Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Manuscript ID	cjfas-2015-0144.R2
Manuscript Type:	Article
Date Submitted by the Author:	23-Sep-2015
Complete List of Authors:	Caldwell, Timothy; University of Nevada - Reno, Department of Biology Wilhelm, Frank; University of Idaho Dux, Andrew; Idaho Department of Fish and Game,
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Non-native pelagic macro-invertebrate alters population dynamics of herbivorous zooplankton in a large deep lake.

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Abstract

Establishment of non-native species can alter native species populations and re-structure lake food webs through complex trophic interactions such as intra-guild predation or classic trophic cascades. Although the freshwater shrimp, *Mysis diluviana*, is well known for its ability to impact both primary and secondary productivity through omnivorous feeding in aquatic ecosystems in which it has been introduced, empirical evidence of mysid consumption of zooplankton prey and associated impacts on cladoceran communities from the same lake is uncommon. Furthermore, recent literature has suggested that mysids may impact other zooplankton populations outside of cladocerans. To test the hypothesis that introduced mysids negatively affect the seasonal abundance of cladocerans in Lake Pend Oreille, a large and deep (348 km², max. depth - 352 m) lake in Idaho, USA, we quantified the seasonal diet and consumption rates of mysids, and compared them to cladoceran production rates. During isothermal conditions, mysids opportunistically fed on copepods, diatoms, and rotifers. However, during stratification, mysids strongly selected cladocerans. In addition, during isothermal conditions, mysids consumed 100% of cladoceran production and selected reproductive-sized individuals. We interpret this to show that mysids regulate the production of cladocerans when the lake is not stratified. The suppression of cladocerans in the spring coincides with the appearance of kokanee fry whose growth and survival may be negatively affected by the lack of abundant cladocerans, a preferred prey. This suggests a possible cascading effect to higher trophic levels.

Keywords: Mysis, Intraguild predation, Trophic cascades, Predator-prey interactions, Cladoceran

Lake ecosystems are often altered by large-scale extrinsic factors such as climatic change (Winder and Schindler 2004), nutrient loading (Carpenter et al. 1985) and anthropogenic activities, which undoubtedly influence the population regulation of aquatic organisms. However, it is the introduction or removal of predators that can cause immediate shifts in biological populations by initiating trophic cascades or creating a new IGP regime (Pace et al. 1999; Vander Zanden et al. 1999; Hyatt et al. 2005; Ellis et al. 2011). Therefore, it is critical that we examine and understand the complex and often unanticipated interactions that result from predator introductions, as their occurrence continues to increase in frequency and impact global biodiversity (Sala et al. 2000).

The freshwater shrimp, *Mysis diluviana* (previously *Mysis relicta*, Audzijonytė and Väinölä 2005), is an invertebrate omnivore with the ability to consume significant portions of zooplankton populations (Johannsson et al. 1994; 2001; Gal et al. 2006; O'Malley and Bunnell 2014). Described as opportunistic, mysids consume food from the benthos while they are on the lake bottom during the day (Van Duyn-Henderson and Lasenby 1986; Johannsson et al. 2001; Sierszen et al. 2011) and prey on pelagic zooplankton at night during diel vertical migration (DVM) (Johannsson et al. 1994; 2001; Viherluoto et al. 2000; Nordin et al. 2008). As young, or when zooplankton are scarce, mysids filter feed on algae (Bowers and Grossnickle 1978; Branstrator et al. 2000; Schindler et al. 2012) and some adults are cannibalistic on juveniles (Nordin et al. 2008). Although capable of consuming a variety of zooplankton species, the selection of prey by mysids is governed by prey availability and ease of capture, thus mysids prefer and typically select large, slow moving cladocerans (Cooper and Goldman 1980; Spencer et al. 1999; Nordin et al. 2008; Whall and Lasenby 2009), however recent research has suggested they can also impact copepod populations (Schindler et al. 2012). Because the abundance of cladocerans is seasonally dynamic in many lakes, omnivorous traits of mysids (Branstrator et al. 2000) are important to their energetics (France 2012; Schindler et al. 2012) and often result in additional impacts on food webs besides the reduction or elimination of zooplankton. These traits, coupled with predator avoidance (i.e., DVM; Beeton and Bowers 1982; Boscarino et al. 2007) make mysids a formidable predator in lentic ecosystems that play a significant role in structuring food webs.

Because of its high lipid content (Adare and Lasenby 1994), large size (1-2 cm), and its importance to fish throughout its native range (Wells and Beeton 1963; Issac 2010; Gamble et al. 2011a; 2011b), fisheries managers introduced *M. diluviana* into numerous lakes across the North

American Pacific Northwest and Scandinavia with the intent to increase fish production (Lasenby et al. 1986). Although, some introductions were successful (e.g., Sparrow et al. 1964), the majority resulted in the decline of some fish populations and caused significant changes to cladoceran population dynamics and entire lake food webs (Rieman and Falter 1981; Richards et al. 1991; Ellis et al. 2011).

Based on correlation between mysid abundance after their introduction and the seasonal decline of cladocerans, Rieman and Falter (1981) suggested that mysids in Lake Pend Oreille, Idaho, USA reduced the prey available to newly released kokanee fry which emerge from April to June. Only during stratification (July-Sep), when mysids are excluded from the epilimnion by warm water temperatures, did cladoceran abundance reach high densities after mysids became established in the lake (Rieman and Falter 1981). Chipps and Bennett (2000) used a general mysid bioenergetics model (Rudstam 1989), to estimate that mysids consumed $186 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ of cladoceran biomass in Lake Pend Oreille, which represents up to 70% of daily cladoceran standing stock. In contrast, cladoceran consumption by kokanee was estimated to be $45 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (Chipps and Bennett 2000). However, neither of the conclusions reached by Rieman and Falter (1981) or Chipps and Bennett (2000) have been empirically tested using data from mysid gut contents. Given the variety of effects observed as a result of the introduction of mysids in other lake ecosystems (Schindler et al. 2012), empirical data from LPO are needed to support this hypothesis.

Here we use gut content analyses to examine the seasonal diet of mysids in Lake Pend Oreille, paired with simultaneous measurements of cladoceran production to empirically test the hypothesis that consumption of cladocerans by mysids limits cladoceran production.

109 **Methods**

110 ***Study Site:***

111 Lake Pend Oreille (LPO), is a large (383 km²) and deep (352 m maximum depth, 164 m
112 mean depth) temperate oligotrophic (total phosphorus - TP < 7 µg·L⁻¹, chlorophyll *a* < 5.5
113 mg·m⁻³) natural lake, located in the panhandle of northern Idaho, USA (Falter and Ingman 2003).
114 The main inflow to the lake is the Clark Fork River which enters LPO from Montana. The lake
115 outlet forms the Pend Oreille River which flows west into the State of Washington (Fig. 1). The
116 lake can be grossly separated into two major basins; the northern basin located to the north and
117 west of the Clark Fork delta which is shallower (< 200 m maximum depth) than the southern
118 basin located south of the Clark Fork delta (> 250 m maximum depth; Fig. 1). The water level of
119 LPO is controlled at the outlet by the Albeni Falls Dam, for flood control, power production and
120 augmentation of flow into the Columbia River Power System. Typically the lake level is
121 maintained at maximum pool elevation from June to September, while in the winter it is dropped
122 by up to 3 meters (Maiolie et al. 2006). The lake is typically thermally stratified between late
123 June and September to an average depth of approximately 10-18m.

124 Each year from 1966 to 1970, 50,000 to 300,000 mysids from Waterton Lake, Alberta,
125 Canada and Kootenay Lake, British Columbia, Canada were introduced to LPO (Rieman and
126 Falter 1981). Annual surveys confirmed that mysids had established a self-sustaining population
127 by 1972, reaching a density of 1,980 mysids·m⁻² by 1978 (Rieman and Falter 1981). During the
128 2000's mysid densities fluctuated from approximately 300 to 1200 mysids·m⁻² in the 2000's
129 (Maiolie et al. 2006; Wahl et al. 2013); however, maximum densities of 2,471 +386 -334
130 individuals·m⁻² (geometric mean ± SE) were reported in 2009-2012 (Caldwell 2010; Caldwell
131 and Wilhelm 2012). Following the introduction of mysids, kokanee salmon (*Oncorhynchus*
132 *nerka*), declined precipitously after the 1960's but have recovered in recent years to re-open a

recreational fishery (Wahl et al. 2013); however, the role of mysids in the decline is unclear. Kokanee have multiple ecological roles in LPO and are utilized as a primary food source by bull trout (*Salvelinus confluentus*; Clarke et al. 2005), currently listed as threatened under the US Endangered Species Act of 1973, and by Gerrard-strain Rainbow Trout (*Oncorhynchus mykiss*). Native fish in LPO include Bull Trout, Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*), and Mountain Whitefish (*Prosopium williamsoni*). Kokanee salmon, Gerrard rainbow trout, lake trout (*Salvelinus namaycush*), Lake Whitefish (*Coregonus clupeaformis*), Smallmouth Bass (*Micropterus dolomieu*), Largemouth Bass (*Micropterus salmoides*), and Walleye (*Sander vitreus*) are all non-native fish that have become established in the ecosystem.

