Forecasting the ecological impacts of the *Hemimysis anomala* invasion in North America: Lessons from other freshwater mysid introductions

Anthony Ricciardi [a,*], Suncica Avlijas [b], Jérôme Marty [c]

[a] *Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6*
[b] *Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada K3A 2K6*
[c] *St. Lawrence River Institute, 2 Belmont Street, Cornwall, Ontario, Canada K6H 4Z1*

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ABSTRACT

The bloody red mysid shrimp *Hemimysis anomala* is the most recent Ponto-Caspian invader of the Great Lakes. At present, there is a paucity of data that can be used to forecast its ecological impacts in North America; however, published studies of other invasive freshwater mysids (i.e. *Mysis diluviana* introduced to North American lakes and *Mysis relicta* introduced to Scandinavian lakes) reveal potentially valuable predictive information. A frequent impact of *Mysis* introductions is a drastic decline in zooplankton (particularly cladoceran) abundance, which can release phytoplankton populations from grazer control and alter the abundance and growth of pelagic fishes. Other impacts include enhanced bioaccumulation of contaminants, new pathways of parasite transmission to fishes, and altered nutrient cycling. Like *Mysis* spp., *H. anomala* has the potential to affect all trophic levels in lakes. It has reduced the abundance and diversity of zooplankton in European reservoirs, where it achieved mean densities higher than those recorded for other introduced mysids elsewhere. It can colonize a broader range of habitats than *Mysis* throughout the year, including the nearshore areas of lakes and large rivers. Within river systems, the impacts of *H. anomala* will likely be most pronounced in backwater lakes, impounded areas and reservoirs. Understanding the environmental factors that limit the local abundance of *H. anomala* and mediate its species interactions is essential for developing predictive models of its impact.

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Introduction

Since the 1980s, the North American Great Lakes have been invaded by over a dozen species of protists, mussels, crustaceans and fishes indigenous to the fresh- and brackish-water margins of the Black, Caspian and Azov seas (Ricciardi, 2006). Prior to their arrival, these Ponto-Caspian species invaded several major European ports and thus gained opportunities for overseas transport by ships (bij de Vaate et al., 2002; Janas and Wysocki, 2005; Ricciardi and MacIsaac, 2000). The most recent among these invaders is the bloody-red mysid shrimp *Hemimysis anomala*, which was discovered simultaneously in Lake Michigan and Lake Ontario in 2006 (Pothoven et al., 2007) and whose arrival was anticipated (Ricciardi and Rasmussen, 1998). This species has spread rapidly throughout the Great Lakes basin in recent years (Brooking et al., 2010; Kestrup and Ricciardi, 2008; Marty et al., 2010) and in western Europe over the past two decades (Dumont, 2006; Janas and Wysocki, 2005; Lundberg and Svensson, 2004; Minchin and Boelens, 2010; Stubbington et al., 2008). It was deliberately stocked in reservoirs of the Dnieper and Volga Rivers

during the 1950s and 1960s to enhance food resources for fish (Pligin and Yemel'yanova, 1989). In 1991, it was discovered in the Baltic Sea within the Gulf of Finland and subsequently spread 200 km along the Scandinavian coast (Lundberg and Svensson, 2004; Salemaa and Hietalahti, 1993). It was also recorded in the Rhine River basin in 1997, the River Main in 1998, the Danube River in 1999, the Trent River and surrounding areas of the English Midlands by 2004, and the River Shannon in Ireland by 2009 (bij de Vaate et al., 2002; Borcherding et al., 2006; Dumont, 2006; Minchin and Boelens, 2010; Stubbington et al., 2008).

Ponto-Caspian species now occupy virtually every trophic level of Great Lakes' food webs and have produced substantial ecological changes in the basin and elsewhere in their invaded range (Ojaveer et al., 2002; Vanderploeg et al., 2002). Ponto-Caspian crustaceans, in particular, have been shown to be aggressive predators (Dick and Platvoet, 2000; Kestrup et al., 2011). One possible reason for their disproportionate impacts is that they are often functionally distinct from native freshwater species in invaded systems and thus more likely to use resources differently and to encounter naïve predators and prey (Ricciardi and Atkinson, 2004). Although *H. anomala* is morphologically similar to the only native freshwater mysid in the Great Lakes — the opossum shrimp *Mysis diluviana* (formerly *M. relicta*), there are major ecological differences that render the

