mg/L), light intensity at ≥3 mg/L of dissolved oxygen (I_3, lx), pH, turbidity (NTU), depth at 3 mg/L of oxygen (Z_3), and Secchi depth (Z_{SD}, m).

Cluster	Number of observations	Conductivity	DO	I_3	pH	Turbidity	Z_3	Z_{SD}
1	6	71.82 (116.60)	6.22 (1.68)	0.05 (0.09)	8.02 (0.43)	0.86 (0.16)	90.33 (48.82)	6.92 (1.88)
2	4	42.38 (36.91)	0.24 (0.28)	5730.90 (4209.89)	8.30 (0.63)	1.59 (0.55)	8.25 (2.99)	4.24 (0.53)

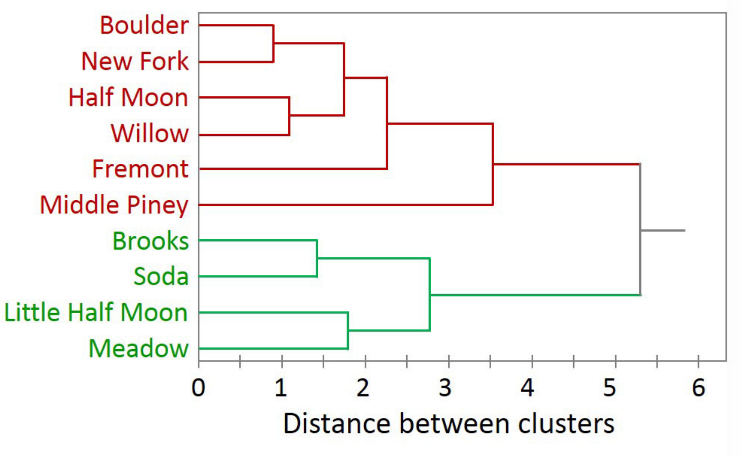

Figure 4. Hierarchical cluster analysis dendrogram using seven physicochemical characteristics of the 10 lakes sampled for *Mysis diluviana* highlighting lakes grouped into two primary clusters (red and green).

Discussion

Mysis persisted in two of the four lakes where they were originally introduced. The *Mysis* populations in Half Moon and Willow lakes have been relatively stable since they were introduced, perhaps because physicochemical conditions have not changed greatly over the period. Grabowski and Ahern (1982) sampled *Mysis* in Half Moon and Willow lakes with comparable methods in August 1981 yielding density estimates (895 individuals/m^2 and 608 individuals/m^2, respectively) that were not significantly different from ours. Dissolved oxygen at 60 m was well above 3 mg/L, and a daytime predation refuge was available, in both lakes during both periods. Surface conductivities in 1981 were slightly lower (16 µS/cm), and Secchi depths slightly greater (8 m) than in 2017, but natural seasonal and interannual variation in these parameters may explain some of the difference. There were few historical data on limnological conditions on the other lakes but the available data suggest that lake conditions in the area have been stable for many years. Brooks Lake has experienced hypolimnetic hypoxia since at least 2001 (WDEQ 2015). Dissolved oxygen profiles and conductivity in Fremont and New Forks lakes in August 1984

(Peterson et al. 1987) were similar to our measurements, but surface temperatures may have increased in Fremont, Half Moon and New Fork lakes since the 1970s (Leopold 1980).

The densities of *Mysis* in Half Moon and Willow lakes were relatively high compared to some other introduced populations of the species in western North America. *Mysis* density averaged 288 individuals/m^2 (range: 1–495 individuals/m^2) at 15 Colorado reservoirs sampled during 1991–2017 (Martinez et al. 2010; BMJ, unpublished data), and averaged 51 individuals/m^2 (range: 1–129 individuals/m^2) over 30 years at Flathead Lake, Montana (Devlin et al. 2016). Seasonal density estimates averaged 352 individuals/m^2 (range: 56–2,471 individuals/m^2) at Lake Pend Oreille, Idaho (Caldwell and Wilhelm 2012). Morgan and Threlkeld (1982) reported 319 individuals/m^2 in Lake Tahoe, California. Our densities are also higher than average densities in the Laurentian Great Lakes (≤ 299 individuals/m^2), where *Mysis* are native (Jude et al. 2018). It is difficult to say why *Mysis* densities are so high in the Wyoming lakes without more detailed information about phytoplankton and zooplankton production, and the intensity of fish predation.