To characterize and examine the spatial and seasonal diet of mysids, we selected one site each in the north (north site; 161 m; N48°13.000' W116°20.687'; Fig. 1), and south basin (south site; 287 m; N47°58.035' W116°29.218'; Fig. 1). This selection was intentional to examine if mysid predation is similar in the two basins.

Temperature profiles:

To determine the seasonal thermal regime in LPO, we used an Amphibian logger connected to a Manta multi-probe sonde (Eureka Environmental, Austin, Texas, USA) which was lowered in 0.5 m increments from the surface to 35 m during each sampling event. Standard limnological isopleths were plotted to show the seasonal thermal regime in the lake at both sites. Additionally, we used a relative thermal resistance to mixing (RTRM) model (Kortmann and Henry 1981) to determine time periods and depths of stratification in LPO during 2009-2010. We also gathered historical profiles (1952, 1953) from Stross (1954), records (1976-1978, 1998-2003) from the Idaho Department of Fish and Game, and records (1989-1990) from the United States Geological Survey (USGS) to determine if the stratification patterns we observed were

similar to other years. The RTRM model was used to determine depth of stratification for all historical profiles during the months of August and plotted as a function of time.

Collection of mysid samples for gut content analysis and density:

To determine the density, and examine the diet of mysids in LPO, individuals were collected during the new moon phase at monthly intervals between May and November 2009 and at bi-monthly intervals between November 2009 and March 2010. To ensure that mysids had completed the upward part of the DVM cycle, all samples were collected around 12:00 AM, well after dusk. In addition, an echosounder was used to confirm that they had reached the upper 40 m of the water column. Triplicate samples of mysids were collected using a vertical net haul with a 1 m diameter hoop net with 1 mm-mesh and a 500 μm -screened cod end (Chippis and Bennett 1996). The net was lowered to 40 m, allowed to settle for several minutes, and then retrieved at approximately $0.33 \text{ m} \cdot \text{s}^{-1}$ with the aid of an electric winch. Samples were preserved in 8% formalin until analysis. Samples were not collected at the north site during November due to inclement weather.

Mysid density at each site was determined by enumerating all mysids in each sample. Each mysid was measured from the tip of the rostrum to the base of the telson, aged, and sexed (Morgan 1980; Caldwell and Wilhelm 2012). Areal density ($\text{individuals} \cdot \text{m}^{-2}$) was calculated as the average number of the triplicate samples, divided by the area of the net (0.785 m^2). Volumetric density ($\text{individuals} \cdot \text{m}^{-3}$) was determined by dividing the average number of mysids collected in each of the three net hauls by the tow volume (31.6 m^3).

Gut contents and prey composition indices:

Ten adult ($> 10 \text{ mm}$) mysids from each month and site were haphazardly selected to evaluate gut contents. Mysids $> 10 \text{ mm}$ were selected because they are abundant throughout the

year, and because mysids < 10 mm are primarily herbivorous (Branstrator et al. 2000). With the aid of a dissecting microscope, mysid foreguts were dissected and spread onto a glass microscope slide with melted glycerol jelly, covered with a coverslip, and allowed to cool. Mysids from which guts were broken or spilled were not used for analysis and were replaced with new individuals. Gut contents of mysids were identified and enumerated with the aid of a compound microscope. Zooplankton were identified and counted based on the presence and number of mandibles (cf. Chess and Stanford 1998; Johannsson et al. 2001). To quantify the number of cladocerans eaten by mysids, mandibles were counted and divided by two using the assumption that two mandibles indicated that one cladoceran was consumed. This may slightly underestimate the actual number of cladocerans consumed.

The size of cladocerans eaten by mysids was estimated from a LPO-specific cladoceran body length to mandible length relationship. The body size of thirty cladocerans spanning the entire size range encountered in samples from LPO was first measured then followed by removal and measurement of the mandibles to the nearest 1 μm . Because mandibles of different cladoceran species could not be differentiated during the analysis of guts, the relationship between mandible length and total body length was established using all cladocerans (*Daphnia* and *Diaphanosoma*) encountered in LPO samples.

The number of prey eaten by mysids per night (individuals eaten $\cdot \text{m}^{-3} \cdot \text{night}^{-1}$) was quantified on a monthly basis, using the equation:

$$(1) \quad P_{im} = i_m D_m G P_m$$

$$\text{and } G P_m = GRT * NL$$

$$\text{and } GRT = 10.367T^{-0.580}$$

$$\text{and } NL = 24 - (\text{sunset time} - \text{sunrise time}) - 2$$

201 where P_{im} is the number of prey i consumed per night (individuals eaten $\cdot m^{-3} \cdot \text{night}^{-1}$) in month m ;
 202 i_m is the mean number of cladocerans consumed in month m ; D_m is the density of large (> 10
 203 mm) mysids (adult individuals $\cdot m^{-3}$) in month m ; and GP_m is gut passages per night in month m ;
 204 GRT is gut residence time which is a temperature (T) dependent metabolic function; T is water
 205 temperature ($^{\circ}\text{C}$) 1 m above the thermocline during month m ; 10.367 and -0.580 are regression
 206 coefficients; NL is night length in decimal hours; 24 is the number of decimal hours in a day; and
 207 sunset and sunrise times are in Pacific Standard Time converted to decimals. Two hours were
 208 subtracted to account for the time needed for ascent and descent (Chipps 1997). The equation
 209 for GRT was established with laboratory experiments using mysids from LPO (Chipps 1997,
 210 1998). Water temperature just above the thermocline was used given the frequent observation of
 211 mysids at this depth via an echosounder (Caldwell, personal observation). Sunset and sunrise
 212 times were obtained from the United States Naval Observatory (USNO 2010).

213 Diet and feeding strategy was described using the prey-specific index (PSI), a
 214 modification of the Costello method (Amundsen et al. 1996). PSI is defined as the volumetric
 215 percentage a certain prey taxon comprises of all prey taxa for only those predators in which the
 216 prey occurs (Amundsen et al. 1996). PSI is calculated as:

$$(2) \quad PSI_i = \sum S_i / \sum S_{it} \times 100$$

217 where PSI_i is the prey-specific index of prey i ; S_i is the gut content volume comprised of prey i in
 218 individual mysids; and S_{it} is the gut content volume of only those predators with prey i present
 219 in the gut. PSI was plotted against the frequency of occurrence to determine prey importance
 220 and feeding strategy. Frequency of occurrence was calculated as:

$$(3) \quad O = P_{it} / P$$

221 where O is the frequency of occurrence, P_{it} is the number of predators with prey i present in their
222 gut, and P is the total number of predators sampled. The volume of mysid foreguts is small (< 2
223 mm diameter) and direct measurement of the volume that a certain prey taxon occupied was
224 difficult. Instead, we subjectively estimated volume using a “points” method (cf. Wilhelm et al.
225 1999). First, each gut regardless of fullness was assigned a value of ten points. Then all prey in
226 each taxon found in the gut were visually assigned a value of points from 1 to 10, based on their
227 contribution to the entire gut contents. For example, if diatoms and copepods contributed 70%
228 and 30%, respectively, of an individual mysid gut, they received scores of 7 and 3. To describe
229 the seasonal feeding strategy of mysids, PSI was calculated for each monthly sample.

230 Typically PSI is plotted against frequency of occurrence, showing prey importance,
231 feeding strategy, and diet niche (see Amundsen et al. 1996 for a complete description). Instead,
232 we plotted the product of PSI and frequency of occurrence as a function of time. This
233 represented the seasonal diet of the mysid population and will be referred from here on as the
234 “Population Prey Specific Index” (PPSI).