invader unique in North American inland waters. The native *M. diluviana* is a glacial relict species that lives primarily below the thermocline of boreal lakes, whereas *H. anomala* inhabits a broad range of depths and nearshore environments (Table 1). Ponto-Caspian mysids are metabolically adapted to higher temperatures than cold-water *Mysis* spp. (Bondarenko and Yablonskaya, 1979; Johannsson et al., 2008); therefore, it is not surprising that *H. anomala* has become abundant in littoral areas of the Great Lakes basin where *M. diluviana* does not exist (Marty et al., 2010; Walsh et al., 2010). Moreover, *H. anomala* can invade lotic environments historically devoid of freshwater mysids (bij de Vaate et al., 2002; Minchin and Boelens, 2010; Stubbington et al., 2008; Wittmann, 2007), including the St. Lawrence River (de Lafontaine et al., 2012–this issue; Kestrup and Ricciardi, 2008).

Advance knowledge of the potential impacts of a species introduction is valuable to environmental management and risk assessment (Ricciardi and Rasmussen, 1998) and can help formulate testable hypotheses. Here, we develop predictions concerning the community-level and ecosystem-level effects of *H. anomala*, based on a review of its life history characteristics, its impact history in Europe, and the impact histories of other invasive freshwater mysids.

Ecology of *Hemimysis*: an overview

Population dynamics

H. anomala is a dioecious species that produces at least two generations per year (Borcherding et al., 2006; Mordukhai-Boltovskoi, 1960). Ovigerous females usually appear when the water temperature reaches 8–9 °C and young individuals can be observed in the marsupium at 11–12 °C. Constrained by these temperatures, *H. anomala* breeds from April to September in Dutch reservoirs (Ketelaars et al., 1999), although ovigerous females were found as late as November in Lake Michigan (Pothoven et al., 2007) and December in Lake Ontario (Marty et al., 2010). The number of eggs per brood varies from 2 to 70, depending on the size of the female (Borcherding et al., 2006; Ketelaars et al., 1999; Pothoven et al., 2007; Salemaa and Hietalahti, 1993), and is often higher in the spring (29 ± 10.9) than at the end of summer (20 ± 3.6) (Borcherding et al., 2006). The development of individuals involves 4 to 6 instar stages (differentiated according to body length; Borodich and Havlena, 1973), where a chitinous exoskeleton is shed at each stage. Individuals reach sexual maturity and start to breed within 45 days (Pothoven et al., 2007). The abundance of adults within a population generally peaks at the end of summer (Ketelaars et al., 1999; Pothoven et al., 2007). Local densities of mysids can vary greatly over spatial and temporal scales, and adults swim actively within an aggregated reproductive swarm that, during winter months, can comprise tens of thousands of individuals and cover several square meters (Dumont, 2006; Dumont and Muller, 2010).

Habitat preferences

Because *H. anomala* can tolerate a broad range of physico-chemical conditions (Table 1) and disperse through canals and river systems (Dumont and Muller, 2010; Stubbington et al., 2008; Wittmann, 2007), it can rapidly expand its distribution following its initial introduction to a region. In contrast to other freshwater mysids (Table 1), *H. anomala* can survive and reproduce even in brackish waters (up to 18 ppm; Wittmann, 2007), which may facilitate its survival during transoceanic voyages in ship ballast tanks. It occurs in water temperatures of 0–28 °C, but prefers 9–20 °C (Ioffe et al., 1968; Wittmann, 2007). As temperatures approach freezing, individuals appear to suffer lower growth rates and higher mortality (Borcherding et al., 2006). However, the increasing number of invaded sites reported in nearshore areas of Lake Ontario since 2006 suggests that the species can form viable populations at temperatures as low as 2 °C (Marty et al., 2010). This is further supported by observations of large swarms under ice cover in a European lake (Dumont, 2006) and in the St Lawrence River (J. Marty, pers. obs.), as well as the recent finding of a population in Oneida Lake (New York), where winter temperatures may remain near 1 °C for up to three months (Brooking et al., 2010).

H. anomala occurs primarily in surface waters and sublittoral depths (Borcherding et al., 2006; Salemaa and Hietalahti, 1993). Infrequently, it is reported in deeper waters, e.g. 20–30 m in the Black and Caspian Seas (Bacescu, 1954) and >50 m in the Dnieper reservoir (Zhuravel, 1960). In the Great Lakes basin, *H. anomala* is generally found in nearshore areas down to 10 m, although boat surveys in southern Lake Ontario have reported the occurrence of swarms at 20 m (Walsh et al., 2010).

