Factors affecting the distribution and abundance of an invasive freshwater mysid

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Abstract

The freshwater shrimp *Hemimysis anomala* is a recent Ponto-Caspian invader of the Great Lakes – St. Lawrence River basin. Based on its invasion history, high predation rate and the naiveté of the ecosystems in which it has been introduced, it has the potential to exert strong impacts on native food webs. Risk assessment and effective monitoring of the spread of this invader require information about the environmental factors that limit its local abundance and distribution. A literature review suggests that *H. anomala* has broad environmental tolerances but may be limited by low water conductivity levels, high local flow, and low dissolved oxygen. An empirical model derived from results of a field study in the St. Lawrence River identified specific conductivity and shoreline heterogeneity as important predictors of *H. anomala* occurrence and abundance across sites. The relationship between conductivity and *H. anomala* occurrence is further supported by experimental evidence that demonstrates lower functional responses at lower conductivity levels. Distance from shore and depth were also good predictors of *H. anomala* abundance, which was maximal in areas close to shore and at depths above 2 m.

Résumé

La crevette d'eau douce *Hemimysis anomala* est une espèce envahissante provenant de la région Ponto-Caspienne qui a été découverte récemment dans le bassin des Grands Lacs et du fleuve Saint-Laurent. En raison de ses fortes tendances envahissantes, de son taux de prédation élevé et de la naïveté des écosystèmes dans lesquels elle a été introduite, elle pourrait avoir des impacts considérables sur les réseaux alimentaires locaux. Afin d'évaluer les risques et de surveiller de manière efficace la dispersion de cette espèce, point est besoin d'avoir accès à de l'information sur les facteurs environnementaux qui limitent son abondance locale et sa distribution. Une recension de la littérature suggère que *H. anomala* fait preuve de tolérance environnementale, mais qu'une basse conductivité d'eau, de hauts courants locaux et une basse concentration d'oxygène dissous peuvent diminuer cette tolérance. Un modèle empirique, mis au point à partir des résultats d'une étude de terrain menée dans le fleuve Saint-Laurent, démontre que la conductivité spécifique et l'hétérogénéité du rivage constituent des facteurs de prédiction de la présence et de l'abondance de *H. anomala* à travers les sites. La relation entre la conductivité de l'eau et la présence de *H. anomala* est, en outre, soutenue par des preuves expérimentales qui mettent en exergue une réponse fonctionnelle réduite à de bas niveaux de conductivité. La distance du rivage et la profondeur sont aussi de bons indices d'abondance de *H. anomala*; la concentration de crevettes atteint d'ailleurs son point le plus haut près du rivage et à plus de deux mètres de profondeur.

Contribution of Authors

This thesis was completed under the supervision of Dr. Anthony Ricciardi and in collaboration with Dr. Susan Doka of Fisheries and Oceans Canada. Chapter two in this thesis is prepared for future submission to a peer-reviewed journal, and Dr. Ricciardi and Dr. Doka will be co-authors on the submitted manuscript. Both Dr. Ricciardi and Dr. Doka were instrumental in this project by suggesting research questions and sampling designs. Dr. Ricciardi also edited drafts of this manuscript. The methods and statistical analysis for the functional experiments were designed in collaboration with Dr. Jamie Dick and graduate students in his lab. I planned and conducted all field sampling in 2010 and 2011, analyzed the data and produced the original drafts for this thesis. Chapter one cites results of an experiment and a literature review which I produced that are published as contributions in peer-reviewed journal articles where I am not the first author.

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Chapter 1: Factors affecting the distribution and abundance of invasive freshwater mysids

Abstract

Rates of dispersal of invasive species have increased exponentially over the past century, becoming a global problem with troubling impacts. Freshwater mysids have a long history of being stocked in new habitats, resulting in unpredictable consequences including cascading food web effects observed after the introduction of *Mysis diluviana* (a native of profundal zones in the Great Lakes) in Kootenay Lake. A comparison of functional responses between *M. diluviana* and *H. anomala*, the newest Ponto-Caspian invader of the St. Lawrence River, indicates that the latter has higher predation rates which creates concerns regarding potential impacts on food webs in areas where it is becoming established. Literature indicates that *H. anomala* has broader environmental tolerances than *M. diluviana* which allow it to inhabit littoral and lotic habitats in the Great Lakes – St. Lawrence system that are naïve to mysids. However, there are also some reports suggesting parameters that may limit establishment: low specific conductivity, high rates of flow and low dissolved oxygen levels. Identifying environmental parameters that favour dense local populations of *H. anomala* will be essential for prioritizing areas for protection from invasion and for early detection which are indispensable for successful management of invasives.

Invasive Species: a Global Problem

Invasive species are an increasing global problem (Gherardi 2007). They are a major cause of the loss of biodiversity (Wilcove et al. 1998; Clavero and Garcia-Berthou 2005), they disrupt ecosystems worldwide, and are a growing economic burden to industry and governments (Pimentel et al. 2005). The combined, estimated yearly cost of invasive species is $1.4 trillion, a full order of magnitude greater than that caused by natural disasters (Ricciardi et al. 2011). Only a fraction of introduced species create what we recognize as significant problems (Williamson and Fitter 1996); however, growing globalization and the resulting exponential increase in trade have led to the intentional and inadvertent transport of plant and animal matter across the planet at unprecedented speeds and spatial scales (Ricciardi 2006, 2007, Hulme 2009). This means that a greater number of exotics are introduced successfully, increasing the probability of negative impacts, to habitats they would have never reached under normal circumstances.

In the Laurentian Great Lakes this is highlighted by the strong correlation between the increase in international shipping traffic over the last century and the number of introduced species discovered in that ecosystem (Ricciardi 2006). The ballast water of transoceanic cargo vessels has been the principal vector for unintentional transport of aquatic species, giving them a ride from port to port, to new watersheds on the other side of the globe (Holeck et al. 2004). Moreover, as transport ships are becoming larger and faster, their ballast water is becoming more hospitable to life and the trips shorter, both of which favour the survival of organisms being transported (Hulme 2009). Other important vectors of aquatic invaders in the Great Lakes, such as the aquarium trade, bait shops and live fish markets, are alarmingly unregulated (Padilla and Williams 2004, Rixon et al. 2005). Freshwater habitats are especially vulnerable to the effects of invasive species (Saunders et al. 2002) partly because they are more isolated than their marine counterparts which means their native inhabitants lack evolutionary experience with the stress brought on by some of the introduced organisms (Cox and Lima 2006).

Managing the risk of negative impacts caused by invasions becomes possible with the aid of predictive information on new and potential invaders. Information on environmental tolerances of potential invaders guides the development of appropriate ballast water regulations (Ovcarenko et al. 2006, Gray et al. 2007) and laws prohibiting the sale of high risk species to the public (Padilla and Williams 2004, Rixon et al. 2005). Identifying habitats capable of supporting abundant and established populations of the invader allows for prioritization of areas for management or exclusion efforts. Moreover, knowledge of habitat preferences of invaders enhances monitoring efficiency, allowing early detection, which is often crucial for the success of management and eradication efforts (Nunn and Cowx 2012, Walsh et al. 2012).

Impacts of invasive freshwater mysids

Mysid shrimp (mysidacea) have extensive invasion histories in Europe and North America (Nesler and Bergersen 1991). Introductions of these predatory invertebrates have resulted in trophic cascades impacting the invertebrate communities, fish populations, and even extending effects to primary producers and non-aquatic species. *M. diluviana*, the only mysid native to the Great Lakes, and the closely related European *M. relicta* have been intentionally stocked in hundreds of watersheds (Hanson 1966, Kay 1999) to encourage the growth of commercially desirable fishes by providing them with a novel, exploitable resource (Martinez and Bergersen 1991). However, in many stocked lakes, targeted fish populations actually declined (Kay 1999). The mysids were not only able to escape predation, but also managed to out-compete their potential predators in consumption of zooplankton (Martinez and Bergersen 1991). A striking example of cascading effects was reported in Kootenay Lake where the decline of Kokanee salmon due to competition from *M. diluviana* caused a crash in the Bald Eagle population which depended on the salmon for food (Spencer et al. 1999). Similar impacts were observed in Europe, where introduction of *M. relicta* in Swedish lakes resulted in changes of zooplankton relative abundances and community composition (Koksvik et al. 2009), Ricciardi et al. 2012). Given these costly outcomes, mysid stocking has since been terminated.

Hemimysis anomala introduction to North America

The freshwater invasive mysid, *Hemimysis anomala* (from here on *H. anomala*) is the most recent Ponto-Caspian introduction to the Great Lakes – St. Lawrence River. Its first record was identified in 2006 from a sample taken in Muskegon Channel, which is connected to Lake Michigan (Pothoven et al 2007). Subsequently, it has spread to connected watersheds, including all the Great Lakes with the possible exception of Lake Superior (Marty et al. 2009). It was detected in the St. Lawrence River in 2008 (Kestrup and Ricciardi 2008), in August 2009 it was found in the stomach contents of a White Perch from Oneida Lake, the first inland lake to be invaded (Walsh 2009) and in 2010 it was captured in samples taken in adjacent Finger Lakes (Brown et al. 2012). Nearly a decade prior to the first detection, *H. anomala* was identified as a potential invader to the Great Lakes based on its ability to survive a partial ballast water exchange, its invasion of European watersheds, which are connected to North American ports through shipping traffic, and its environmental tolerance (Ricciardi and Rasmussen 1998). A genetic analysis of the Muskegon Channel population substantiates that it arrived to North America via the ballast water of transoceanic freighters originating from large ports in the Rhine River system in Europe (Audzijonyte et al. 2008), which was invaded in the 1990s (Ketelaars et al. 1999).