In addition to updating the distribution of *Mysis diluviana* in Wyoming, our investigation provides some insights into the invasion biology of this species, including the conditions needed for establishment, persistence and secondary invasions. The likelihood of establishment and persistence were higher when *Mysis* entered systems with physicochemical conditions similar to those typical of the species' native range: deep, oligotrophic lakes with a well-oxygenated hypolimnion (Dadswell 1974). Further, we found that the only lakes with established populations of *Mysis* also had very low light intensities near the bottom. Despite relatively high water transparency, the lakes with *Mysis* (Half Moon Lake, Willow Lake) were deep enough (85 m) that *Mysis* could retreat to water below the light threshold for visual-feeding by fish during daytime. Only one other lake in the study (Fremont Lake) had a daytime predation refuge.

The two lakes with established *Mysis* populations clustered together, and these lakes were nested within a cluster with four other lakes, suggesting that physicochemical conditions might also be suitable for *Mysis* in Boulder, Fremont, Middle Piney, and New Fork lakes. All of these lakes were deeper and had higher dissolved oxygen concentrations in the hypolimnion, lower pH, and higher water clarity than the lakes in cluster 2. Light intensity at the bottom was at least two orders of magnitude lower in the lakes in cluster 1 than the lakes in cluster 2, but still above the fish feeding threshold at Boulder, Middle Piney, and New Fork lakes. The cluster analysis also showed that Middle Piney Lake was most dissimilar to the other lakes in cluster 1. This suggests that conditions may be less suitable for *Mysis* here, and may also explain why the initial introduction failed at Middle Piney Lake. We believe there are two plausible mechanisms. Mysids are highly sensitive to rapid changes in conductivity (Fürst 1965; Gosho 1975). The conductivity at Middle Piney Lake was at least three times higher than at any of the other lakes in the study, or at the source lake (Twin Lakes, CO; Britton and Wentz 1980). Thus, stocked mysids may have died from osmotic shock upon release. A second explanation is the lack of daytime predation refuge in this, the shallowest lake in cluster 1. Lake trout, a predominant predator on *Mysis* in its introduced range (Lasenby et al. 1986), are also more abundant in Middle Piney Lake than in other area lakes (P.A. Cavali, Wyoming Game and Fish Department, personal communication). Thus, it is possible that fish predation may have prevented establishment of *Mysis* at Middle Piney Lake.

The four lakes in cluster 2 (Brooks, Little Half Moon, Meadow, and Soda) did not have established *Mysis* populations, although one lake (Brooks Lake) was stocked and *Mysis* were immigrating to another (Little Half Moon Lake). All of these lakes appeared to be less suitable for *Mysis* than the lakes in cluster 1: they were shallow, exhibited low dissolved oxygen in the hypolimnion, and had a higher pH than lakes in cluster 1. These conditions were negatively associated with the presence of *Mysis* in 327 lakes in its native range (Dadswell 1974). Further, because they were shallow and moderately clear lakes, *Mysis* would be forced to occupy depths that were well above the minimum light intensity for fish feeding, increasing predation risk. Low hypolimnetic dissolved oxygen caused obligatory habitat shifts in closely related *M. relicta*, resulting in population collapse due to intense predation by fish (Horppila et al. 2003) which may explain the failure of the introduction at Brooks Lake: an interaction between unsuitable oxygen conditions, light penetration and fish predation. These conditions could also prevent *Mysis* from establishing in Meadow and Soda lakes, if the lakes were ever exposed to *Mysis*. Although we captured one mysid in Little Half Moon Lake, we believe that *Mysis* have not established a population there because surface temperature exceeded the upper lethal temperature and depths with suitable temperatures were hypoxic. We believe the single individual we captured had emigrated from Half Moon Lake, just 400 m upstream.