Mysid swarms avoid direct light by aggregating in deeper water, under rocks, or within crevices during the day (Dumont, 2006; Salemaa and Hietalahti, 1993); at dusk, individuals will migrate to the upper water column and remain there until dawn (Borcherding et al., 2006; Janas and Wysocki, 2005). Being more transparent, juveniles are less vulnerable to predation than adults and tend to stay in the upper water column throughout the day (Borcherding et al., 2006), perhaps helping them to avoid cannibalism (Ketelaars et al., 1999). This ontogenetic difference in water column position is also related to light preferences, which successfully predict the mysid's vertical distribution and migration patterns (Boscarino et al., 2012–this issue).

H. anomala favors areas of rocky substrate and is less abundant on soft sediments, especially silty areas (Janas and Wysocki, 2005; Ketelaars et al., 1999; Minchin and Boelens, 2010; Pothoven et al., 2007). Swarms are often found in shaded areas near massive anthropogenic structures such as piers and jetties (de Lafontaine et al., 2012–this issue; Pothoven et al., 2007; Stubbington et al., 2008; Wittmann, 2007), but their occurrence varies through time (Wittmann, 2007). In large rivers, the species is more abundant at sites protected from strong current and heavy wave action (Stubbington et al., 2008; S.

Table 1
Published physico-chemical tolerances of three invasive freshwater mysids in North America and Europe. Most parameters (e.g. D.O., conductivity, pH, water current) are conservative estimates based on field conditions in which live specimens were found.

Species	Depth m	Temperature °C	Dissolved oxygen (minimum) mg/L	Conductivity μS/cm	Water current m/s	pH	Salinity ‰
Mysis diluviana	5[a]–262[b]	Tolerates: 2[i]–22[j] Prefers: 6–8[h] Avoids: >18[h]	>2.5[c,q]	24[s]–267[t]	<0.05–0.1[x]	5.9[y]–8.5[s]	0–3[p]
Mysis relicta	7[d]–94[e]	Prefers: 3[k]–16[l] Avoids: >7[m]	>3[r,d]	23[u]–74[v]		6.5[z]–7.5[v]	0–7[p,e]
Hemimysis anomala	0–60[f,g]	Tolerates: 2[o]–28[n] Prefers: 9–20[n] Avoids: >25[n]	>4[g]	92[w]–29200[g]	0–0.8[g]	6.21[w]–8.65[g]	0–18[g]

Data sources: *a*. Paterson et al., 2010; *b*. Robertson et al., 1968; *c*. Martinez and Bergersen, 1991; *d*. Horppila et al., 2003; *e*. Väinölä, 1986; *f*. Minchin and Holmes, 2008; *g*. Wittmann, 2007; *h*. Boscarino et al., 2007; *i*. Johannsson, 1992; *j*. DeGraeve and Reynolds, 1975; *k*. Naesje et al., 2003; *l*. Griffiths, 2007; *m*. Hakala, 1978; *n*. Ioffe et al., 1968; *o*. Borcherding et al., 2006; *p*. Audzijonytė and Väinölä, 2005; *q*. Sandeman and Lasenby, 1980; *r*. Bailey et al., 2006; *s*. Trippel and Beamish, 1993; *t*. Carrick et al., 2001; *u*. Rippey, 1993; *v*. Koksvik et al., 2009; *w*. Wittmann and Ariani, 2009; *x*. Northcote, 1991; *y*. Schindler et al., 1985; *z*. Moen and Langeland, 1989.

Avlijas and A. Ricciardi, unpubl. data), suggesting that flow velocity limits its distribution in river systems.

Feeding

H. anomala is an opportunistic omnivore that feeds primarily on large zooplankton, but also consumes plant and animal detritus, phytoplankton (particularly filamentous green algae and diatoms) and small benthic invertebrates (e.g. juvenile gammarid amphipods; oligochaetes, insect larvae), and is occasionally cannibalistic (Borcherding et al., 2006; Dumont, 2006; Ioffe et al., 1968; Ketelaars et al., 1999; S. Avlijas and A. Ricciardi, unpubl. data). Its flexible feeding behavior was demonstrated in the nearshore area of Lake Ontario, where carbon stable isotope signatures of the mysid spanned from −24 to −19‰, indicating its use of both pelagic and benthic food sources (Marty et al., 2010). A similar result was observed in the St. Lawrence River, where mysids used pelagic food sources at sheltered sites within Montreal Harbour and benthic food sources at exposed sites outside the harbour (Marty et al., 2012–this issue). Juvenile mysids (<6 mm total length) feed mainly on phytoplankton, whereas adults consume a larger proportion of zooplankton (Borcherding et al., 2006; Ketelaars et al., 1999). In laboratory arenas, individual adult *H. anomala* can consume over a hundred small daphniids in 24 h (S. Avlijas and A. Ricciardi, unpubl. data).