Predicting impacts of *H. anomala*

Most introduced species do not establish successfully and, of those that do, the majority have little impact on native biodiversity (Ricciardi and Kipp 2008). However, there are some criteria we can use to identify which invasive species are most likely to cause problems, and a great deal of evidence implicates *H. anomala* as a probable disruptive invader for the Laurentian Great Lakes.

1) Invasion History

Invasion history is a useful tool for developing predictions of ecological impacts caused by invaders (Kulhanek et al. 2011). Like the glacial relicts, *M. diluviana* and *M. relicta*, in the 1950s *H. anomala* was intentionally transplanted to many reservoirs and lakes in Eurasia with great success (Mordukhai-Boltovskoi 1960). It has also been introduced unintentionally into European watersheds, where it established stable populations and is continuing to extend its range through natural dispersion and unintentional transfer associated with anthropogenic activities (Wittmann and Ariani 2009). To date, it has become locally abundant throughout mainland Western (Ketelaars et al. 1999; Dumont and Muller 2009; Faasse 1998; Wittmann 2007) and Eastern (Borza 2008; Wittmann 2007; (Stubbington et al. 2008) Europe, England (Stubbington et al. 2008) and Ireland (Minchin and Holmes 2008; Minchin and Boelens 2010). European studies found that introductions of *H. anomala* coincided with decreases in biodiversity and abundance of zooplankton (Ketelaars et al 1999). The studies conclude that *H. anomala* is a voracious predator and a top down-regulator of the zooplankton community

(Pienimaki and Leppakoski 2004), with the potential to negatively impact planktivorous fish populations and indirectly, entire food webs (Salemaa and Hietalahti 1993).

2) Functional Response

When field studies of impacts of an invader are scarce, as they are in the case of *H. anomala*, an alternative approach is to compare its functional response curve to that of another functionally similar invader with better-known impacts. *H. anomala*'s functional response, measured as a function of predation was compared to *M. diluviana*'s (Dick et al 2012). Both mysids pose a threat primarily because of their voracity (Ketelaars et al. 1999; Borcherding et al. 2006), and *H. anomala* actually had a higher overall predation rate than *M. diluviana* despite being smaller on average (Dick et al. 2012; Figure 1.1). Since total impact of an invasion is a function of impact per individual and abundance of the invader (Parker et al. 1999), we can expect that in areas where *H. anomala* is successful at establishing dense local populations, at minimum, it will have a significant impact on the zooplankton populations that it feeds on, and that it is likely to also cause cascading impacts throughout the food web.

3) Naïvete of invaded communities

A meta-analysis of literature done in 2004 (Ricciardi and Atkinson 2004) suggests that the magnitude of an aquatic invader’s impact is related to its taxonomic distinctiveness within the recipient community. The communities in the habitats being invaded by *H. anomala* in inland watersheds of North America are entirely naïve to mysids. *H. anomala* colonizes shallow, warm, littoral and river habitats that are outside the range of the only native mysid, *Mysis diluviana* (Audzijonytė and Väinölä 2005). Moreover, because of its distinctiveness, *H. anomala* introduction results in a trophic lengthening of the food web in these communities (Yuille et al. 2012).

Range of Environmental tolerance of *H. anomala*

H. anomala is native to the fresh and brackish water portions of the Black, Azov and Caspian Seas (Porter et al. 2008). Species arriving from the Ponto-Caspian region are of particular concern because they are becoming ubiquitous in the Great Lakes, with far reaching impacts (Ricciardi and MacIsaac 2000). A contributing factor to their success is their broad tolerance of environmental conditions, resulting from their shared evolutionary history in the highly variable hydrology and geology of the Ponto-Caspian basin (Reid and Orlova 2002). It is therefore relevant to assess what we know about *H. anomala* environmental tolerances and preferences. Some data exist in literature about invasive freshwater mysids' environmental preferences and tolerance limits. Table1.1 summarizes the range of some important abiotic parameters for six freshwater mysids: the two glacial relicts, *Mysis diluviana* and *Mysis relicta*, and four Ponto-Caspian mysids, *Hemimysis anomala*, *Limnomysis benedeni, Paramysis lacustris* and *Katamysis warpachowskyi.*

Unlike the glacial relicts, Ponto-Caspian mysids are riverine mysids, which are capable of inhabiting shallower areas where temperature is higher, and withstanding greater flows. From the literature data, it appears that there are some environmental parameters which could lead to the exclusion of *H. anomala* from some freshwater habitats. *H. anomala* and the other Ponto-Caspian mysids appear to be less tolerant to low specific conductivity levels than their glacial-relict counterparts, with a reported lower limit of 92 µS/cm for *H. anomala* (Wittman and Ariani, 2009), compared to 23 µS/cm (Rippey, 1993) and 24 µS/cm (Trippel and Beamish, 1993) for *M. relicta* and *M. diluviana* respectively. Ponto-Caspian invaders studied thus far, seem to have a general preference for higher conductivities (Jones and Ricciardi 2005; Kestrup and Ricciardi 2009). Dissolved Oxygen level tolerance also appears to be slightly more limiting for *H. anomala* than for the glacial relicts, though no direct experiments have been done to confirm this (Martinez and Bergersen, 1991 ; Bailey et al., 2006 ; Wittman, 2007). Flow may also prove to be limiting because, although *H. anomala* has a higher ability to swim against currents than non-riverine mysids, it is limited at 0.8 m/s (Northcote, 1991; Wittman, 2007) which means that it cannot swim against heavy currents, and upstream dispersal is dependent on other vectors.

Biotic effects on *H. anomala* are much less studied. There is evidence of fish predation on *H. anomala* which may be able to control its local densities (Yuille et al.

2012) and a recent study (Marty et al 2012) found a relationship between site and diet quality in *H. anomala* which is presumably dependent on prey availability, and may impact its success. However, no direct comparison of diet and *H. anomala* population density have been done to date.

Managing the Invasion

Predictive information about new invaders is needed for two main reasons: prioritizing locations for management and early detection. The ability to predict which sites are likely to be invaded allows us to concentrate limited resources on invasion prevention programs in areas that are most vulnerable to *H. anomala* impacts. Early detection is crucial to successfully manage invasives (Britton et al 2011); generally once locally dense populations are established it is too late to reverse the invasion and its effects. Therefore, if we can identify areas where *H. anomala* are likely to settle first, based on their habitat preferences, we can improve our ability to detect them in the earliest stages of introduction, before they have become well-established.

With the general aim of improving our ability to predict *H. anomala* spread, this study has two main objectives:

1) Determine the extent, spatially and in terms of density, to which *H. anomala* has been able to colonize the St. Lawrence River.

2) Identify physico-chemical parameters which favour establishment of *H. anomala*, and those that prevent it from reaching high local densities.

Tables

Table 1.1 Published physico-chemical tolerances of invasive freshwater mysids. 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 mg/L**	**Conductivity µS/cm**	**Water Current m/s**	**pH**	**Salinity ‰**
Mysis diluviana	5[a]–262[b]; 3[c] for juveniles	Tolerates: 2[i]–22[j] Prefers: 6–8[h] Avoids: >18[h]	>2–3[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]–4[d]	23[u]–74[v]	?	6.5[z]–7.5[v]	0–7[p,e]
Hemimysis anomala	<1–60[f,g]	Tolerates: 2[o]–28[n]	>4[g]	92[w]–29200[g]	0–0.8[g]	6.21[w]–8.65[g]	0–18[g]

		Prefers: 9–20[n] Avoids: >25[n]					
Limnomysis benedeni	<0.5[ai]-*33* prefers: *0.5-5*[fi]	0[fi]-31[fi] Prefers: 10[fi]-25[fi]	>3.7[g] Prefers >5.9[fi]	Prefers 500-6000[fi] Range: 52-23000[fi]	Prefers: <0.5[ki,ni,] Range: 0-1.5[g]	Prefers:7.3-8.6[fi] Range: 5.4[ji]-9.6[fi]	Occurence: 0–11[li] Range: 0.5[g ,ki]-23[mi] 100% mortality: 34[h]
Paramysis lacustris	prefers:1-3[fi]	Tolerate: 0-32.5[gi] Prefer: 7-28[gi]	>0.9 [gi]	?	?		Occurence: 0–7.5[li] Range: 0-15 [li] 100% mortality: 23[mi]
Katamysis warpachowskyi	0.5[ei]- ?	?	>6[ei]	*? -343*[ei]	>*L. beneden*[ei]	-8.24[ei]	?