235 ***Cladoceran density, size, and production:***

236 Triplicate vertical hauls of zooplankton were collected on each sampling occasion with a
237 Wisconsin-style plankton net (30-cm diameter, 64 μm -mesh) during the same monthly intervals
238 when mysids were sampled. The net was lowered to 20 m, allowed to settle for several minutes
239 and retrieved at $0.33 \text{ m}\cdot\text{s}^{-1}$. Samples were preserved in 8% formalin until analysis. Each sample
240 was brought up to 100 mL from which all zooplankton in a 5 mL sub-sample were enumerated
241 and identified with the aid of a dissecting microscope. Cladocerans were identified to genus.
242 Mean density ($\text{individuals}\cdot\text{m}^{-3}$) of each taxon was estimated by back calculating from the
243 subsamples and dividing the average of the three replicate samples by the tow volume.

To determine cladoceran size, 100 individuals (except in samples from the south site in October, and November which only contained 49 and 44 cladocerans, respectively) were measured by first haphazardly selecting a location in the petri dish containing the entire zooplankton sample and then measuring every individual encountered while working outward in an increasing spiral from the starting point. Each individual was measured from the top of the head to the inflection of the tail spine to the nearest 1 μm with the aid of a dissecting microscope fitted with a calibrated ocular micrometer. In addition the average body length of reproductive cladocerans was determined from gravid females encountered in samples (all gravid individuals were measured from each sample). The mean size of prey in mysid guts was compared to the mean size in the lake using a t-test for each month. All statistics were performed in SYSTAT® version 13.

Production of *Daphnia* and *Diaphanosoma* was calculated with the egg ratio method (Edmondson and Winberg 1971; Edmondson 1972; Paloheimo 1974). To estimate birth rate we used the equation described by Paloheimo (1974):

$$(4) \quad b = \ln \left[\left(\frac{C_t}{N_t} \right) + 1 \right] / D$$

where b is the instantaneous birth rate; C_t is number of eggs, N_t is number of females, and D is the temperature-dependent egg development time in days. We used 2 days for D at 20 °C (Chippis 1997) and adjusted D along the normal Krogh curve (Edmondson and Winberg 1971) to match the observed water temperature. Instantaneous birth rate was multiplied by density for each species during each month, and production was estimated as $\text{births} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$. The sum of *Daphnia* and *Diaphanosoma* production was used to determine total cladoceran production ($\text{births} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$) for each month.

266 ***Comparison of mysid diet between sites:***

267 To test if the diet of mysids differed between sites we used a nonparametric Kolmogorov-
268 Smirnov (K-S) two-sample test, comparing the amount of each prey item consumed at each site.
269 K-S tests were run using SYSTAT® version 13.

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Results

Temperature profiles:

Temperature profiles and the RTRM model indicated that thermal regimes and seasonal stratification of LPO was similar at the north and south sites (Fig. 2a, b). From October to April the lake was isothermal, with a temperature of approximately 4 °C. During late-April and May the surface water began to warm to ~8-10 °C. The lake was weakly stratified to a shallow depth of approximately 5 m during June but deeper (11-14 m), strong stratification did not occur until July and lasted until September, with temperatures reaching 23 °C at the surface, while the epilimnion was about 20 °C (Fig. 2a, b). Historical thermal stratification patterns (1954-2003) for August in LPO were similar to our observations in 2009 (Fig. 2c, d). The average thermocline depth between 1954 and 2010 at the north and south sites was 11.5 m (range 6-16 m) and 13.5 m (range 7-18 m), respectively (Fig. 2c, d).

Gut contents and prey composition:

Mysid diet varied seasonally (Fig. 3a, b), but was similar between sites (Table 1). A significant portion of the mysid gut content consisted of 'other' material that was amorphous, and unidentifiable (Fig. 3a, b). The highest volume of 'other' material occurred in October ranging from 100% to 84% at the north and south sites, respectively (Fig. 3a, b). During mid-to late spring (May and early June) mysid gut contents included diatoms, pollen grains, rotifers, and copepods which contributed up to 42% and 35% of gut contents at the north and south sites, respectively (Fig. 3a, b). Pollen was more prevalent in the diet of mysids at the south site in May and June (21% and 6%) compared to the north site (0% and 5%; Fig. 3). During July, rotifers were the most abundant prey in mysid gut contents, contributing approximately 31% and 60% to the gut volume at the north and south sites, respectively (Fig. 3a, b). Diatoms generally

293 contributed a higher percentage of material to gut contents at the north site than at the south site
294 (Fig. 3a, b).

295 Cladocerans contributed $< 1\%$ to mysid gut contents during May, June and July (Fig. 3a,
296 b) while the lake was isothermal, however, after stratification in August and September, mysids
297 at both sites strongly selected cladocerans (Fig. 3a, b). During September, cladocerans
298 contributed 70% and 82% to gut contents at the north and south sites, respectively (Fig. 3a, b).
299 After the breakdown of stratification (October to March) mysids returned to a cosmopolitan diet,
300 (Fig 3a, b). In summary, mysids were generalist feeders when the lake was isothermal and had a
301 high within-phenotype component (Amundsen et al. 1996) and broad niche width, while during
302 stratification, mysids strongly selected cladocerans.

303 ***Cladoceran density and production:***

304 Cladocerans in lake samples were rarely observed when the lake was isothermal (Table
305 2). Interestingly, we noted the occurrence of cladoceran remains in the gut contents of mysids
306 approximately 1 month before we obtained any in zooplankton tows. Total cladoceran density at
307 the north site increased from 114 ± 57 (mean $\pm$ SE) individuals $\cdot$ m $^{-3}$ in July to 4941 ± 250
308 individuals $\cdot$ m $^{-3}$ in August, then decreased until November when they were no longer detected in
309 lake samples (Table 2). A similar trend was observed at the south site (Table 2). The cladoceran
310 community consisted of *Diaphanosoma* and *Daphnia* spp. *Diaphanosoma* was more abundant
311 than *Daphnia* spp. during July and October, while *Daphnia* spp. made up $> 85\%$ of all
312 cladocerans in August and September at both sites (Table 2). When the lake was isothermal
313 (October- July), *Diaphanosoma* was detected at low densities ($< 24 \pm 22$ individuals $\cdot$ m $^{-3}$) during
314 January at the north site, and November at the south site.

315 Cladoceran production was low during late spring and early summer (May-July) but
316 peaked at > 2000 births $\cdot$ m $^{-3}\cdot$ d $^{-1}$ in August at both sites (Table 2). In September, production

317 decreased to 505 and 843 births·m⁻³·d⁻¹, at the north and south sites, respectively (Table 2).
318 Production continued to decrease during October, and was < 120 births·m⁻³·d⁻¹ at both sites
319 (Table 2). *Diaphanosoma* made up > 90% of the total cladoceran production during July,
320 October, and November at both sites (Table 2). In August and September *Daphnia* spp.
321 accounted for > 80% of overall cladoceran production (Table 2). During January gravid
322 cladocerans were not found in any samples, thus production was set to 0 births·m⁻³·day⁻¹.

323 ***The effects of mysid consumption on cladoceran production:***

324 Because we found cladocerans in the gut contents of mysids during some time periods
325 when they were not detected in the lake, we calculated the production of cladocerans as zero.
326 However, the consumption of cladocerans by mysids indicates that some production occurred,
327 but without several variables required by the egg:ratio method (Edmondson and Winberg 1971;
328 Edmondson 1972; Paleheimo 1974) we could not calculate a production rate. Because
329 cladoceran parts were observed in mysid guts, we assumed that mysids consumed close to 100%
330 of the cladoceran production during these time periods.

331 In May and June we calculated that mysids consumed between 9 and 11 cladocerans·m⁻³·
332 night⁻¹, respectively (Table 2), at the north site. No cladocerans were found in mysid guts in
333 May at the south site, while we calculated that 5 cladocerans·m⁻³·night⁻¹ were removed in June
334 (Table 2). During stratification (July – September) mysids consumed considerably more (21-651
335 cladocerans·m⁻³·night⁻¹) cladocerans at both sites (Table 2). Mysid consumption of cladocerans
336 decreased at both sites between October and November, and during winter few cladocerans (0-5
337 cladocerans·m⁻³·night⁻¹) were detected in mysid guts (Table 2).

338 Mysids removed 100% of cladoceran production at both sites in early spring (May-June
339 north site; June-July south site; Fig.4a, b). The percentage of cladoceran production consumed

by mysids at both sites declined to 14-40% (depending on the month) once the thermocline deepened (August or September). At the north site, mysids consumed 100% of cladoceran production during September but only about 20% of production in October (Fig. 4a). At the south site, consumption of cladoceran production by mysids returned to 100% in October upon the return of isothermal conditions (Fig. 4b). March was the only month when cladocerans were not detected in the lake or consumed by mysids, thus both consumption and production rates were zero.