Invasion history as a guide to predicting the impacts of mysids

The simplest and most reliable method of gaining predictive information about an invader's impacts is to compare its effects across different ecosystems and geographic regions in which it has been introduced (Grosholz and Ruiz, 1996; Ricciardi, 2003). An analysis of the type and magnitude of impacts across invaded sites can determine if the effects of an invader are consistent – and therefore predictable – across different environments (Grosholz and Ruiz, 1996), or whether they vary predictably with habitat conditions (Ward and Ricciardi, 2007). When the invader lacks a sufficiently detailed impact history, we might benefit from examining the histories of functionally similar organisms, under the assumption that species that use resources in similar ways (e.g. other invasive mysids) are likely to exert similar impacts. Here, we use both of these empirical approaches to forecast *H. anomala*'s potential impacts in the Great Lakes basin.

Documented impacts of H. anomala on food webs

In the few European reservoirs where its impacts have been studied (Ketelaars et al., 1999), *H. anomala* has severely reduced zooplankton biomass and diversity, with cladocerans, rotifers and ostracods being most affected. Phytoplankton biomass increased concomitantly with the loss of herbivorous zooplankton. However, when small-sized (juvenile) mysids are predominant, their grazing can reduce local phytoplankton (Borcherding et al., 2006; Ketelaars et al., 1999). Furthermore, *H. anomala* competes with or preys upon other invertebrate planktivores, such as the large predatory cladocerans *Bythotrephes longimanus* and *Leptodora kindti* (Ketelaars et al., 1999). *Hemimysis* feeds rapidly even at low prey densities, and its fecal pellets may alter the local physico-chemical environment (Ketelaars et al., 1999; Olenin and Leppäkoski, 1999).

In the Great Lakes basin, the effect of *H. anomala* on nearshore food webs is as yet unclear and difficult to assess, owing to variation in population characteristics, food sources, and foodweb structure across sites. The feeding activities of a dense mysid population could reduce energy flow between benthic and pelagic food webs. The importance of littoral production for supporting the pelagic food web has been well documented (Hecky and Hesslein, 1995; Vander Zanden and Vadeboncoeur, 2002). Recent shifts in nutrient pools from pelagic to benthic zones following dreissenid mussel invasions have dampened

the coupling between littoral and pelagic food webs in the Great Lakes (Fahnenstiel et al., 2010; Hecky et al., 2004). We hypothesize that *H. anomala* will exacerbate this trend, if its populations are not sufficiently limited by fish predation.

H. anomala has begun to be observed in the diets of several littoral and pelagic fishes in the Great Lakes basin (Brooking et al., 2010; Lantry et al., 2010). Owing to its lipid content, this species is a high-quality food source that can enhance the growth of planktivores (Borcherding et al., 2006). Preliminary data from Lake Ontario suggest that the caloric content of the *H. anomala* is lower than that of the native *M. diluviana*, but higher than that of other resident zooplankton, and thus offers a relatively energy-rich prey item for nearshore fishes (Walsh et al., 2010). Young-of-the-year (YOY) European perch (*Perca fluviatilis*) in a Dutch gravel-pit lake increased their predation on *H. anomala* from 20% in August to 100% in November, and this diet shift was accompanied by an increased lipid content in the perch (Borcherding et al., 2006). However, other introduced mysids have had mixed effects on fish growth and productivity (see below).

We expect the impacts of *H. anomala* to be correlated with its local abundance (Parker et al., 1999; Ricciardi, 2003). System-wide population densities recorded at the time of discovery (2006) in southeastern Lake Michigan (0.5 ± 0.1 individuals/L; Pothoven et al., 2007) and subsequently in southern Lake Ontario (1.3 ± 1.2, max = 6.2 individuals/L in 2007; Walsh et al., 2010) were already as high as those found in some European reservoirs invaded by *H. anomala* and even higher than the maximum densities of several other mysid species introduced elsewhere (Ketelaars et al., 1999). However, it is difficult to predict the carrying capacity of *H. anomala* in the Great Lakes. There are virtually no published studies on its longterm dynamics, but strong temporal fluctuations are expected (as observed for other mysids, cf. Bowles et al., 1991; Koksvik et al., 2009; Langeland et al., 1991b; Spencer et al., 1991). A once abundant and expanding *H. anomala* population subsequently disappeared from a Dnieper River reservoir, apparently in response to water quality degradation (Pligin and Yemel'yanova, 1989). In northeastern France, a population decline was observed over two consecutive winters and was attributable to strong predation pressure (Dumont and Muller, 2010).