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*. Wittman, 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*. Audzijonyte 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*. Wittman and Ariani, 2009; *x*. Northcote, 1991; *y*. Schindler et al., 1985; *z*. Moen and Langeland, 1965 ; *ai* Gergs et al. 2008 ; *bi* Steinman 2009 ; ci Semenchenko 2007 ; *di* Szalontai et al 2003 ; *ei* Hanselmann 2010 ; *fi* Wittmann 2012 ; *gi* Khmeleva 1987 ; *hi* Lazauskiene et al. 1995 ; *ji* Szalontai et al. 2003 ; *ki* Wittmann 1995 ; *li* Lazauskiene et al. 1995 ; *mi* Ovarecenko et al 2006 ; *ni* Wittmann and Ariani 2000 ;

Figures

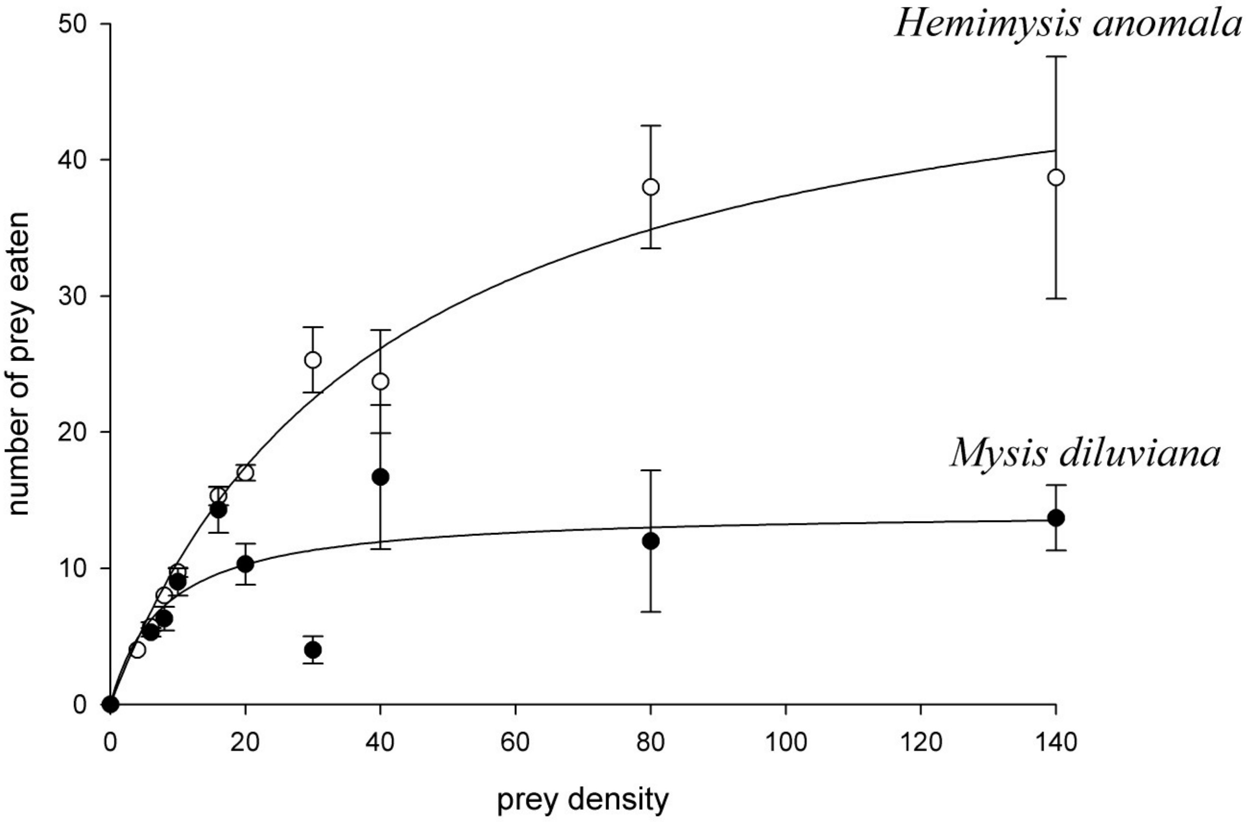

Figure 1.1 Functional response curves of *H. anomala* and *M. diluviana*, as a function of predation on *D. pulex* over 12 hours, at 12°C (Dick et al. 2012).

Linking Statement

In chapter 1 I reviewed the literature on physico-chemical factors affecting the distribution of mysids in general and Hemimysis in particular using European and recent North American published data. This review identified several limnological and habitat-based variables that collectively may explain the distribution and abundance of *H. anomala* in invaded habitats. Major differences in environmental tolerance between *H. anomala* and the native North American *M. diluviana* include temperature, depth, specific conductivity, and salinity, as well as *H. anomala*'s ability to colonize lotic environments. Guided by some of this information, the next chapter will test specific hypotheses on a fine scale in the St. Lawrence River, the first large river to be invaded in North America.

Chapter 2: Distribution and habitat preferences of *Hemimysis anomala* in the St. Lawrence River

Abstract

A Ponto-Caspian crustacean, the ‘bloody red shrimp’ *Hemimysis anomala*, was discovered in the Great Lakes in 2006 and in the St. Lawrence River in 2008. Surveys conducted in late summer-early fall 2010 and in summer 2011 reveal that the species has colonized the length of the river, from the outflow of Lake Ontario to the freshwater estuary at Quebec City, within four years. Maximum and mean abundances in the St. Lawrence River are comparable to sites in the Great Lakes and European sites that have been invaded for longer periods of time. A multivariate Poisson model related mysid densities to site-specific physico-chemical variables; the model with the greatest explanatory power (based on Akaike's Information Criterion) included specific conductivity, depth, distance from shore and the shoreline heterogeneity index score as predictor variables. Conductivity appears to act as a threshold variable, severely limiting the abundance of mysids in ion-poor waters. This was further supported in a lab experiment that compared the functional response of *H. anomala* across a gradient of conductivities reflecting those found in the river; mysids performed poorly at low conductivities – similar to conditions at sites containing the lowest densities. A comparison of model results for data obtained from net hauls and benthic traps, respectively, suggests that net hauls are a poor method of estimating low abundances such as those expected in the early stages of an invasion and in sub-optimal habitats. Furthermore, owing to the dynamic and patchy distribution of mysids, net hauls are more likely to yield ‘zeroes’ than benthic traps deployed for <24 hrs.

Introduction

Aquatic invasive species have been discovered in the Great Lake – St. Lawrence River Basin at an increasing rate over the past two centuries (Ricciardi 2006). The Ponto-Caspian region has been a frequent donor of invasive species, partly because of its unstable hydrological history – which has produced animals with broad ecological tolerances and rapid colonization abilities – as well as numerous opportunities to interface with international shipping traffic (Ricciardi and Rasmussen 1998; Reid and Orlova 2002). The 'bloody red shrimp' *Hemimysis anomala* is a mysid native to the freshwater and brackish-water margins of the Black, Azov and Caspian Seas (Porter et al. 2008). It is the most recent Ponto-Caspian species to be introduced to North American watersheds, and it shares many of the characteristics that have made other Ponto-Caspian invaders successful.

Widespread establishment of *H. anomala* is considered a potential threat to North American watersheds, owing to its invasion history and novelty. Throughout the 1950s and 1960s, it was stocked in several reservoirs in the Dnieper and Volga River basins in Russia, Ukraine and Moldova as a potential prey item to promote fish biomass (Pligin and Yemel'yanova 1989). It subsequently spread into other basins by natural dispersal through connecting waterways and by unintentional transfer associated with human activities (Wittmann and Ariani 2009). To date, its European range extends to the Baltic Sea, the Gulf of Finland, the Rhine River basin, the River Main, the Danube River and various rivers in the U.K. (Salemaa and Hietalahti 1993, Bij de Vaate et al. 2002, Lundberg and Svensson 2004, Borcherding et al. 2006, Dumont 2006, Holdich et al. 2006). Studies of the impacts of *H. anomala* introductions in Europe identify the species as a top-down regulator of the plankton community (Pienimaki and Leppakoski 2004), with the ability to directly cause changes in macro-zooplankton overall abundance and community composition, thereby indirectly impacting planktivorous fish populations and whole food webs (Salemaa and Hietalahti 1993, Ketelaars et al. 1999). The only mysid native to the Great Lakes, the opossum shrimp *M. diluviana*, is a deep-water glacial relict species (Audzijonytė and Väinölä 2005) that, unlike *H. anomala*, does not occur in littoral zones or lotic systems. Consequently, these systems have no natural ecological analogue to *H. anomala*, and thus are naïve to the effects of this novel predator (Ricciardi and Atkinson 2004).

H. anomala was discovered for the first time in North America in 2006, almost simultaneously in Lake Michigan (Pothoven et al. 2007) and in Lake Ontario (Marty 2008). It is presently established in each of the Great Lakes, except for possibly Lake

Superior (Marty et al. 2009). In 2008, the first specimens were discovered in the St. Lawrence River, near Montreal, approximately 290 km from the outflow of Lake Ontario (Kestrup and Ricciardi 2008). Since then, thriving populations have been found in some inland lakes and canals within the Great Lakes basin (Walsh 2009, Brown et al. 2012). These high rates of spread, coupled with its European invasion history, signal this species as a priority for management in the Great Lakes region (Ricciardi et al. 2011).

The only sustainable strategy for managing invasive species is to prevent their spread through early detection and rapid response (Leung 2002, Vander Zanden 2012). The effective allocation of limited management resources requires prioritization of vulnerable sites, which may be identified using predictive models. There exist few models predicting the distribution and abundance of Ponto-Caspian invaders (Wilson and Sarnelle 2002, Jones and Ricciardi 2005). No such models have been developed for *H. anomala*, despite a recent surge in studies of *H. anomala* ecology on both sides of the Atlantic Ocean. The rapid spread of *H. anomala* since its first detection in North American watersheds highlights the urgency of the need to identify its habitat tolerances and preferences to inform management efforts.

There is a need to identify ecological parameters that permit invaders to spread quickly in some habitats and that limit their establishment in others. Based on published observations in other invaded systems (Chapter 1), we expected to find freshwater habitats that are inaccessible to *H. anomala* establishment. A long-term study reports that while *H. anomala* has persisted in the Kaunas Water Reservoir (Lithuania) since it was stocked there in the 1960s, it has failed to colonize connected watersheds, unlike two other Ponto-Caspian mysids (*Paramysis lacustris and Limnomysis benedeni*) that had been stocked concurrently (Arbaciauskas 2002, 2005). Published data on *H. anomala*'s ecology and invasion history allow us to identify, *a priori,* abiotic variables that have the potential to explain spatial variability in *H. anomala* distribution and abundance in the St. Lawrence River (Table 2.1). Additional abiotic factors that may be important in determining the success of *H. anomala* include dissolved oxygen or salinity; however, these do not vary enough between sites in the freshwater portion of the St. Lawrence River to be useful for discerning any patterns.