Our estimated percentage of cladoceran production consumed by mysids in LPO was approximately 11 to 30% higher than previous estimates using a bioenergetics approach (Table 3). Our estimates were similar to those of Johannsson et al. (1994) for Lake Ontario where they estimated that mysids consumed up to 110% of zooplankton production (Table 3). This is in stark contrast to Gal et al. (2006) who estimated that mysids only consumed up to 4% of zooplankton production in Lake Ontario. We were surprised to find only three studies that quantified mysid consumption as a fraction of zooplankton production or standing stock (Table 3), however, numerous studies have quantified mysid clearance rates and examined prey densities before and after mysid introductions (see discussion).

Size of cladocerans selected by mysids:

At the north site, the mean size of cladocerans increased from 1072.92 ± 25.81 (mean $\pm$ SE) μm in July, to 1507.33 ± 42.32 μm in September, then decreased to 1269.74 ± 25.33 μm in October (Fig. 5). Similarly, the mean size of cladocerans at the south site increased from 895.37 ± 25.86 μm in July, to 1433.42 ± 34.06 μm in September, and then decreased to 1304.12 ± 33.92 μm in October (Fig. 5). The mean size of gravid cladocerans increased from 999 ± 34 μm to

1660 ± 47 µm and 1118 ± 28 µm to 1665 ± 46 µm at the north and south sites, respectively, from July to September (Fig. 5). No gravid individuals were observed in October.

Cladoceran body size was positively related ($R^2 = 0.80$, $n = 33$, $P = < 0.001$) to mandible length and described by the equation:

$$TBL = 9.69(ML) + 926.63$$

where *TBL* is total body length of cladocerans in µm; *ML* is mandible length in µm; and 9.69 and 926.63 are regression coefficients. This relationship was used to estimate the size of cladocerans consumed by mysids.

At the north and south sites, cladocerans in mysid gut contents were significantly larger than those in the lake during July, while they were similar in August, September and October (Fig. 5). Mysids also consumed cladocerans that were significantly larger than the average size of gravid females detected in the lake during July, but not in August or September (Fig. 5). After turnover, the size of gravid females declined to <1400 µm in October at both sites (Fig. 5).

374 **Discussion**

375 *The impacts of mysid predation on the cladoceran population*

376 Classic food web theory and hypotheses suggest that predators often regulate and control
377 population dynamics of herbivores and/or primary producers (Hairston et al. 1960; Brooks and
378 Dodson 1965), however, the complete domination of certain trophic levels or species populations
379 is rarely observed. The impact of consumption by a macro-zooplankter such as mysids on the
380 production of lower trophic levels has been examined in several ecosystems, albeit, many of
381 these were modeled using a bioenergetics approach (e.g., Johannsson et al. 1994; Chipps and
382 Bennett 2000; Gal et al. 2006). Consumption rates of prey by predators are rarely equal to or
383 greater than production rates of the prey (Yan et al. 1991). We provide direct empirical evidence
384 including predation rates based on gut content analyses and simultaneous calculations of
385 zooplankton production which suggests that predation by mysids in LPO is commensurate with
386 cladoceran production rates until LPO becomes thermally stratified and the epilimnion is
387 sufficiently warm to provide a refuge for zooplankton from mysids. To our knowledge, the
388 impact of mysid consumption on zooplankton populations presented here is the greatest that has
389 been directly quantified via empirical evidence (Table 3), however, the extirpation of
390 cladocerans in other lake ecosystems after the introduction and establishment of mysids suggests
391 it may occur in other lakes (Richards et al. 1991; Ellis et al. 2011). Our results provide empirical
392 evidence suggesting that mysids are responsible for the reduction or extirpation of cladoceran
393 populations in several lakes which received mysid introductions (Lasenby et al. 1986).

394 The intra-guild predation (IGP) theory (Polis and Holt 1992) is often supported by
395 pelagic food webs that have mysid shrimp because they and planktivorous fish tend to consume
396 similar prey, and often the fish can and do consume the mysids (Hyatt et al. 2005). However,

our research suggests that planktivorous fish (kokanee salmon) have little to no effect on the mysid population, suggesting a more classic trophic cascade model (e.g., Carpenter et al. 1985; Pace et al. 1999) with regards to the upper trophic levels of LPO. It should be noted that we only collected one year of mysid diet and cladoceran production data and more complex intra-guild effects may occur based on the variability in fish abundance or lake primary productivity among years (Hyatt et al. 2005). However, an analysis of the LPO community using stable isotopes does not indicate a strong link between kokanee and mysids, but that kokanee rely on cladocerans and chironomids (Clarke et al. 2005).

Our empirical data on the seasonal diet of mysids lends support to various hypotheses and inferences made about the LPO food web in the past. For example, Rieman and Falter (1981) used historical zooplankton data to infer that the suppression of cladocerans was caused by the introduction of mysids. Similarly, bioenergetic model simulations by Chipps and Bennett (2000) suggested that the removal of cladoceran production by mysids in early spring and fall was significant. Because mysids do not typically tolerate water temperatures above 17 °C (Rudstam 1989; Boscarino et al. 2007), their vertical migration does not extend into the epilimnion (20°C), affording cladocerans a warm-water predator refuge from mysids. Thus, in the absence of mysids, they can reach high densities in the epilimnion. It is likely that mysids make metalimnetic excursions (Murtaugh 1981) to consume cladocerans. These short migrations into the metalimnion to briefly feed in prey rich waters do not appear to impact the population of cladocerans. Breakdown of thermal stratification in the fall removes the thermal barrier allowing mysids access to cladocerans again. Because our data show that predation by mysids removes 100% of cladoceran production during this time period, we conclude that predation by mysids also contributes to the collapse of the cladoceran population in fall.

Mysids have been described as “sloppy” feeders because they consume the soft portion of *Daphnia* while often discarding the hard and difficult to digest parts (i.e., exoskeleton, mandibles, claws; Grossnickle 1982; Smokorowski et al. 1998). Because we used the detection of mandibles to quantify the number of cladocerans consumed by mysids, our consumption estimates are likely conservative and underestimate the impact of mysid predation on cladocerans. Indirect effects, such as the consumption of resting eggs by mysids, may further limit the production of cladocerans (Lehtiniemi et al. 2009).

Mysids have been shown to reduce the biomass and change the community structure of phytoplankton and diatoms through direct consumption in other systems (e.g., Lindén and Kuosa 2004; Lehtiniemi et al. 2009; Schindler et al. 2012). During isothermal conditions in LPO (Nov-Mar), 26-48% of the mysid diet consisted of diatoms. The role of mysid consumption in the primary productivity of lakes has not been satisfactorily explored, given that adults are omnivorous and juveniles are primarily herbivorous (Branstrator et al. 2000) it certainly deserves further investigation.

The selection of large zooplankton by mysids suggests another mechanism by which they delay the onset of an abundant cladoceran population in LPO. At the onset of stratification, the mean size of cladocerans consumed by mysids was larger than the mean size of gravid cladocerans in the lake. Thus mysids removed the largest individuals which would cause declines in cladoceran production rates because reproductive output is related to cladoceran body size (Lynch 1980). In the absence of large individuals that are highly fecund, the cladoceran intrinsic rate of increase would be reduced, and lead to slow population growth in spring and early summer.

Seasonal diet and prey selection:

Cooper and Goldman (1980) hypothesized that the selection of prey by mysids depended on; i) availability of prey; ii) prey escape ability; and iii) efficiency of prey capture. In LPO, the diet of mysids was highly plastic, similar to that reported in other lakes (Schindler et al. 2012; O'Malley and Bunnell 2014). For example, during winter, when diatoms were abundant, they occurred in mysid guts at both sites in LPO. This is similar to other systems in which mysids also feed on diatoms (Viherluoto and Viitasalo 2001; Lehtiniemi et al. 2009; Schindler et al. 2012). While the density of copepods is high in LPO (Caldwell and Wilhelm, unpublished data) they did not contribute significantly to the gut contents of mysids, however they select for copepods elsewhere (Schindler et al. 2012; O'Malley and Bunnell 2014). Ramcharan et al. (1985) and Nero and Sprules (1986) suggested that the rapid escape response of copepods reduces the ability of mysids to efficiently capture them. This may also be the case in LPO.