Lessons from other mysid introductions

Studies of other mysid invasions yield predictive information for *H. anomala*. Throughout much of the previous century, *Mysis diluviana* and *M. relicta* were transplanted beyond their natural ranges into lakes across North America and Scandinavia, respectively, to provide a supplementary food source for freshwater fishes (Lasenby et al., 1986; Northcote, 1991; Pligin and Yemel'yanova, 1989). A frequent impact of these introductions is a reduction of macrozooplankton — particularly cladocerans (Fig. 1; Table 2), upon which *Mysis* feeds preferentially (Lasenby and Fürst, 1981; Spencer et al., 1999). Cladoceran biomasses have been reduced by 55–99% following *Mysis* invasions (Koksvik et al., 1991; Koksvik et al., 2009; Langeland et al., 1991b). Although cladocerans are preferred prey, copepods may also be severely reduced in abundance (Spencer et al., 1999). Overall, strong (>60%) declines in macrozooplankton density and biomass are typically observed within 1 or 2 decades following mysid introduction. The most severe reductions tend to occur at high mysid densities (Table 2), but the relationship between impact and mysid density is weak (Fig. 2), suggesting the influence of local environmental variables. Other common impacts are a delay in seasonal peaks in abundance, a shift in species composition, and an increase in the abundance of smaller zooplankton such as rotifers (Kinsten and Olsen, 1981; Koksvik et al., 1991; Martinez and Bergersen, 1991). Impacts on benthic invertebrates have not been well studied, but negative effects have been reported: in two Swedish lakes, the population expansion of *M. relicta* was accompanied by a severe decline in the benthic cladoceran *Eurycercus* (Lasenby and Fürst, 1981).
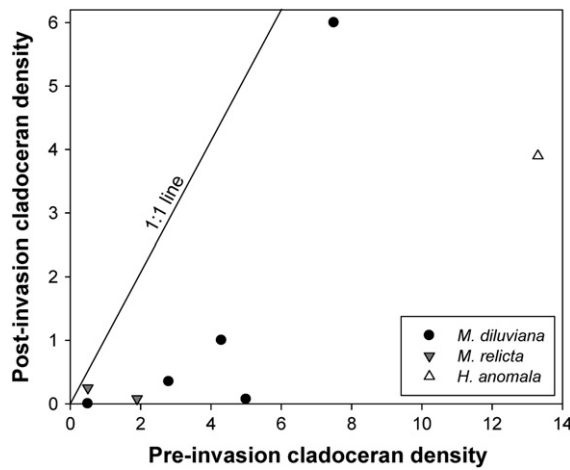
Fig. 1. Mean lakewide cladoceran density (#/L) before and after invasions by *Mysis diluviana* in North American lakes, *Mysis relicta* in Scandinavian lakes, and *Hemimysis anomala* in a Dutch reservoir. Post-invasion densities are significantly lower (paired *t*-test, p = 0.024). See Table 2 for data sources.
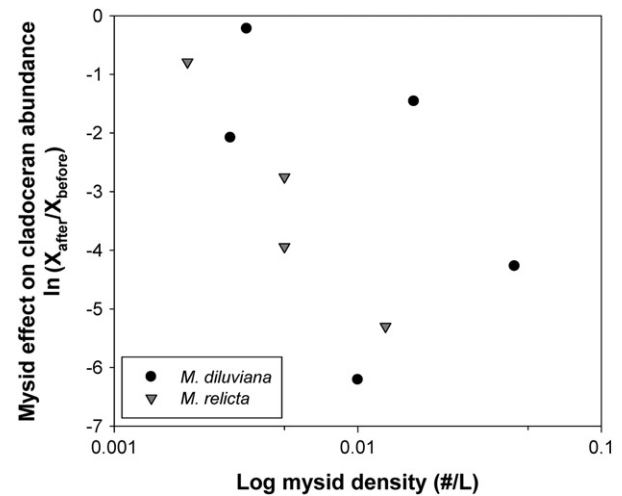

Fig. 2. Effect of *Mysis* invasion on cladoceran abundance in relation to maximum mean mysid density. Effect sizes are $\log_e$–response ratios of mean lakewide cladoceran abundance before and after mysid invasion (Table 2). The relationship is not significant (least-squares regression, p = 0.13, $R^2_{adj} = 0.20$). Data are for *Mysis diluviana* in North American lakes and *Mysis relicta* in Scandinavian lakes.