The goals of the present study were to (1) assess the extent to which the St. Lawrence River has been colonized by *H. anomala* and (2) develop a predictive model of *H. anomala* occurrence and abundance, based on abiotic variables described in Table 2.1. (3) complement the model with experimental evidence for variables that are confounded in the field. The St. Lawrence River was chosen as the site for this field study because of the heterogeneity of its water chemistry, shoreline and flow patterns. It is also the first large North American river to be invaded by *H. anomala*, and thus may provide predictive information for other rivers that are likely to be invaded in the future.

Methods

Field Study

Given that *H. anomala* forms swarms that have a patchy spatial and temporal distribution (Borcherding et al. 2006), we used multiple sampling gears and a nested sampling design to maximize our ability to detect and quantify *H. anomala* populations. As it was not the purpose of this study to measure temporal variation, we minimized bias from seasonal effects by limiting sampling to a period of two months when *H. anomala* is expected to be most abundant (Taraborelli et al. 2012) and by randomizing the order in which sites were sampled.

Sampling and habitat assessments were conducted at 17 sites in the St. Lawrence River from August 16 to October 18, 2010 (Figure 2.1 and Figure 2.2). Sampling was done either from a boat or from shore, depending on the accessibility of the site. Sites were selected to represent a heterogeneous sample of habitat types; parameters considered in the site selection were shoreline development, flow and water conductivity. To capture local variation in micro-habitat within each site, we sampled multiple sub-sites that differed among themselves in substrate type, macrophyte cover, local flow or shoreline slope. Sites and sub-sites were 1 km and 5-10 m in shoreline length, respectively.

The relative abundance and local population density of *H. anomala* were determined using benthic traps and vertical zooplankton net hauls, respectively. A benthic trap consisted of a plastic bucket (30.5 cm width, 38 cm depth) with a black funnel (30.5 cm diameter) secured to its opening with plastic cable ties, and with four holes (5 cm diameter, covered with 400 µm mesh) spaced at 90º angles along the circumference of the bucket to allow water to drain as the trap is lifted from the water column. Pre-cleaned rocks were placed within the bucket prior to its deployment to weigh down the trap, and a float was attached to the bucket handle by a rope to facilitate retrieval. The traps were deployed before dusk to capture mysids as they migrate to the benthos at dawn in search of refuge from visual predators (Borcherding et al. 2006, Boscarino 2012). The funnel's black colour appears to attract *H. anomala* (personal observations). Traps were set in triplicate, adjacent to each other, at five sub-sites within each site – except at two of the sites (Gentilly and Port of Becancour) where we were only able to sample three sub-sites. At some locations, one or more traps from a sub-site were lost to high currents or tampering. Traps were retrieved during daylight, 18-24 hours after deployment. Trap contents were sieved through 500 µm mesh by rinsing the rocks and the inside of the bucket. The sample from the sieve was preserved in 75% ethanol.

Net haul sampling was conducted after dusk using a plankton net (400 µm mesh, 78 cm diameter), which was lowered slowly to the bottom, left undisturbed for 2-3 minutes and then hauled up vertically at a steady speed. This method is effective at capturing mysids while they feed in the water column at night (Pothoven et al. 2007). Net hauls were done at 6-10 sub-sites within each site, within 24 hours of the bucket trap deployment at that site. All samples were immediately preserved in 75% ethanol. We were unable to retrieve traps set at Bainsville, and because sites at Valois Bay were shallow and covered in very dense macrophytes they were unsuitable for vertical net hauls; therefore, data at these two sites were collected with only one sampling gear type, net hauls in the former and traps in the latter.

Mysid samples were sorted in the lab using a dissecting microscope. Individuals were categorized and enumerated as gravid females, non-gravid females, males, or juveniles (length < 6 mm, as measured from the anterior tip of the carapace to the posterior tip of the telson, Figure 2.4). Sex was determined based on the presence of elongated abdominal pleopods (Pothoven et al. 2007); gravid females were identified by the presence of eggs and/or embryos in their brood pouches. Density of *H. anomala* at each site was estimated from net haul samples using the formula:

$$\frac{\text{number of individuals captured}}{\text{area of the net opening X depth of the site}}$$

A habitat assessment was done at each of the sub-sites where bucket traps were deployed. A series of parameters were measured (Table 2.2). Substrate was classified based on a visual assessment as bedrock, boulder, rock, cobble, pebble, gravel, sand, silt or clay. Sediments smaller than cobble were classified after retrieving a sample with a Ponar grab, while the size of larger sediment (rubble or boulders) was estimated from the boat if it was possible to see them through the water column. Subsequently, each sediment category was assigned an average phi value (Valere 1996; Table 2.5), Macrophyte cover was assigned a value between 0 and 4 (Table 2.3) using visual assessments done from a boat at each sub-site, according to the Fisheries and Oceans Canada protocol for habitat assessment (Brousseau et al. 2005). Digital photographs were taken of the shoreline and used to categorize each sub-site's shoreline slope between 0 and 3 (Table 2.4). Aerial images from Google Earth software were used for measuring the Shoreline Heterogeneity Index (SHI) – i.e. the distance between two points measured in total shoreline length divided by their direct Euclidean distance (Archambault and Bourget 1996), calculated using a map with scale 1:2000 and points that are 2 km apart and equidistant from the center of the site. The fluvial distance of each site from the source of the St. Lawrence River at Lake Ontario (44° 6'35.35"N, 76°23'3.10"W) was also measured using Google Earth. All habitat data except secchi depth, sediment size and macrophyte cover – all of which are difficult to measure in the dark – were collected or calculated at the net haul sub-sites using the same methods used at trap sub-sites.

We constructed generalized linear mixed models to relate *H. anomala* relative abundance to habitat variables. Models were fitted with a Poisson distribution (using glmr and log link functions in R) because 1) our dataset included zero-inflated count-data that could not be normalized by transformation, and 2) our sampling protocol employed a nested design with different within-site and between-site predictor variables. Random effects for sub-site were included in the model to account for the spatial correlation between sub-sites within a site. Parameters which did not sufficiently vary between our sites (i.e. did not differ by at least one standard deviation), such as dissolved oxygen and secchi-depth, were removed from the analysis. Akaike Information Criterion scores were generated for all possible models involving the remaining predictor variables, using the dredge function in R. Among the models generated with the lowest AIC scores, we selected the one that retained all the predictor variables that were significant or nearly so ($p<0.08$). Finally, to test for threshold effects, a presence/absence model was similarly constructed from presence/absence trap data, using a binomial distribution and a logit link function in R. All statistical analyses were conducted in R, and data were plotted in Sigma Plot. Statistical methods and R code for constructing the hierarchical models were done as described in Gelman and Hill (2007).

A second field survey was conducted the following year to compare *H. anomala* abundance and population structure at Port of Montreal and Port of Quebec. The sites were chosen because they have similar habitat characteristics: steep shoreline, low local flow, >5 m depth along the shore. The sampling was conducted within the same 48 hours to avoid confounding seasonal effects that affect *H. anomala* population abundance and structure (Table 2.6). Ten net hauls were done at each port and a sample from each haul was preserved in 75% ethanol. All mysids were counted, sexed and measured for the Port of Quebec samples. Some Port of Montreal samples were sub-sampled using the "Beaker method" (Van Guelpen et al. 1982) because of very high densities (>1000 individuals in each sample). Approximately a 2 mL volume of sample was sub-sampled and the total number of individuals in the sample was estimated using the formula:

$$\frac{\text{number of individuals in subsample}}{\text{volume of subsample}} \times \text{volume of sample}$$

Functional Response Experiment

Model results correlating specific conductivity with *H. anomala* relative abundance and occurrence in the field may have been confounded by differential propagule supply (drifting juveniles) in the ion-rich water from the St. Lawrence River mixing with the ion-poor water from the Ottawa River along the southern shore of the island of Montreal (Kestrup and Ricciardi 2009). Based on the premise that an organism's functional response (i.e. its rate of prey consumption in relation to prey supply; Holling 1959) is a good indicator of changes in performance under different environmental conditions (Kestrup and Ricciardi 2009), we examined *H. anomala* functional responses at different conductivity levels in the lab.

Live specimens of *H. anomala* were obtained from the Port of Montreal in September 2011. They were kept in conditioned tap water, in a dark, temperature-controlled chamber at 11ºC prior to use in trials. Low conductivity water (110 µS/cm) was collected from the Ottawa River at Ste-Anne-de-Bellevue (Quebec), whereas high conductivity water (307 µS/cm) was collected from the St. Lawrence River in a fluvial lake (Lac St. François, at Bainsville, Ontario). Water from the two sources was mixed in equal parts to obtain intermediate-conductivity water (214 µS/cm) that is similar to that found at various sites along the southern shoreline of Montreal at the confluence of the two rivers (Kestrup and Ricciardi 2009). All water was filtered through 11 µm filter paper to remove parasites and particulate organic material.

Experimental procedures generally followed Bollache et al. (2008). Prior to the start of a trial, *H. anomala* were acclimated in water at the appropriate experimental conductivity level for 48 hours. Individual *H. anomala* were then placed in cylindrical plastic arenas (5 cm height, 10 cm diameter) and offered prey at initial densities of 4, 6, 8, 10, 16, 20, 30, 40, 80 and 140 individuals of *Daphnia pulex* from laboratory stock. This prey species was selected based on its documented importance in mysid diets in Europe (Ketelaars et al. 1999), and previous experiments that showed it to be readily consumed by *H. anomala* in the lab (S. Avlijas and A. Ricciardi, unpubl. data). All prey densities were run in the dark at each conductivity level (low, intermediate, and high) in triplicate for 12 hours; immediately afterwards, the predator was removed and remaining prey were counted. Dead prey were counted as not consumed. To ensure that all uneaten prey could be accounted for, controls (n=3) were set up with only the prey items and no *H. anomala* at each conductivity level.