Caldwell and Wilhelm (2012) observed little to no growth in mysids during the winter months (Nov – Mar) in LPO. The consumption of less preferred food sources (i.e., diatoms and copepods) may cause the allocation of energy to prey capture rather than to growth and reproduction (Nordin et al. 2008). We hypothesize that low water temperatures associated with winter, coupled with the re-allocation of energy to the capture of prey items (i.e., diatoms and copepods) reduced the efficiency of predation and slowed growth.

Cladocerans are slow moving, high in nutrient content (Anderson and Hessen 1991), and abundant during certain times of the year. It is likely because of these characteristics that mysids in LPO strongly selected cladocerans when available. Similar patterns have been observed in other lakes (Johannsson et al. 2001; Whall and Lasenby 2009). The correlation between the consumption of cladocerans presented here and increased rate of growth by mysids (Caldwell and Wilhelm 2012) suggests that cladocerans may be important prey to mysids.

Potential cascading effects of the mysid-altered zooplankton assemblage on fisheries:

The temporal delay of cladoceran abundance caused by mysid predation on cladocerans has been implicated in the reduction of kokanee salmon (*Onchorhynchus nerka*) stocks (Nesler and Bergersen 1991), and was hypothesized in LPO (Rieman and Falter 1981; Bowles et al. 1991). While all life-stages of kokanee may be influenced by the suppression of cladocerans by mysids, fry may be the most susceptible because their emergence in LPO occurs between April and June at which time they depend on the presence of cladocerans (Rieman and Bowler 1980). This coincides with the apparent complete suppression of cladoceran abundance by mysids (see above). Thus, kokanee fry likely emerge into a food-poor environment, in which their preferred prey is absent and they are forced to find alternate prey, survive on reserves until the lake stratifies and cladoceran abundance increases (although warm epilimnetic water temperatures may preclude kokanee from the epilimnion), or perish. An abundant food supply is known to be important to recruitment of kokanee (Paragamian and Bowles 1995; Clarke and Bennett 2004) and predation pressure by mysids on zooplankton may represent a bottleneck to the kokanee population.

Variables which control the diel vertical migration of kokanee and sockeye salmon fry (the anadromous form of *Onchorhynchus nerka*) are not well understood (Beauchamp et al. 1997; Stockwell and Johnson 1999; Scheuerell and Schindler 2012). If kokanee spend a disproportionate time below the thermocline, their growth and survival may be reduced by the lower abundance of zooplankton due to the presence of mysids (see above). Thus, studies by Clarke and Bennett (2002a; 2002b; 2004) which concluded that the presence of mysids did not negatively influence kokanee growth and survival in LPO or the zooplankton assemblage

available to them may have been confounded by the shallow (2 m) depth at which they were conducted. Spatial overlap between mysids, kokanee fry, and other life stages of kokanee, along with the effects of predation on cladoceran density, may be more significant below the thermocline and underestimated in this and other studies (e.g., Chipps and Bennett 2000; Clarke and Bennett 2002a; 2002b; 2004).

The introduction of mysids to LPO has had a multi-pronged effect on the population of cladocerans. We observed a classic trophic cascade mechanism in the upper trophic levels (kokanee and mysids) but also observed evidence for intra-guild predation by mysids on cladocerans and their primary forage base (diatoms). Based on empirical quantification of the gut contents of mysids, we concluded that; i) direct consumption by mysids was commensurate to production by cladocerans during isothermal conditions (spring and fall); ii) mysids exhibited diet plasticity associated with the seasonal distribution and abundance of prey; and iii) mysids selected large-sized gravid cladocerans. Because of the effects-mysids have on cladoceran density, kokanee growth and survival in LPO is likely negatively influenced by mysids. Specifically, the temporal overlap of the recruitment of kokanee fry and the suppression of cladoceran production by mysids may represent a food bottleneck to the kokanee population. These results suggest that certain non-native predators have the ability to significantly alter the production and temporal dynamics of lower trophic levels, causing lake-wide changes to food webs.

Acknowledgements

We thank Andrew Waldo, Cindy Adams, William Ament, William Harryman, Nick Wahl, Tyson Fehringer, Caeylan Coyler, Rick Hartson, Andrew Baker, Rosalinda Gonzalez, Susan Bury, and Ben Ho for assistance with field work. The Idaho Department of Fish and

512 Game provided occasional use of research vessels, especially in winter. Funding for this project
513 was provided by the Bonneville Power Administration through a grant to the Idaho Department
514 of Fish and Game. T.J. Caldwell was supported by scholarships from the International
515 Association of Great Lakes Research, the Washington State Lakes Protection Association and
516 the Idaho Chapter of the American Fisheries Society. We thank Dr. Marion Wittmann, Dr.
517 Clinton Davis, Dr. Sudeep Chandra, Jason Barnes, and Annie Caires for constructive comments
518 that improved the manuscript. We also appreciate constructive comments from the associate
519 editor and one anonymous reviewer that greatly improved the manuscript.

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References

- 522 Adare, K.I., and Lasenby, D.C. 1994. Seasonal changes in the total lipid content of the opossum
523 shrimp, *Mysis relicta* (Malacostraca: Mysidacea). Can. J. Fish. Aquat. Sci. **51**(9): 1935–
524 1941. doi: 10.1139/f94-195.
- 525 Amundsen, P.-A., Gabler, H.-M., and Staldivik, F.J. 1996. A new approach to graphical analysis
526 of feeding strategy from stomach contents data—modification of the Costello (1990)
527 method. J. Fish Biol. **48**(4): 607–614. doi: 10.1111/j.1095-8649.1996.tb01455.x.
- 528 Anderson, T., and Hessen, D.O. 1991. Carbon, nitrogen, and phosphorus content of freshwater
529 zooplankton. Limnol. Oceanogr. **36**(4): 807–814. doi: 10.4319/lo.1991.36.4.0807.
- 530 Audzijonytė, A., and Väinölä, R. 2005. Diversity and distributions of circumpolar fresh- and
531 brackish-water *Mysis* (Crustacea: Mysida): descriptions of *M. relicta* Lovén, 1862, *M.*
532 *salemaai* n. sp., *M. segerstralei* n. sp. and *M. diluviana* n. sp., based on molecular and
533 morphological characters. Hydrobiologia **544**(1): 89–141. doi: 10.1007/s10750-004-8337-7.
- 534 Beauchamp, D.A., Luecke, C., Wurtsbaugh, W.A., Gross, H.G., Budy, P.E., Spaulding, S.,
535 Dillenger, R., and Gubala, C.P. 1997. Hydroacoustic assessment of abundance and diel
536 distribution of sockeye salmon and kokanee in the Sawtooth Valley Lakes, Idaho. North
537 Am. J. Fish. Manag. **17**(2): 253–267. doi: 10.1577/1548-8675
- 538 Beeton, A.M., and Bowers, J.A. 1982. Vertical migration of *Mysis relicta* Lovén. Hydrobiologia
539 **93**: 53–61. doi: 10.1007/978-94-009-8012-9_6.
- 540 Boscarino, B.T., Rudstam, L.G., Mata, S., Gal, G., Johannsson, O.E., and Mills, E.L. 2007. The
541 effects of temperature and predator—prey interactions on the migration behavior and
542 vertical distribution of *Mysis relicta*. Limnol. Oceanogr. **52**(4): 1599–1613. doi:
543 10.4319/lo.2007.52.4.1599.
- 544 Bowers, J.A., and Grossnickle, N.E. 1978. The herbivorous habits of *Mysis relicta* in Lake
545 Michigan. Limnol. Oceanogr. **23**(4): 767–776. doi: 10.4319/lo.1978.23.4.0767.
- 546 Bowles, E.C., Rieman, B.E., Mauser, G.R., Bennett, D.H., Nesler, T.P., and Bergersen, E.P.
547 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. In *Mysis* in
548 fisheries: hard lessons from headlong introduction. American Fisheries Society. pp. 65–74.
- 549 Branstrator, D.K., Cabana, G., Mazumder, A., and Rasmussen, J.B. 2000. Measuring life-history
550 omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. Limnol.
551 Oceanogr. **45**(2): 463–467. doi: 10.4319/lo.2000.45.2.0463.
- 552 Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science
553 **150**(3692): 28–35. doi: 10.1126/science.150.3692.28.