Predicting the longterm changes to zooplankton populations under the influence of introduced mysids is complicated by temporal fluctuations in mysid abundance, indirect effects and chance events. Preferential predation on daphniids may promote the enhancement of other zooplankton through competitive release (Nero and Sprules, 1986; Rieman and Falter, 1981; Spencer et al., 1999). In Lake Tahoe (California/Nevada, USA), the formation of dense mysid populations led to the near total disappearance of three dominant cladocerans: *Daphnia rosea*, *D. pulex* and *Bosmina longirostris*. A subsequent decline in mysid density coincided with the reappearance of *B. longirostris*, whose recolonization was facilitated by wind-induced advection from an isolated source population and annual variability in mortality inflicted by another predator (Goldman et al., 1979; Threlkeld, 1981).

Cascading multitrophic level effects were observed in Flathead Lake (Montana, USA), where cladocerans declined by nearly 80% after the introduced *M. diluviana* exploded in abundance (Spencer et al., 1999). The loss of macrozooplankton and other foodweb changes led to the extirpation of an abundant planktivore — kokanee salmon (*Oncorhynchus nerka*), and the subsequent disappearance of bald eagles (*Haliaeetus leucocephalus*) that depended on kokanee spawners for food (Spencer et al., 1991). The kokanee population crashed one year after mysids reached peak density. Mysids provided a new food source for an introduced salmonid, lake trout (*Salvelinus namaycush*),

a deepwater forager that had remained at low densities for 80 years but now dominates the lake fishery at the expense of native bull trout and cutthroat trout, both imperiled species. The proliferation of lake trout is also thought to have contributed to the collapse of kokanee (Ellis et al., 2011).

In some lakes, introductions of mysids have stimulated the increased growth of salmonids (Lasenby et al., 1986; Stafford et al., 2002); in most other lakes, they are associated with declines in the growth, abundance and productivity of planktivorous fishes (Bowles et al., 1991; Langeland et al., 1991a,b; Lasenby et al., 1986; Rieman et al., 1979; Spencer et al., 1991; Tohtz, 1993). In lakes where kokanee salmon have collapsed following mysid introductions, lake trout may switch from piscivory to planktivory and suffer reduced growth, although their population may increase (Bowles et al., 1991; Morgan et al., 1978; Stafford et al., 2002). In a Norwegian lake where cladoceran biomass declined by over 90% following the introduction of *M. relicta*, planktivorous arctic char (*Salvelinus alpinus*) did not switch to mysid prey and consequently diminished in number and body size, whereas benthic arctic char fed on mysids and their density remained unchanged (Langeland et al., 1991b). Similarly, adult lake whitefish (*Coregonus clupeaformis*) are less sensitive to reduced zooplankton abundance because they also feed

Table 2
Cladoceran abundance in lakes before and after invasion by freshwater mysids. Cladoderan abundances are lakewide means taken across years, where possible. The maximum of mean mysid densities were taken from reported values. Cladoceran and mysid abundances were normally measured in the summer.

Location	Mysid species	Years since introduction	Max. mean mysid density (#/m²)	Max. mean mysid density (#/L)	Initial mean cladoceran density (#/L)	Final mean cladoceran density (#/L)	Initial mean cladoceran biomass (mg/m²)	Final mean cladoceran biomass (mg/m²)	Source
Pend Oreille Lake, USA	*M. diluviana*	16	1980	0.044	5	0.07	.	.	1
Priest Lake, USA	*M. diluviana*	13	500	0.017	4.3	1	.	.	2, 3
Upper Priest Lake, USA	*M. diluviana*	13	100	0.0035	7.5	6	.	.	3
Lake Selbusjoen, Norway	*M. relicta*	14	200	0.005	.	.	470	30	4
Lake Jonsvatn, Norway									
Kilvatn embayment	*M. relicta*	8	100	0.005	.	.	360	7	5
Lille Jonsvatn	*M. relicta*	7	252	0.013	.	.	1200	6	6
Store Jonsvatn	*M. relicta*	15	110	0.002	.	.	265	120	6
Lake Mesvattnet, Sweden	*M. relicta*	5	.	.	1.9	0.08	.	.	7
Lake Smavattnet, Sweden	*M. relicta*	5	.	.	0.5	0.25	.	.	7
Flathead Lake, USA	*M. diluviana*	7	130	0.003	2.8	0.35	.	.	8, 9
Lake Tahoe, USA	*M. diluviana*	5	380	0.01	0.5	<0.001	.	.	10–12
Honderd en Dertig reservoir, Netherlands	*H. anomala*	>1	200	3	13.3	3.9	.	.	13