A two-factor ANOVA was used to examine the mean number of prey consumed at the three conductivity levels. A Tukey HSD posthoc test was used to check for significant effects of specific conductivity levels. Logistic regression analysis on proportion of prey consumed against initial prey density was used to obtain parameter estimates for low, intermediate and high specific conductivity water to determine the shape of the curve (type I, II or III). Functional response parameters were then modelled at low, intermediate and high conductivities by the Rogers random-predator equation to obtain estimates for attack rate, handling time and estimated maximum feeding rate (Juliano 2001):

$$N_e = N_0 (1 - \exp(a (N_e h - T)))$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental time available. Bootstrapping was used to generate multiple estimates (n=15) of the response parameters of attack rate a and handling time h and maximum feeding rate ($1/hT$), which were then compared in an ANOVA with a Tukey HSD post-hoc analysis.

Results

Distribution and spread in the St. Lawrence River

In the 2010 field study, *H. anomala* was detected at 15 of 17 sites sampled in the St. Lawrence River (Figure 2.3). *H. anomala* was not detected using either gear type at Repentigny and Beaconsfield, the two sites that were the most highly influenced by the Ottawa River and therefore subject to the lowest conductivity levels. *H. anomala* was present at the westernmost site sampled in the river (Lac St-François, at Bainsville, Ontario) and as far downstream as the Quebec City Old Port, 284 km from the site where *H. anomala* was first discovered in the river in 2008 (Kestrup and Ricciardi 2008). It seems unlikely that *H. anomala* was present in the river undetected for longer than a year, because areas where it is most abundant were frequently sampled for limnological studies (e.g. Kestrup 2009; Kipp 2012). Therefore, assuming it arrived in 2007, we can infer a downstream rate of spread of ~71 km/year, colonizing the entire freshwater section of the river in less than four years.

H. anomala was most abundant at the Port of Montreal site sampled in 2011, which supported a maximum density (1432.4 mysids/m^3) that is among the highest recorded for the species anywhere outside its native range. The only recorded density that is higher is at Bronte Park, in Lake Ontario (1817 mysids/m^3; Figure 2.5). The mean density in the 2010 St. Lawrence survey (14.33± 5.82 mysids/m^3) appears low compared to that of other systems (Figure 2.5), but this is likely an artefact of other field surveys having focused on ports and marinas, whose environmental conditions favour dense mysid populations.

Comparison between invaded ports in the St. Lawrence River

Of the 2096 mysids processed from Port of Montreal samples collected in 2011, 95.6% are juveniles, 2.4% are adult females (0 gravid), and 2% are adult males. The length distribution for this population of mysids appears to be bimodal (Figure 2.6), representing two distinct reproductive events. The first and second cohorts have peaks at 3 mm and 5 mm, respectively. Overall, the mean juvenile length is 4.23 mm, mean female length is 6.70 mm, and mean male length is 6.88 mm. Port of Quebec samples consisted of 2178 individuals: 90.8% juveniles, 6.2% adult females (0.1% gravid females), and 3% adult males. The three gravid females present were carrying broods containing 6 neonates, 21 embryos, and 19 embryos respectively. Mean juvenile length is 3.96 mm, mean female length is 6.88 mm, and mean male length is 8.03 mm. The size frequency distribution of the Port of Quebec population, unlike the Port of Montreal population, does not exhibit distinct peaks; however, given the span of its size range, it is likely that multiple cohorts are obscured by the combination of local reproduction and immigration of individuals from upstream populations. At the Port of Montreal the two distinct peaks represent two distinct cohorts resulting from reproduction events. Considering the comparatively low densities of populations at all sites immediately upstream of Port of Montreal, the contribution to population growth by immigration is likely very small compared to local reproduction.

The mean mysid density at the Port of Montreal 2011 site was 658.7±142.6 mysids/m^3 (range 266.7 to 1432.4 mysids/m^3). Port of Quebec had a mean density of 54.9±15.8 mysids/m^3 (range 5.9 to 266.7 mysids/m^3), which was comparable to those of a different Port of Montreal site where *H. anomala* was found at mean densities of 67.5±36.0 mysids/m^3, with a maximum of 239.3 mysids/m^3 in 2010. In 2011, *H. anomala* were collected at a site within the Port of Montreal, where densities were much higher than at the 2010 site. Data collected in 2009 by de Lafontaine et al. (2011) at both sites in Port of Montreal during the same month, suggests that this difference in densities is due to spatial (rather than temporal) variation.

Sampling Gear Efficiency

At three sites (Ile de la Paix, St. Bernard, and La Salle), *H. anomala* specimens were collected in the traps, but were not detected in net hauls (Figure 2.7 and Figure 2.8). However, the relationship between the results obtained with each gear type was positive, i.e. sites with higher relative abundances in traps also had higher densities as measured by net hauls. The correlation between average density from net haul data and average abundance from traps at the 15 sites where both gears were used was nearly significant (n=15; p=0.08; r^2=0.15) if all sites were considered, and very significant when one outlier (LaRonde) was removed (n=14; p=0.0004; r^2=0.63). The outlier was likely due to the very wavy conditions at the time of sampling which made it more difficult than normal to do net hauls.

Success of various gear type seemed to be dependent on habitat. At sites that are covered in dense macrophyte beds, net hauls often fail to detect mysids because the net rests on top of the macrophyte mat surface and does not capture the mysids inhabiting the interior. It is impractical to deploy traps at some sites, such as high traffic areas where they are likely to be tampered with, and at sites with strong local flow where they are moved by the current and sometimes lost.

Variation Across Sites

H. anomala mean and maximum densities across all sites sampled in 2010 were 14.33 ± 5.82 mysids/m^3 and 427 mysids/m^3, respectively. Between-site variation (Figure 2.7 and 2.8) was high for both densities estimated by net hauls and for relative abundances measured in traps.

Variation in *H. anomala* abundance across sites was explained by water chemistry and physical habitat characteristics. Multivariate models generated using trap data are shown in Table 2.7, 2.8 and 2.9. The best fitting models, according to the Akaike Information Criterion, were ones that retained specific conductivity, depth, distance from shore, Shoreline Heterogeneity Index and distance from Lake Ontario. While distance from shore did not have a significant p value in this model, it was retained, as suggested in Gelman and Hill (2007) because the coefficient is negative, as expected (i.e. it decreases as abundance increases) and evidence from literature strongly suggests it is important (deLafontaine et al. 2012; Fitzsimons et al. 2012; Walsh et al. 2012).

H. anomala abundance increased non-linearly with conductivity: mysids are fairly scarce until 250 µS/cm, and then their numbers increase rapidly as specific conductivity reaches 300 µS/cm, suggesting a threshold effect (Figure 2.9). Abundance declines precipitously with distance from shore (Figure 2.11), falling to zero after 2 m from shore. The effect of depth seems to have two trends (Figure 2.10). The first spike is caused by high abundances at sites where depth is 2-3 m immediately next to shore, while the second, more gradual increase is mitigated by the fact that at those sites, as depth increases, distance from shore does as well, and distance from shore is negatively correlated with relative abundances (Figure 2.9). Depth and distance from shore had a fairly low correlation (0.15), which can be explained by the fact that many of our sites have steep artificial shorelines, where it is quite deep immediately by the shore (e.g. at a port). Surprisingly, flow did not appear to be significant in any of our models; however, effects of flow were likely accounted in the SHI parameter. The higher the SHI score is, the more habitat that is sheltered from high flows on a local scale, will be available (Figure 2.12). The outlier in the SHI-abundance graph is at La Ronde, a small island, whose shape creates problems for calculating the SHI: the side of the island sampled was narrower than the standardized 2 km for the Euclidean distance used to calculate SHI, so a side of the island far from the area sampled, and with a much less heterogeneous shoreline was included in the calculations.

Distance from Lake Ontario came up as an important factor, negatively correlated with *H. anomala* abundance in the model: it was significant and lowered the AIC value. However, looking at the plot of abundances versus distance from Lake Ontario (Figure 2.13) it becomes apparent that this relationship is created by outliers (Gentilly and Port de Becancour) which had low-medium densities, but were almost twice the distance from Lake Ontario than any other site. In fact, if these sites are omitted, it appears the direction of the relationship becomes positive, although no longer significant. If more sites had been included between Pointe Marie and Port de Becancour, or if we had sampled at a dense port location downstream (e.g. Port of Quebec) this parameter would not have been significant in the model.

Results from the presence/absence analysis corroborate the implications of the relative abundance models (Table 2.10). The model with the lowest AIC score includes specific conductivity, SHI, depth, distance from shore, and local flow. Flow and distance from shore, however, are not significant ($p>0.1$). The similarity between the occurrence and abundance models suggests that most of the parameters we measured which appear to be important in our relative abundance models are threshold effects.

Functional Response in relation to Conductivity

We did not test the long-term survival of *H. anomala* in low conductivity waters, but observations of the mysids held in tanks during the functional response experiments indicated that they can survive at least 2 weeks in water as low as 110 μS/cm.

The functional response we calculated was a measure of performance, quantified by predation rate under different water chemistry conditions. ANOVA analysis revealed significant effects of conductivity and initial prey density on proportion of prey consumed (Table 2.11). Tukey HSD posthoc tests for conductivity effects indicate an overall reduction in feeding between high and low, and intermediate and low water conductivity levels, but no difference between high and low conductivities (Table 2.12). Posthoc tests were not done for main effects of prey density as densities were manipulated and the effect is an artefact of the experiment.