The fact that *Mysis* have not invaded the other lakes in the study area should be some consolation to managers in the region charged with conserving imperiled native species in the face of growing numbers of nonnative species. However, just as the invasion of virile crayfish *Orconectes virilis* Hagen, 1870, facilitated increased piscivory of native fishes by nonnative smallmouth bass *Micropterus dolomieu* Lacepède, 1802, elsewhere in the region (Martinez 2012), the presence of *Mysis* in some of the lakes may facilitate the invasion of other species, such as burbot *Lota lota* Linnaeus, 1758. Burbot are highly piscivorous as adults but *Mysis* are an important food for their young (Scott and Crossman 1973) as they are for young lake trout (Schoen et al. 2015). Burbot are expanding their range in Wyoming and threatening native fishes, after having been illegally transplanted from across the Continental Divide into Big Sandy and Fontenelle reservoirs during the 1990s (Gardunio et al. 2011). Although burbot have not been detected in the Upper Green River basin, there are no barriers preventing them from moving upstream into Little Half Moon and Half Moon lakes (P. Cavalli, Wyoming Game and Fish Department, personal communication). If burbot become established in the Half Moon Lake system they would further threaten the unique population of roundtail chub there. Thus, the presence of introduced *Mysis* could set the stage for an invasional meltdown that would amplify impacts on native species (Simberloff and Von Holle 1999). Because it would not be feasible to eliminate *Mysis* (Lasenby et al. 1986; Martinez and Bergersen 1989) conserving the native fishes of these natural lakes will depend on preventing the spread of *Mysis* and the arrival of new invasive organisms.

Interconnected lakes and reservoirs can act as stepping stones for invasive aquatic species (Havel et al. 2005) and another invasive mysid (*Hemimysis anomala*) is currently spreading across Europe and the Great Lakes region of North America via inland waterways (Kestrup and Ricciardi 2008; Minchin and Boelens 2010). We believe that *Mysis* from Half Moon Lake are regularly being flushed into Little Half Moon Lake and rivers downstream. *Mysis* may be emigrating to these rivers via the outlet at Willow Lake also. The outlets from these lakes flow into the headwaters of the Green River which has two large, coldwater reservoirs that could support *Mysis* approximately 110 km (Fontenelle Reservoir), and 220 km (Flaming Gorge Reservoir) downstream. Thus, waters downstream of the *Mysis* lakes in Wyoming could, in principle, experience secondary invasion. There are some reasons to expect this risk to be low. Unlike *Hemimysis anomala*, *M. diluviana* is an obligate lacustrine species and it is improbable that *Mysis diluviana* could survive such extensive transit in a riverine environment. It is unlikely that *Mysis* could survive the turbulence and fish predation in these rivers to traverse these distances (Gregg and Bergersen 1980). In Colorado, which has dozens of introduced *Mysis* populations, the only cases of successful long distance (> 20 km) dispersal among interconnected lakes occurs via pipelines, not surface rivers. Moreover, mysids dispersing from the Wyoming study lakes would encounter rapidly increasing and an order of magnitude higher conductivity and salinity as they moved downstream in the Green River (Godwin et al. 2015). Such changes in water chemistry have been shown to inhibit translocation success of *M. diluviana* (Gosho 1975) and *M. relicta* (Fürst 1965).

We found no published accounts, agency reports, or database entries documenting sightings of *Mysis* in any other waters of Wyoming (B. Bear, AIS Coordinator, WGFD, personal communication; L. Tronstad, Lead Invertebrate Zoologist, University of Wyoming, personal communication). The absence of evidence for established populations outside of the stocked lakes during the nearly 50 years that the species has been present in Wyoming strongly suggests that *Mysis* have not expanded their range in Wyoming. Thus, it appears that the prospects for secondary invasions by *Mysis* in Wyoming are limited without human assistance. Maintaining the state's strong AIS regulations and penalties for illegal stocking (WGFD 2017) should help to reduce the risk of human-facilitated invasions of *Mysis* in Wyoming. Future studies could formally evaluate the risk of *Mysis* establishing in other waters in Wyoming, and elsewhere in the region. Based on our findings, there are several environmental characteristics that may increase this risk. Lakes with short connections to established populations seem to be more invasible to downstream dispersants. The presence of a daytime predation refuge from fishes, and cold (< 14 °C) hypolimnetic temperatures coupled with adequate (> 3 mg/L) dissolved oxygen concentrations also seem to favor colonization and persistence of *Mysis* in Wyoming. A more comprehensive comparison of limnological conditions in lakes where *Mysis* invasions have succeeded and failed across their introduced range would provide more insights into habitat requirements and a better understanding of future invasion risk.

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