Sources: 1. Rieman and Falter, 1981; 2. Bowles et al., 1991; 3. Rieman et al., 1979; 4. Langeland et al., 1991b; 5. Koksvik et al., 1991; 6. Koksvik et al., 2009; 7. Kinsten and Olsen, 1981; 8. Spencer et al., 1991; 9. Spencer et al., 1999; 10. Goldman et al., 1979; 11. Morgan et al., 1978; 12. Richards et al., 1975; 13. Ketelaars et al., 1999.

on benthic invertebrates (Tohtz, 1993). Benthivorous fishes such as percids, centrarchids and small-sized burbot (*Lota lota*) seem to benefit from the availability of mysid prey (Bowles et al., 1991; Langeland et al., 1991b). Mysids are able to evade many pelagic predators through their rapid escape response and by hiding amongst bottom sediments during daylight hours (Northcote, 1991), but strong upwelling currents in some reservoirs (e.g. Kootenay Lake, B.C.; Martin and Northcote, 1991) probably render mysids more vulnerable to predation and thus contribute to the situations in which the introduction was beneficial to the target fish population (Northcote, 1991).

Through direct transmission and indirect effects on the food web, introduced mysids can enhance parasitism by nematodes, cestodes and acanthocephalans in pelagic fishes (Lasenby et al., 1986; Northcote, 1991; Rieman et al., 1979). In addition to serving as intermediate hosts for a variety of fish parasites, they affect host–parasite relationships by altering the composition of zooplankton. Following mysid introductions in Swedish lakes, the incidence of parasitism by cestodes increased in arctic char, driven by an increased abundance of copepods replacing cladocerans in fish diets (Lasenby et al., 1986).

Enhanced phytoplankton production has been observed in some lakes during the development of dense mysid populations, although such effects vary greatly over time (Kinsten and Olsen, 1981; Koksvik et al., 1991; Koksvik et al., 2009). A few years after the introduction of *Mysis relicta* to a Scandinavian lake, the phytoplankton biomass nearly doubled (Koksvik et al., 1991), likely in response to the reduction of large-sized cladocerans and to benthic feeding activities that release phosphorus from sediments (Northcote, 1991). Dissolved organic carbon and silica are also released by mysid feeding activities, which involve the fragmentation of diatom frustules (Northcote, 1991). Nutrient cycling may be limited to deeper areas of lakes, where most mysids remain throughout much of the day (Chipps and Bennett, 2007).

Mysids recycle contaminants by grazing on floating detritus in the water column, consuming contaminated sediments or by preying on benthic invertebrates, before themselves being consumed by fish (Evans et al., 1982; Van Duyn-Henderson and Lasenby, 1986). Their vertical migrations result in the transport of heavy metals between benthic and open-water food webs (Northcote, 1991). Moreover, through a lengthening of the food chain, a mysid introduction may increase the biomagnification of contaminants in higher consumers; thus, concentrations of polychlorinated biphenyls and mercury in lake trout have been shown to be higher in lakes containing mysids than in mysid-free lakes (Cabana et al., 1994; Rasmussen et al., 1990).

Challenges to predicting the impacts of *H. anomala*

The European literature does not provide sufficient information to make confident predictions of the impacts of *H. anomala* in North American lakes and rivers. We must therefore refer to its life history traits and the invasion history of mysids in general. The few ecological studies of this species highlight its strong potential for trophic disruptions in lakes, consistent with the effects of other introduced freshwater mysids. Investigations of introduced *Mysis* have demonstrated the potential for severe declines and compositional shifts of macrozooplankton communities, reduced abundances and growth rates of pelagic fishes, and altered nutrient and contaminant cycling. These studies also reveal the importance of environmental variables that influence the availability of mysids to diurnal predators (e.g. the presence of upwelling currents; Martin and Northcote, 1991). Water clarity is thought to limit mysid migration into shallow waters and thereby provide epilimnetic refugia for cladoceran populations (Koksvik et al., 2009). Lake productivity is another plausible moderator of impact; some evidence suggests that mysid introductions are particularly disruptive in nutrient-poor systems because of stronger competitive effects (Li and Moyle, 1981; Nero and Sprules, 1986; Northcote, 1991), whereas in more productive waters higher birth rates of zooplankton

might offset predation losses (Morgan et al., 1981). Peak summer temperatures could limit the occurrence and impact of *H. anomala* in nearshore areas, but predictions cannot be made without better knowledge of its thermal tolerances and temperature-avoidance behavior (Ioffe et al., 1968). Within rivers, the impacts of *H. anomala* should be most pronounced in backwater lakes, impounded areas and reservoirs, where the mysid can develop locally abundant populations (Stubbington et al., 2008; Wittmann, 2007).