Logistic regressions of the proportion of prey consumed against initial prey density indicates a type II functional response curve for each conductivity level (Table 2.13, Figure 2.14), and the functional response parameters, attack rate, handling time and maximum feeding rate, as modeled by the Rogers random-predator equation are summarized in Table 2.14. Bootstrapped values of attack rate, handing time and maximum feeding rate (Table 2.15) were analyzed using ANOVA. The main effect of conductivity was significant ($p<0.001$) (Table 2.16). Posthoc Tukey HSD tests indicate a significant difference between all three levels of conductivity (high-low, intermediate-low and high-intermediate) for attack rate ($p<0.001$). Handling time and maximum prey consumed estimates were only significantly different between high and low, and intermediate and low conductivities ($p<0.001$, Table 2.17) but not between high and intermediate conductivities. The results of the experiment lend support to our predictive model's conclusion that *H. anomala* is less successful at low conductivities.

Discussion

H. anomala spread and establishment

High rates of spread and maximum densities in the St. Lawrence River that are comparable to the highest densities reported worldwide, suggest that *H. anomala* has the potential to spread and establish rapidly in lotic systems. Moreover, in rivers, upstream populations can influence abundance and population structure at downstream sites (Brittain and Eikeland 1988; Casper and Thorp 2007), as seems to be the case in the Port of Quebec. This influx of individuals, particularly juveniles, may further aid in speeding up colonization of downstream sites once *H. anomala* enters the system and reaches high densities at upstream locations. If *H. anomala* has sufficiently low mortality rates during drift, as is suggested by Van Riel et al 2011, we can expect it to spread faster throughout rivers, than in lentic systems like the Great Lakes.

H. anomala habitat preferences

H. anomala most likely arrived into the St. Lawrence River from Lake Ontario, because 1) Lake Ontario is where the first specimens of *H. anomala* in North America were detected (Walsh et al. 2010), and 2) while it has been hypothesized that the Port of Montreal may be a point of introduction (de Lafontaine et al. 2012), *H. anomala* was first detected in the St. Lawrence River about 30 km upstream of the port (Kestrup and Ricciardi 2008, de Lafontaine et al. 2012). However, only three years after invasion, site to site variation in abundance of *H. anomala* seems better explained by local environmental variables than proximity to the Lake Ontario source population. It is probable that proximity to Lake Ontario would have been a significant predictor much earlier in the invasion, before dense local populations established throughout the river.

The most important predictors for presence and abundance of *H. anomala* among the ones we measured, at a site scale are specific conductivity and the Shoreline Heterogeneity Index. *H. anomala* is not likely to be successful at establishing dense populations at sites where specific conductivity is lower than 200µS/cm. The Shoreline Heterogeneity Index is an indicator of the quantity of micro-habitat available to *H. anomala* for refuge from currents that would otherwise flush it downstream (Archambault and Bourget 1996). More complex shorelines allow *H. anomala* populations to become established locally and remain at that particular site. Conversely, stretches of the river where the shoreline is fairly smooth and there are few or no inlets, are not expected to support dense local populations. Local flow did not appear to be significant in any of our models; however, in the St. Lawrence, local flow is very variable on the small scale (1 - 5 m) relevant for *H. anomala*, which can be difficult to measure, particularly from a boat (personal observation). On a large scale, effects of flow are accounted for in the SHI parameter: increased SHI scores will decrease negative effects of high flow on *H. anomala* abundance because high SHI scores indicate that areas of locally low flow are present where *H. anomala* can become entrained. Moreover, because flow aids downstream drift of *H. anomala* (Van Riel et al. 2011), on a large scale, we could expect that increased flow will flush more individuals into the area, and if the shoreline is complex enough to entrain them, increased flow will actually be positively correlated with abundance.

On a smaller scale, the best predictors of *H. anomala* presence and abundance within a site are depth and distance from shore. A previous study in the Shannon River (Ireland) reported that depth was negatively related with *H. anomala* abundance (Minchin and Boelens 2010); however, they did not consider proximity to shore as a factor. In fact, it is likely that the low abundances at the very deep sites are driven by those sites being very far from shore, rather than the depth itself. In the St. Lawrence River, *H. anomala* seems to congregate at locations where depth drops at least ~2 m very close to shore (within 1 to 2 m from shore). This is why *H. anomala* is often found in ports where there are vertical walls, and depths are above 2 m. Shoreline slope and presence of artificial structure were not strong enough predictors to be included in our model, possibly because there are numerous sites where the shoreline is artificial, with vertical cement walls, that are also very shallow. Ultimately depth next to shore seems to be more important than presence of a steep shoreline itself.

Macrophyte cover does not appear to be related to presence or abundance of *H. anomala*; however, it is possible that both our gear types were biased against catching representative numbers of *H. anomala* in dense macrophyte beds. Sites like Ile de La Paix, where nearly the entire site bottom was covered in dense macrophyte beds, meant that the zooplankton net was not able to sample the water column; the net would rest on top of the macrophyte bed, 0.5-1 m below the water surface, unable to capture the mysids taking shelter below. Traps did capture some *H. anomala* at these sites; however, as the entire habitat is sheltered by the plants, the black funnel would not have attracted the mysid in the same way it does in areas with no macrophyte cover, giving us a lower relative estimate of abundance. Alternately, it is possible that effects of macrophyte cover are confounded by effects of depth and distance from shore: all of our sites with very dense macrophyte cover were quite shallow near shore.

Despite expectations that substrate size would be important for *H. anomala* because of the interstitial spaces formed by larger sediment, which *H. anomala* is hypothesized to use as daytime refuge from visual predators (Kelleher et al. 1999), we did not find any significant effects of substrate size on abundance or presence of *H. anomala*. At the sites which had highest abundances, like Port of Montreal or La Ronde, areas where substrate was fine supported dense *H. anomala* populations, thanks to the complexity of the walls along the shoreline which provided refuge areas (Ketelaars et al. 1999) even if the substrate itself did not. A recent study (Claramunt et al. 2012) suggests that, rather than having a preference for larger substrates, *H. anomala* is associated with quality of interstitial spaces, which is a function of substrate size and shape. The optimal substrate identified by that study is uniformly rounded rocks approximately 9 cm in diameter. These characteristics allow the substrate to provide more tightly-packed interstitial spaces that provide higher quality refuge and they would be a better factor to include in a predictive model than a continuous measure of sediment size.

Effects of conductivity on *H. anomala*

Our predictive model suggests that areas with low conductivity will not support dense populations of *H. anomala* and the two sites that were below our detection limits are among the lowest water conductivity areas sampled. We addressed the issue of differential propagule pressures between the St. Lawrence and the Ottawa rivers, which could have confounded the relationship between water specific conductivity and *H. anomala* abundance, by running functional response experiments at three different water conductivity levels, representative of the water chemistry conditions found in the areas we sampled. Functional responses are a unique way of looking at performance (Bollache et al. 2008). The significantly lower functional response of *H. anomala* at low conductivity levels, compared to intermediate and high conductivities corroborates our predictive model's conclusion that *H. anomala* are less successful at low than at intermediate and high conductivities. Intermediate and high conductivity results were not significantly different from each other suggests that conductivity is a threshold effect, which is further supported by the presence/absence model results which indicate that conductivity is important for determining occurrence.

These results do not mean that *H. anomala* is not capable of invading low conductivity sites. For example, it is able to survive in Ottawa River water with conductivity as low as 110µS/cm for at least two weeks (personal observation). However, we do not expect it to become established and form dense local populations at those sites. Long-term exposure effects of low Specific Conductivity on survivorship and reproductive capability have not been tested, but our experiments show that performance in terms of predatory ability is compromised. This is consistent with other Ponto-Caspian species, like *Echinogammarus ischnus* (Kestrup and Ricciardi 2009) and *Dreissena polymorpha* (Jones and Ricciardi 2005), which are limited by ion-poor water. *E. ischnus* also showed decreased functional response in low conductivity waters in experiments using a similar methodology to ours (Kestrup and Ricciardi 2009). *E. ischnus* predation rates on the native *Gammarus fasciatus* is decreased in lower conductivity waters, which hampers its competitive ability in respect to the native gammarid and has thus far prevented it from establishing dense populations at low conductivity sites.

Specific Conductivity is representative of the relationship between ion-poor waters and Ponto-Caspian invaders in the section of the St. Lawrence River we sampled, however concentration of calcium ions may be a more metabolically-relevant parameter (e.g. Hessen et al. 1999, Vanderploeg et al. 2002). Disentangling effects of specific conductivity from effects of calcium may be significant in areas where the two are not correlated, for example in areas that have a high magnesium ion concentration. The implication of the relationship between *H. anomala* density and calcium has meaningful consequences for potential limits to its spread to inland lakes on the Canadian Shield, which are being depleted of calcium (Jeziorski, A., N. D. Yan, et al. 2008).

Sampling Gear comparison

Net hauls are a poor method of estimating low abundances, such as those encountered in the early stages of an invasion and in sub-optimal habitats. Furthermore, owing to the dynamic patchy distribution of mysids, single net hauls are more likely to yield zeroes than benthic traps left for periods of time. Similar conclusions were reached by Claramunt et al. (2012) who detected *H. anomala* using passive benthic traps, with "egg funnels" originally meant to sample fish eggs during spawning, in an area where net haul surveys failed to capture them. One advantage of employing bucket traps instead of egg funnels is that no diving is required, as they can be easily deployed and retrieved from a boat.

Net haul data, however, are important for estimating density levels, since traps are a passive capture method and can only yield information about relative abundance between sites. There are also areas where it is unfeasible to sample with traps, for example, busy ports, or areas with exceptionally high currents, where traps are likely to be lost. In these cases, net hauls may be the best method for sampling *H. anomala,* with the understanding that their detection limits are inferior. Net hauls also yield much larger samples, per unit effort; therefore, if the aim is to obtain large numbers of *H. anomala* for analysis, from sites that are densely populated, net hauls are a more appropriate choice.