- 554 Caldwell, T.J. 2010. The role of the non-native freshwater opossum shrimp *Mysis diluviana*, in
555 the nutrient and food web dynamics of Lake Pend Oreille, Idaho. M.Sc. Thesis. University
556 of Idaho, Moscow, Idaho.
- 557 Caldwell, T.J., and Wilhelm, F.M. 2012. The life history characteristics, growth and density of
558 *Mysis diluviana* in Lake Pend Oreille, Idaho, USA. J. Great Lakes Res. **38**: 58–67. doi:
559 10.1016/j.jglr.2011.07.010.
- 560 Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L.,
561 Essington, T.E., Houser, J.N., and Schindler, D.E. 2001. Trophic cascades, nutrients, and
562 lake productivity: whole-lake experiments. Ecol. Monogr. **71**(2): 163–186. doi:
563 10.1890/0012-9615
- 564 Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake
565 productivity. Bioscience **35**(10): 634–639 doi: 10.2307/1309989.
- 566 Chess, D.W., and Stanford, J.A. 1998. Comparative energetics and life cycle of the opossum
567 shrimp (*Mysis relicta*) in native and non-native environments. Freshw. Biol. **40**(4): 783–
568 794. doi: 10.1046/j.1365-2427.1998.00373.x.
- 569 Chipps, S.R. 1997. *Mysis relicta* in Lake Pend Oreille: seasonal energy requirements and
570 implications for mysid-cladoceran interactions. University of Idaho.
- 571 Chipps, S.R. 1998. Temperature-dependent consumption and gut-residence time in the opossum
572 shrimp *Mysis relicta*. J. Plankton Res. **20**(12): 2401–2411. doi: 10.1093/plankt/20.12.2401.
- 573 Chipps, S.R., and Bennett, D.H. 1996. Comparison of net mesh sizes for estimating abundance of
574 the opossum shrimp *Mysis relicta* from vertical hauls. North Am. J. Fish. Manag. **16**(3):
575 689–692. Taylor & Francis. doi: 10.1577/1548-8675.
- 576 Chipps, S.R., and Bennett, D.H. 2000. Zooplanktivory and nutrient regeneration by invertebrate
577 (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: Implications for trophic
578 interactions in oligotrophic lakes. Trans. Am. Fish. Soc. **129**(2): 569–583. doi:
579 10.1577/1548-8659.
- 580 Clarke, L.R., and Bennett, D.H. 2002a. A net-pen experiment to evaluate kokanee growth rates
581 in autumn in an oligotrophic lake with *Mysis relicta*. Trans. Am. Fish. Soc. ... **131**(6): 1061–
582 1069. doi: 10.1577/1548-8659.
- 583 Clarke, L.R., and Bennett, D.H. 2002b. Newly emerged kokanee growth and survival in an
584 oligotrophic lake with *Mysis relicta*. Trans. Am. Fish. Soc. **131**(1): 176–185. doi:
585 10.1577/1548-8659.
- 586 Clarke, L.R., and Bennett, D.H. 2004. Zooplankton community changes at Pend Oreille Lake,
587 Idaho: Testing implications for age-0 kokanee prey selection, digestion, and growth. Trans.
588 Am. Fish. Soc. **133**(5): 1221–1234. doi: 10.1577/T03-184.1.

- 589 Clarke, L.R., Vidergar, D.T., and Bennett, D.H. 2005. Stable isotopes and gut content show diet
590 overlap among native and introduced piscivores in a large oligotrophic lake. *Ecol. Freshw.*
591 *Fish* **14**(3): 267–277. doi: 10.1111/j.1600-0633.2005.00103.x.
- 592 Cooper, S.D., and Goldman, C.R. 1980. Opossum shrimp (*Mysis relicta*) predation on
593 zooplankton. *Can. J. Fish. Aquat. Sci.* **37**(6): 909–919. doi: 10.1139/f80-120.
- 594 Duyn-Henderson, J.A. Van, and Lasenby, D.C. 1986. Zinc and cadmium transport by the
595 vertically migrating opossum shrimp, *Mysis relicta*. *Can. J. Fish. Aquat. Sci.* **43**(9): 1726–
596 1732. doi: 10.1139/f86-216.
- 597 Edmondson, W.T. 1972. Instantaneous birth rates of zooplankton. *Limnol. Oceanogr.* **17**(5):
598 792–795. doi: 10.4319/lo.1972.17.5.0792.
- 599 Edmondson, W.T., and Winberg, G.G. 1971. A manual on methods for the assessment of
600 secondary productivity. Blackwell Scientific Publications, Oxford, England.
- 601 Ellis, B.K., Stanford, J.A., Goodman, D., Stafford, C.P., Gustafson, D.L., Beauchamp, D.A.,
602 Chess, D.W., Craft, J.A., Deleray, M.A., and Hansen, B.S. 2011. Long-term effects of a
603 trophic cascade in a large lake ecosystem. *Proc. Natl. Acad. Sci.* **108**(3): 1070–1075. doi:
604 10.1073/pnas.1013006108.
- 605 Falter, C.M., and Ingman, G. 2003. Lake Pend Oreille littoral periphyton community: An
606 updated trophic status assessment: final report submitted to the Tri-State Water Quality
607 Council.
- 608 France, R.L. 2012. Omnivory, vertical food-web structure and system productivity: Stable
609 isotope analysis of freshwater planktonic food webs. *Freshw. Biol.* **57**(4): 787–794. doi:
610 10.1111/j.1365-2427.2012.02744.x.
- 611 Gal, G., Rudstam, L.G., Mills, E.L., Lantry, J.R., Johannsson, O.E., and Greene, C.H. 2006.
612 Mysid and fish zooplanktivory in Lake Ontario: quantification of direct and indirect effects.
613 *Can. J. Fish. Aquat. Sci.* **63**(12): 2734–2747. doi: 10.1139/f06-156.
- 614 Gamble, A.E., Hrabik, T.R., Stockwell, J.D., and Yule, D.L. 2011a. Trophic connections in Lake
615 Superior Part I: The offshore fish community. *J. Great Lakes Res.* **37**(3): 541–549. doi:
616 10.1016/j.jglr.2011.06.003.
- 617 Gamble, A.E., Hrabik, T.R., Yule, D.L., and Stockwell, J.D. 2011b. Trophic connections in Lake
618 Superior Part II: The nearshore fish community. *J. Great Lakes Res.* **37**(3): 550–560. doi:
619 10.1016/j.jglr.2011.06.008.
- 620 Grossnickle, N.E. 1982. Feeding habits of *Mysis relicta* — an overview. *Hydrobiologia* **93**(1-2):
621 101–107. doi: 10.1007/BF00008103.

- 622 Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control,
623 and competition. *Am. Nat.* **94**(879): 421–425. doi: 10.2307/2458808.
- 624 Hiltunen, T., Jones, L.E., Ellner, S.P., and Hairston, N.G. 2012. Temporal dynamics of a simple
625 community with intraguild predation: an experimental test. *Ecology* **94**(4): 773–779. doi:
626 10.1890/12-0786.1.
- 627 Hyatt, K.D., Ramcharan, C., McQueen, D.J., and Cooper, K.L. 2005. Trophic triangles and
628 competition among vertebrate (*Oncorhynchus nerka*, *Gasterosteus aculeatus*) and
629 macroinvertebrate (*Neomysis mercedis*) planktivores in Muriel Lake, British Columbia,
630 Canada. *Ecoscience* **12**(1): 11–26. doi: 10.2980/i1195-6860-12-1-11.1.
- 631 Issac, E.J. 2010. An Evaluation of the importance of *Mysis relicta* to the Lake Superior fish
632 community. M.Sc. Thesis, University of Minnesota, Duluth, MN.
- 633 Johannsson, O.E., Leggett, M.F., Rudstam, L.G., Servos, M.R., Mohammadian, M.A., Gal, G.,
634 Dermott, R.M., and Hesslein, R.H. 2001. Diet of *Mysis relicta* in Lake Ontario as revealed
635 by stable isotope and gut content analysis. *Can. J. Fish. Aquat. Sci.* **58**(10): 1975–1986. doi:
636 10.1139/f01-118.
- 637 Johannsson, O.E., Rudstam, L.G., and Lasenby, D.C. 1994. *Mysis relicta*: Assessment of
638 metalimnetic feeding and implications for competition with fish in Lakes Ontario and
639 Michigan. *Can. J. Fish. Aquat. Sci.* **51**(11): 2591–2602. doi: 10.1139/f94-259.
- 640 Kortmann, R.W., and Henry, J.D. 1981. Relative thermal resistance to mixing. *LakeLine* **1**(1): 7.
- 641 Lane, P. A. 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton
642 communities. *Nature* **280**: 391–393. doi: 10.1038/280391a0.
- 643 Lasenby, D.C., Northcote, T.G., and Fürst, M. 1986. Theory, practice, and effects of *Mysis*
644 *relicta* introductions to North American and Scandinavian Lakes. *Can. J. Fish. Aquat. Sci.*
645 **43**(6): 1277–1284. doi: 10.1139/f86-158.
- 646 Lehtiniemi, M., Kiljunen, M., and Jones, R.I. 2009. Winter food utilisation by sympatric mysids
647 in the baltic sea, studied by combined gut content and stable isotope analyses. *Mar. Biol.*
648 **156**(4): 619–628. doi: 10.1007/s00227-008-1113-x.
- 649 Lindén, E., and Kuosa, H. 2004. Effects of grazing and excretion by pelagic mysids (*Mysis* spp.)
650 on the size structure and biomass of the phytoplankton community. *Hydrobiologia* **514**: 73–
651 78. doi: 10.1023/B:hydr.0000018207.42449.fb.
- 652 Morgan, M.D. 1980. Life history characteristics of two introduced populations of *Mysis Relicta*.
653 *Ecology* **61**(3): 551–561. doi: 10.2307/1937421.
- 654 Murtaugh, P. A. 1981. Selective predation by *Neomysis mercedis* in Lake Washington. *Limnol.*
655 *Oceanogr.* **26**(3): 445–453. doi: 10.4319/lo.1981.26.3.0445.