Assuming that *H. anomala* becomes a significant prey item for planktivorous fishes, it will increase bioaccumulation of contaminants in piscivorous fish and waterfowl. If predation is relatively low and the mysid maintains high abundances, we predict that *H. anomala* will negatively impact the growth and abundance of YOY and planktivorous fishes in nearshore areas. Low predation pressure from fishes is thought to have exacerbated the impacts of *H. anomala* in Dutch reservoirs (Ketelaars et al., 1999). Thus, a major question is whether predators can limit its local abundance and spatial distribution. In the Great Lakes, there are efficient planktivores such as alewife (*Alosa pseudoharengus*), which feed selectively on *M. diluviana* and are able to adjust their own diel vertical migrations to coincide with the mysid (Janssen and Brandt, 1980; Pothoven and Vanderploeg, 2004; Stewart et al., 2009). However, in Lake Ontario, which has the highest degree of planktivory among the Great Lakes (Rand et al., 1995), the presence of alewife and other planktivorous fishes has not prevented *H. anomala* from spreading widely and becoming locally abundant (Walsh et al., 2010), even though alewife have increased their consumption of native mysids (*M. diluviana*) in recent decades (Stewart et al., 2009) and can feed substantively on *H. anomala* (Lantry et al., 2010).

Accurate forecasts of the foodweb effects of *H. anomala* require a predictive understanding of its interspecific interactions, which are likely to be complex (Fig. 3). The presence of abundant dreissenid mussel populations should alter *H. anomala*'s impact on phytoplankton populations. High filtering rates by mussels consume most of the phytoplankton production in Lake Ontario, suggesting that intense mysid predation on zooplankton may not necessarily lead to increased algal standing stocks, but instead promote an increase in mussel density (Koops et al., 2010). Subsequent competition between mussels and
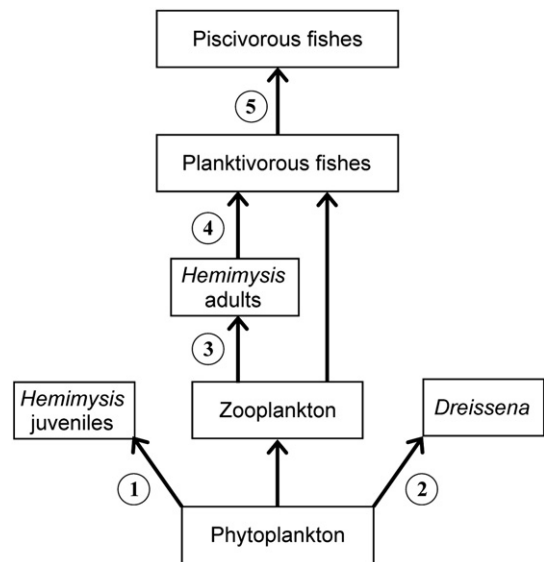
Fig. 3. Hypothesized pelagic foodweb effects of *H. anomala*. Pathways #4 and #5 facilitate bioaccumulation of contaminants (e.g. mercury, PCB) in fishes. If mysid consumption of zooplankton (pathway #3) is not constrained by fish predation on mysids (pathway #4), it may reduce fishery productivity and (if pathways #1 and #2 are relatively weak) promote algal blooms. Alternatively, pathways #2 and #3 may lead to increased production by dreissenid mussels, if the mussels are food-limited. Positive effects on dreissenids may create a negative feedback, owing to competition between juvenile mysids and dreissenid mussels.

juvenile mysids could conceivably generate negative feedbacks on *H. anomala* populations.

Finally, the impacts of *H. anomala* are expected to vary over temporal and spatial scales, owing to the dynamics of mysid populations. A fluctuating, patchy distribution of *H. anomala* will create heterogeneity in its impacts on fish populations by locally depressing zooplankton concentrations below the needs of YOY fishes at some locations, and creating refugia for zooplankton elsewhere. Thus, a key avenue of research will be to quantify the environmental factors that contribute to patchiness and the formation of *H. anomala* swarms.

Acknowledgments

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