Caveats to interpretation

While we identified some important factors that help us explain and predict *H. anomala* spread and abundances, we did not measure every possible parameter, and some of the ones we left out may have large effects, limiting our predictive power if we do not expand our model. For, example, we did not include any biotic effects, and these should be tested and included in future models. Relevant parameters that could limit *H. anomala* are availability of food, presence of competitors and predation pressure. Variables to be measured could include Chlorophyll-a concentration, zooplankton and fish abundances and community compositions. A recent study (Marty et al. 2012) found that *H. anomala* diet, while omnivorous, is very site-dependent in terms of quality. This suggests that quality of food available at a site may affect *H. anomala* growth and reproduction, potentially limiting its local abundance and spread.

Moreover, our study is just a snapshot of *H. anomala* populations in the St. Lawrence during a few months in 2010. Other papers have identified the importance of characterizing temporal variability within sites, as abundance and population structure change between seasons (Nunn and Cowx 2012).

Conclusion

Studies of *H. anomala* spread in North American lentic systems showed that its tolerance to a broad range of environmental conditions allowed it to spread quickly and colonize all the Great Lakes except Lake Superior (Walsh 2010), including nearly the entire shoreline of Lake Ontario (Marty 2009), and inland lakes, like Lake Oneida (Walsh 2009). This study demonstrates *H. anomala*'s high capacity for rapid spread throughout a lotic system, the St. Lawrence River. If management measures are not put in place, we can expect *H. anomala* to spread relatively rapidly throughout large North American rivers, like the Illinois River which flows out of Lake Michigan and into the Mississippi, if environmental conditions in these systems can support local populations.

Our results show that the invasion success of *H. anomala* populations is highly context-dependent. We identified site-specific variables that explain the distribution and abundance of *H. anomala* within a large river: specific conductivity and the Shoreline Heterogeneity Index predict between-site variation, and depth and distance from shore predict where it is most likely to be found within a site. As the St. Lawrence is the first large river to be invaded in North America, these results provide predictive information for other large rivers on the continent, at risk of future invasions. In particular they provide guidance as to where monitoring efforts are most likely to detect incipient populations early in the invasion.

Tables

Table 2.1 Physico-chemical variables hypothesized to explain variation in the local distribution and abundance of *H. anomala* in large rivers.

Variable	**Prediction**	**Rationale**	**Reference**
Conductivity	Low densities in low conductivity areas	Evolutionary history is in an ion-rich environment. Other Ponto-Caspian invaders' spread is limited by low conductivity waters.	Kestrup, Å. and A. Ricciardi (2009)
Shoreline Heterogeneity Index (SHI)	Higher densities are expected in areas with high shoreline heterogeneity	Shorelines with higher heterogeneity indices provide more complex habitat for *Hemimysis* swarms to take shelter in. Studies done on invertebrates show a correlation of invert abundance and diversity with higher SHI.	Archambault and Bourget (1996)
Flow	Areas with high local flow are not expected to support high densities of *Hemimysis*	Mysids have a limited ability to swim against current, and areas high in local flow will likely flush out populations of *Hemimysis* from the area.	Wittman et al. (2008)
Shoreline Slope	Steep shorelines are expected to be correlated with high *Hemimysis* densities	Literature reports that *Hemimysis* were found near steep concrete walls.	Pothoven et al. (2007)
Distance from	*Hemimysis* are expected in higher	Literature and preliminary studies suggest that densities drop	Taraborelli et al.

shore	densities closer to shore.	off with increasing distance from shore. It is possible that there is more shelter near the shore than off shore.	(2012)
Presence of Artificial Structure	*Hemimysis* are expected to be associated with the presence of artificial structures.	*Hemimysis* have been found in large densities at sites with vertical concrete walls sheltered from currents (e.g. marinas).	Pothoven et al. (2007)
Vegetation	*Hemimysis* are expected to be abundant in areas with dense vegetation	*Hemimysis* have been reported to present in vegetated areas, which may be acting as a refuge from predators.	Minchin and Holmes (2008)
Depth	*Hemimysis* are expected to be found in higher densities at greater depths	*Hemimysis* are light sensitive and in near-shore areas, deeper sites provide more refuge from light and predators than shallower sites.	Boscarino et al. (2012)
Sediment Size	*Hemimysis* abundance is expected to increase with increasing sediments size	*Hemimysis* has been reported to favour areas with sediment that is cobble or larger over sand or clay because the former provides interstitial spaces for refuge.	Claramunt et al. (2012)
Distance from L. Ontario	Distance from L. Ontario is not going to be associated with *Hemimysis* density	We expect that local variables will be more significant in determining *Hemimysis* abundances than distance from their most likely source population.	-

Table 2.2 Parameters measured in the habitat survey.

Parameter	**Gear**	**Method**
Geographic coordinates	Garmin Handheld GPS unit	Digital reading
Depth	WildCo Depth Meter	Digital reading
Distance from shore	Laser distance meter	Digital reading, and visual estimate for short (<10m) distances
Local Flow	Mechanical Flow Meter	Meter reading
Specific Conductivity	YSI probe	Digital reading
Dissolved Oxygen	YSI probe	Digital reading
Temperature	YSI probe	Digital reading
Secchi Depth	Secchi Tube	Secchi tube reading
Substrate Size	Petite Ponar Grab	Visual assessment
Macrophyte cover	N/A	Visual assessment
Shoreline type	Digital camera	Visual assessment
Presence of artificial structure	N/A	Visual assessment

Table 2.3 Macrophyte cover variable classification. Percent cover categories from Brousseau et al. 2005.

Variable	Percent Cover	Description
0	0.00%	none
1	1-19%	sparse
2	20-69%	moderate
3	70-89%	dense
4	90-100%	very dense

Table 2.4 Shoreline slope categories and the corresponding slope (in degrees).

Variable	Description
0	Flat beach (0º-10º)
1	Gentle slope (11º-30º)
2	Medium slope (31º-50º)
3	Steep slope (51º-80º)
4	Vertical wall (81º-90º)

Table 2.5 Values (mm) corresponding to substrate categories are from Valere (1996). Φ= -log2 (particle diameter).

Substrate category	Diameter (mm)	Phi value (Φ)
Clay	<0.0039	9
Silt	0.0039-0.0625	4.91
Sand	0.0625-2	-0.04
Gravel	2 – 16	-3.17
Pebble	16-64	-5.32
Cobble	64-256	-7.32
Boulder	256-300	-8.12
Bedrock	>300	-10.67

Table 2.6 Environmental conditions (Dissolved Oxygen in mg/l and %, Temperature, Specific Conductivity, Salinity, Depth, Date and Time) at time of sampling at Port of Montreal and Port of Quebec.

Site	DO mg/l	DO %	Temp ˚C	SCond µS/cm	Sal ppt	Depth m	Date	Time
Port of Montreal	10	115.1	19.6	257.2	0.1	9	26/09/2011	21h-23h
Port of Quebec	8.93	94.8	18.6	232.4	0.1	6	25/09/2011	20h-22h

Table 2.7 Results of Multivariate Model 1, AIC= 362.7

Variable	Coefficient	Standard Error	p-value
Specific Conductivity (large scale)	0.021	0.006	0.0003**
Depth (local scale)	0.718	0.141	3.16e-07**
Distance from shore (local scale)	-0.015	0.009	0.114
SHI (large scale)	0.998	0.281	0.0004**
Distance from L. Ontario (large scale)	-0.009	0.004	0.0399*

Table 2.8 Results of Multivariate Model 2, AIC= 364.8

Variable	Coefficient	Standard Error	p-value
Specific Conductivity (large scale)	0.020	0.006	0.0007**
Depth (local scale)	0.830	0.142	5.14e-09**
SHI (large scale)	1.237	0.279	9.20e-06**
Distance from L. Ontario (large scale)	-0.010	0.005	0.0225*

Table 2.9 Results from Multivariate Model 3, AIC= 365.1

Variable	**Coefficient**	**Standard Error**	**p-value**
Specific Conductivity (large scale)	0.023	0.0058	0.0001**
Depth (local scale)	0.618	0.135	3.50e-06**
Distance from shore (local scale)	-0.0177	0.009	0.0775
SHI (large scale)	0.81	0.261	0.0018**

Table 2.10 Model with the lowest AIC for Presence/Absence data

Variable	**Coefficient**	**Standard Error**	**p-value**
Specific Conductivity (large scale)	0.015	0.005	0.0006**
Depth (local scale)	0.521	0.162	0.001**
Distance from shore (local scale)	-0.011	0.007	0.12
SHI (large scale)	0.792	0.236	0.0008**
Local flow (local scale)	-0.297	0.182	0.10

Table 2.11 Summary table of ANOVA analysis testing effects of Conductivity, Initial Prey density and their interaction on proportion of prey consumed.

Parameter	Df	Sum Sq	Mean Sq	F value	p
Conductivity	2	678.16	339.08	14.1767	<0.001
Initial Prey density	1	265.84	265.84	11.1147	<0.01
Conductivity * Initial Prey density	2	7.38	3.69	0.1542	0.857342
Residuals	84	2009.11	23.92		

Table 2.12 Tukey HSD posthoc test results for conductivity

Comparison	Difference	Lower	Upper	p
intermediate-high	-0.9333333	-3.946199	2.079533	0.74
low-high	-6.2333333	-9.246199	-3.220467	<0.001
low-intermediate	-5.3000000	-8.312866	-2.287134	<0.001

Table 2.13 Parameter estimates (and significance levels) from second-order logistic regression analyses of proportion of prey consumed against initial prey density. Values for intercept, first order (N0) and second order terms (N20) are presented with p values.