- 656 Nero, R.W., and Sprules, W.G. 1986. Predation by three glacial opportunists on natural
657 zooplankton communities. *Can. J. Zool.* **64**(1): 57–64. doi: 10.1139/z86-009.
- 658 Nesler, T.P., and Bergersen, E.P. 1991. Mysids in fisheries: hard lessons from headlong
659 introductions. American Fisheries Society, Bethesda, Maryland.
- 660 Nordin, L.J., Arts, M.T., Johannsson, O.E., and Taylor, W.D. 2008. An evaluation of the diet of
661 *Mysis relicta* using gut contents and fatty acid profiles in lakes with and without the invader
662 *Bythotrephes longimanus* (Onychopoda, Cercopagidae). *Aquat. Ecol.* **42**(3): 421–436. doi:
663 10.1007/s10452-007-9098-y.
- 664 O'Malley, B.P., and Bunnell, D.B. 2014. Diet of *Mysis diluviana* reveals seasonal patterns of
665 omnivory and consumption of invasive species in offshore Lake Michigan. *J. Plankton Res.*
666 **36**(4): 989–1002. doi: 10.1093/plankt/fbu038.
- 667 Pace, M.L., Cole, J.J., Carpenter, S.R., and Kitchell, J.F. 1999. Trophic cascades revealed in
668 diverse ecosystems. *Trends Ecol. Evol.* **14**(12): 483–488. doi: 10.1016/S0169-
669 5347(99)01723-1.
- 670 Paloheimo, J.E. 1974. Calculation of instantaneous birth rate. *Limnol. Oceanogr.* **19**(4): 692–
671 694. doi: 10.4319/lo.1974.19.4.0692.
- 672 Paragamian, V.L., and Bowles, E.C. 1995. Factors affecting survival of kokanees stocked in
673 Lake Pend Oreille, Idaho. *North Am. J. Fish. Manag.* **15**(1): 208–219. doi: 10.1577/1548-
674 8675.
- 675 Polis, G.A., and Holt, R.D. 1992. Intraguild predation: The dynamics of complex trophic
676 interactions. *Trends Ecol. Evol.* **7**(5): 151–154. doi: 10.1016/0169-5347(92)90208-S.
- 677 Polis, G.A., and Strong, D.R. 1996. Food web complexity and community dynamics. *Am. Nat.*
678 **147**(5): 813–846. doi: 10.2307/2463091.
- 679 Ramcharan, C., Sprules, W.G., and Nero, R.W. 1985. Notes on the tactile feeding behavior of
680 *Mysis relicta* Loven (Malacostraca: Mysidacea). *Verhandlungen der Int. Vereinigung der*
681 *Limnol.* **22**(5): 3215–3219.
- 682 Richards, R., Goldman, C., Byron, E., and Leviatan, C. 1991. The mysids and lake trout of Lake
683 Tahoe: A 25-year history of changes in the fertility, plankton, and fishery of an alpine lake.
684 *In Mysids in fisheries: hard lessons from headlong introduction. Edited by E.P. Nesler, T.P.,*
685 *Bergerson. American Fisheries Society, Bethesda. pp. 30–38.*
- 686 Rieman, B.E., and Bowler, B. 1980. Kokanee trophic ecology and limnology in Lake Pend
687 Oreille. Idaho Department of Fish and Game Fisheries Bulletin.

- 688 Rieman, B.E., and Falter, C.M. 1981. Effects of the establishment of *Mysis relicta* on the
689 macrozooplankton of a large lake. Trans. Am. Fish. Soc. **110**(5): 613–620. Taylor &
690 Francis. doi: 10.1577/1548-8659.
- 691 Rudstam, L.G. 1989. A bioenergetic model for *Mysis growth* and consumption applied to a
692 Baltic population of *Mysis mixta*. J. Plankton Res. **11**(5): 971–983. doi:
693 10.1093/plankt/11.5.971.
- 694 Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E.,
695 Huenneke, L.F., Jackson, R.B., Kinzig, a, Leemans, R., Lodge, D.M., Mooney, H. a,
696 Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000.
697 Global biodiversity scenarios for the year 2100. Science **287**(2000): 1770–1774. doi:
698 10.1126/science.287.5459.1770.
- 699 Scheuerell, M.D., and Schindler, D.E. 2012. Diel vertical migration by juvenile sockeye salmon:
700 empirical evidence for the antipredation window. Ecology **84**(7): 1713–1720.
- 701 Schindler, D.E., Carter, J.L., Francis, T.B., Lisi, P.J., Askey, P.J., and Sebastian, D.C. 2012.
702 *Mysis* in the Okanagan Lake food web: A time-series analysis of interaction strengths in an
703 invaded plankton community. Aquat. Ecol. **46**: 215–227. doi: 10.1007/s10452-012-9393-0.
- 704 Sierszen, M.E., Kelly, J.R., Corry, T.D., Scharold, J. V., Yurista, P.M., and Sprules, G. 2011.
705 Benthic and pelagic contributions to *Mysis* nutrition across Lake Superior. Can. J. Fish.
706 Aquat. Sci. **68**(6): 1051–1063. doi: 10.1139/f2011-033.
- 707 Smokorowski, K.E., Lasenby, D.C., and Evans, R.D. 1998. Quantifying the uptake and release of
708 cadmium and copper by the opossum shrimp *Mysis relicta* preying upon the cladoceran
709 *Daphnia magna* using stable isotope tracers. Can. J. Fish. Aquat. Sci. **55**(4): 909–916. doi:
710 10.1139/cjfas-55-4-909.
- 711 Sparrow, R.A.H., Larkin, P.A., and Rutherglen, R.A. 1964. Successful introduction of *Mysis*
712 *relicta* Lovén into Kootenay Lake, British Columbia. J. Fish. Res. Board Canada **21**(5):
713 1325–1327. doi: 10.1139/f64-110.
- 714 Spencer, C.N., Potter, D.S., Bukantis, R.T., and Stanford, J.A. 1999. Impact of predation by
715 *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. J. Plankton Res. **21**(1): 51–
716 64. doi: 10.1093/plankt/21.1.51.
- 717 Stockwell, J.D., and Johnson, B.M. 1999. Field evaluation of a bioenergetics-based foraging
718 model for kokanee (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **56**(S1): 140–151. doi:
719 10.1139/cjfas-56-S1-140.
- 720 Stross, R.G. 1954. A limnological study of Lake Pend Oreille, Idaho, with special consideration
721 of the ecology of kokanee salmon. M.Sc Thesis. University of Idaho, Moscow, ID.

- 722 Viherluoto, M., Kuosa, H., Flinkman, J., and Viitasalo, M. 2000. Food utilisation of pelagic
723 mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea.
724 Mar. Biol. **136**(3): 553–559. doi: 10.1007/s002270050715.
- 725 Viherluoto, M., and Viitasalo, M. 2001. Temporal variability in functional responses and prey
726 selectivity of the pelagic mysid, *Mysis mixta*, in natural prey assemblages. Mar. Biol.
727 **138**(3): 575–583. doi: 10.1007/s002270000478.
- 728 Wells, L.R., and Beeton, A.M. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan.
729 Trans. Am. Fish. Soc. **92**(3): 245–255. doi: 10.1577/1548-8659.
- 730 Whall, J.D., and Lasenby, D.C. 2009. Differences in the trophic role of *Mysis diluviana* in two
731 intermontane lakes. Aquat. Biol. **5**(3): 281–292. doi: 10.3354/ab00162.
- 732 Wilhelm, F.M., Parker, B.R., Schindler, D.W., and Donald, D.B. 1999. Seasonal food habits of
733 bull trout from a small alpine lake in the Canadian Rocky Mountains. Trans. Am. Fish. Soc.
734 **128**(6): 1176–1192. doi: 10.1577/1548-8659.
- 735 Winder, M., and Schindler, D.E. 2004. Climatic effects on the phenology of lake processes.
736 Glob. Chang. Biol. **10**(11): 1844–1856. doi: 10.1111/j.1365-2486.2004.00849.x.
- 737 Yan, N.D., Keller, W., MacIsaac, H.J., and McEachern, L.J. 1991. Regulation of zooplankton
738 community structure of an acidified lake by *Chaoborus*. Ecol. Appl. **1**(1): 52–65. doi:
739 10.2307/1941847.
- 740 Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for
741 the food web consequences of species invasions in lakes. Nature **401**(6752): 464–467.
742 Available from <http://dx.doi.org/10.1038/46762>.
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Table 1: Results of nonparametric Kolmogorov-Smirnov tests
comparing mysid diet between the north and south site in Lake
Pend Oreille, ID.

Test	Max difference	<i>p</i> value
Cladocerans	0.111	1.00
Copepods	0.444	0.31
Diatoms	0.111	1.00
Pollen	0.333	0.67
Rotifers	0.556	0.11
Other	0.333	0.66

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Table 2. Cladoceran density (mean individuals·m⁻³±SE), production (births·m⁻³·d⁻¹), and the consumption (individuals consumed·m⁻³·d⁻¹) of cladocerans by mysids, with percent contribution from each species in Lake Pend Oreille, Idaho, from May 2009 to March 2010.

	North									South								
	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Mar
	Cladoceran Density																	
<i>Daphnia</i> (%)	0	0	7	93	80	22	n/a	14	0	0	0	7	87	88	21	0	0	0
<i>Diaphanosoma</i> (%)	0	0	93	7	20	78	n/a	86	0	0	0	93	13	12	79	100	0	0
Total cladocerans	0	0	114±57	4940±250	1242±151	599±146	n/a	9±5	0	0	0	231±107	5097±1103	2000±697	597±271	24±12	0	0
Cladoceran production																		
<i>Daphnia</i> (%)	0	0	6	93	80	0	n/a	0	0	0	0	5	89	87	0	0	0	0
<i>Diaphanosoma</i> (%)	0	0	94	7	20	100	n/a	0	0	0	0	95	11	13	100	100	0	0
Total cladocerans	0	0	60	2163	505	76	n/a	0	0	0	0	73	2262	843	110	3	0	0
Mysid consumption																		
<i>Daphnia</i> (%)	10	55	22.5	95.25	85.93	27.57	20	10	0	0	21	7	90	92	34	20	10	0
<i>Diaphanosoma</i> (%)	90	45	78	4.7	14	72	80	90	0	0	79	93	10	8	66	80	90	0
Total consumption	9	11	43	545	651	21	6	2	0	0	5	82	330	346	44	26	5	0

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750 **Table 3:** The consumption rate of cladocerans by *Mysis diluviana* in Lake Pend Oreille, Idaho, and other lakes in North America.

751 Consumption rate is presented as a fraction of production or standing stock of cladocerans. Depending on the study, consumption

752 rates were calculated using either bioenergetics (B) or empirical diets (ED), while production (P) was estimated using the egg ratio

753 method Paleheimo (1974). In cases where production was not calculated, standing stock was presented (SS). We retained the original

754 units of consumption and production published by the authors of each study due to the variability of methods, depths sampled and

755 conversion factors (i.e., dry weight to wet weight, etc.).

Lake	Estimation Method			Percent Consumed	Citation
	Consumption	Production/Standing Stock	Units		
Ontario*	≈ 0.5 (B)	0.031 - 1.327 (P)	(kcal·m ⁻² ·d ⁻¹)	38-110%	Johannsson et al. 1994
Lake Pend Oreille (1994)	0.08 - 2.4 (B)	0.89 – 14.12 (SS)	(kg cladocerans·ha ⁻¹ ·d ⁻¹)	9-17%	Chipps and Bennett 2000
Lake Pend Oreille (1995)	0.06 – 2.8 (B)	1.2 – 4.0 (SS)	(kg cladocerans·ha ⁻¹ ·d ⁻¹)	5-70%	Chipps and Bennett 2000
Lake Ontario**	.0026 – 1.3 (B)	0.51 - 3.08 (SS)	(g·wet weight zooplankton·m ⁻² ·d ⁻¹)	1-4%	Gal et al. 2006
Lake Pend Oreille (South)	9 – 651 (ED)	0 - 2163 (P)	(ind·births·m ⁻³ day ⁻¹)	18-100%	This Study
Lake Pend Oreille (North)	5 – 346 (ED)	0 – 2262 (P)	(ind·births·m ⁻³ day ⁻¹)	32-100%	This Study

756 * These consumption/production rates and percentages are based on the production of the entire zooplankton community, and

757 approximated from Figure 5 and Table 6 in Johannsson et al. (1994). We used values from the >200 m deep site to be comparable to

758 the site depths in our study (>300m).

759 ** These consumption rates, standing stock estimates and percentages are based on the production of the entire zooplankton

760 community. Consumption, standing stock, and percentage consumed were taken from Table 2, Table 4 and Table 6, respectively in

761 Gal et al. (2006). Production rates were estimated by adding values from depth categories for the deepest site during each season, we
762 presented the range in (g·wet weight zooplankton·L⁻¹).

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765 Figure 1. Map of Lake Pend Oreille, ID and surrounding areas, and north (N) and south (S)
766 sampling locations (modified from Caldwell and Wilhelm 2012). Contour lines are at 50 m
767 intervals.

768 Figure 2. Water temperature isopleths for Lake Pend Oreille, ID at the north (a) and south (b)
769 sites during 2009-2010; and historical (1954-2005, and 2009) thermal stratification depths during
770 August from the north (c) and south (d).

771 Figure 3. Seasonal population prey-specific index (PPSI) plot of *Mysis diluviana* as a function of
772 time at the north (a) and south (b) sites in Lake Pend Oreille, Idaho, USA. Prey-specific index
773 (Amundsen et al. 1996) was plotted as a function of time to describe the seasonal diet of mysids.

774 Figure 4. The percentage of cladoceran production ($\text{births} \cdot \text{m}^{-3} \cdot \text{day}^{-1}$) removed by mysid
775 consumption ($\text{individuals} \cdot \text{m}^{-3} \cdot \text{night}^{-1}$) and the depth of stratification at the north (a) and south (b)
776 sites of Lake Pend Oreille, Idaho. The depth of stratification for each month is plotted as dark
777 horizontal bars.

778 Figure 5. Average size of cladocerans eaten by mysids (gut – black filled circles), gravid
779 females present in the lake (lake – open squares), and gravid females in guts of mysids (gravid
780 females – grey filled triangles) as a function of time in Lake Pend Oreille, Idaho, at the north (a)
781 and south (b) sites. Horizontal bars beneath monthly data sets indicate statistical differences
782 between size of cladocerans eaten and those present in the lake.

783

Figure 1. Map of Lake Pend Oreille, ID and surrounding areas, and north (N) and south (S) sampling locations (modified from Caldwell and Wilhelm 2012). Contour lines are at 50 m intervals.
215x279mm (300 x 300 DPI)

Figure 2. Water temperature isopleths for Lake Pend Oreille, ID at the north (a) and south (b) sites during 2009-2010; and historical (1954-2005, and 2009) thermal stratification depths during August from the north (c) and south (d).
279x361mm (300 x 300 DPI)

Figure 4. The percentage of cladoceran production (births·m⁻³·day⁻¹) removed by mysid consumption (individuals·m⁻³·night⁻¹) and the depth of stratification at the north (a) and south (b) sites of Lake Pend Oreille, Idaho. The depth of stratification for each month is plotted as dark horizontal bars.
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