Conductivity	**Intercept** **(*p* value)**	N_0 **(*p* value)**	N^2_0 **(*p* value)**	**Functional response**
110 µS/cm	-9.835e-01 (<0.001)	-2.531e-02 (<0.001)	7.961e-05 (NS)	II
214 µS/cm	1.858e+00 (<0.001)	-8.013e-02 (<0.001)	3.565e-04 (<0.001)	II
307 µS/cm	1.257e+00 (<0.001)	-4.590e-02 (<0.001)	1.387e-04 (<0.001)	II

Table 2.14 Functional response parameters at low, intermediate and high conductivities as modelled by the Rogers random-predator equation. (a = attack rate, h = handling time, 1/ht = estimated maximum feeding rate.)

Conductivity	**a**	**h**	**1/ht**
110 µS/cm	0.409698	0.132793	0.6275431
214 µS/cm	4.7022638	0.0816978	1.020019
307 µS/cm	3.2864393	0.0673667	1.237011

Table 2.15 Bootstrapped functional response parameters at low, intermediate and high conductivities as modelled by the Rogers random-predator equation. (a = attack rate, h = handling time, 1/ht = estimated maximum feeding rate. Means presented with standard errors

Conductivity	**a**	**h**	**1/ht**
110 µS/cm	0.476 ± 0.049	0.134 ± 0.006	0.644 ± 0.033
214 µS/cm	4.957 ± 0.292	0.085 ± 0.0025	0.998 ± 0.0308
307 µS/cm	3.676 ± 0.285	0.076 ± 0.003	1.119 ± 0.041

Table 2.16 ANOVA analysis testing for conductivity effects on bootstrapped functional response parameters

	DF	**Sum Sq**	**Mean Sq**	**F value**	**p**
Attack rate					
Conductivity	2	0.029230	0.0146149	54.557	<0.001
Residuals	42	0.011251	0.0002679		
Handling time					
Conductivity	2	0.029230	0.0146149	54.557	<0.001
Residuals	42	0.011251	0.0002679		
Maximum feeding rate					
Conductivity	2	1.82832	0.91416	49.254	<0.001
Residuals	42	0.77953	0.01856		

Table 2.17 Tukey HSD posthoc test results for differences in attack rate, handling time and maximum estimated feeding rate between the three conductivity levels.

Comparison	**Difference**	**Lower**	**Upper**	**p**
Attack Rate				
int-high	1.281585	0.4657873	2.097383	<0.01
low-high	-3.199951	-4.0157490	-2.384154	<0.001
low-int	-4.481536	-5.2973339	-3.665739	<0.001
Handling time				
int-high	0.00861776	-0.005901999	0.02313752	0.329
low-high	0.05785587	0.043336116	0.07237563	<0.001
low-int	0.04923812	0.034718357	0.06375787	<0.001
Maximum feeding rate				
int-high	-0.1216800	-0.2425380	-0.0008219358	0.048
low-high	-0.4752399	-0.5960979	-0.3543818248	<0.001
low-int	-0.3535599	-0.4744179	-0.2327018387	<0.001

Figures

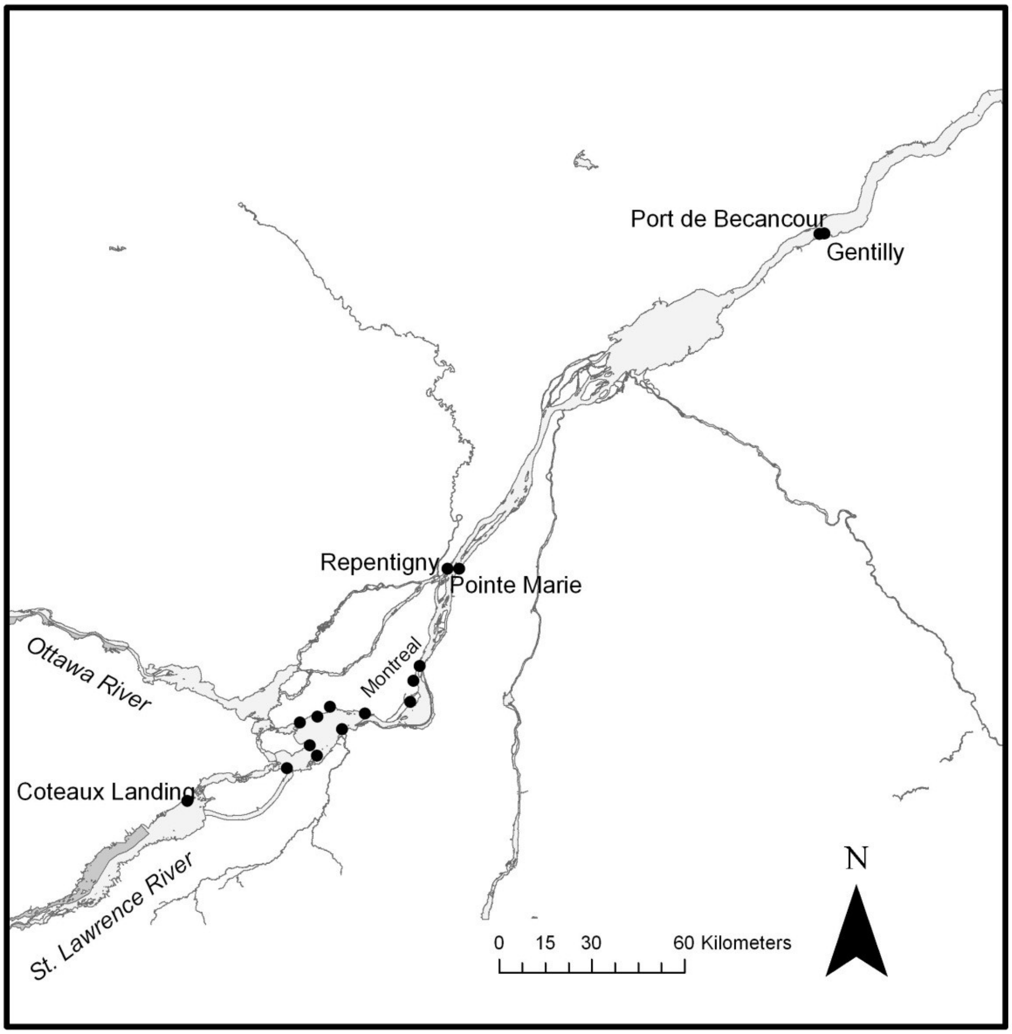

Figure 2.1 Map of sites sampled in the St. Lawrence River in 2010.

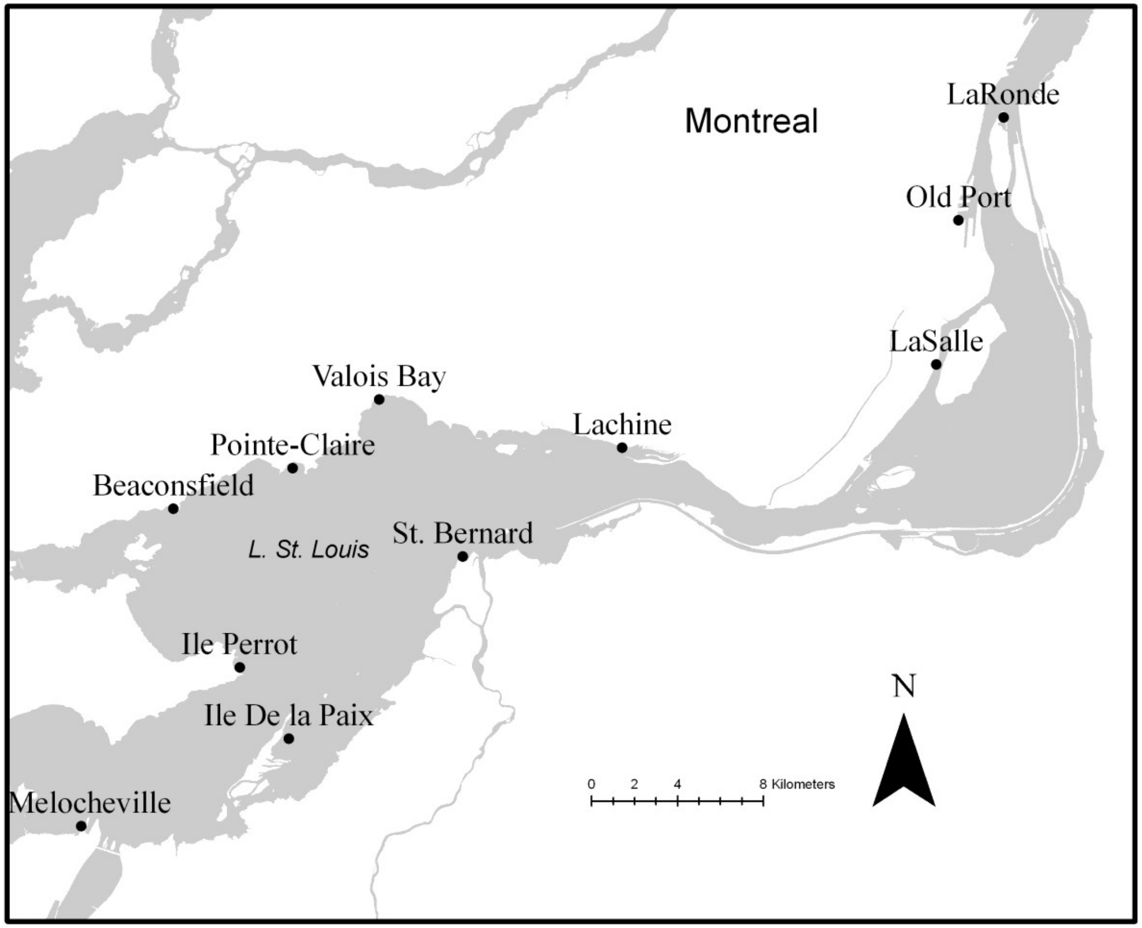

Figure 2.2 Map of sites around Lac-St. Louis sampled in the St. Lawrence in 2010.

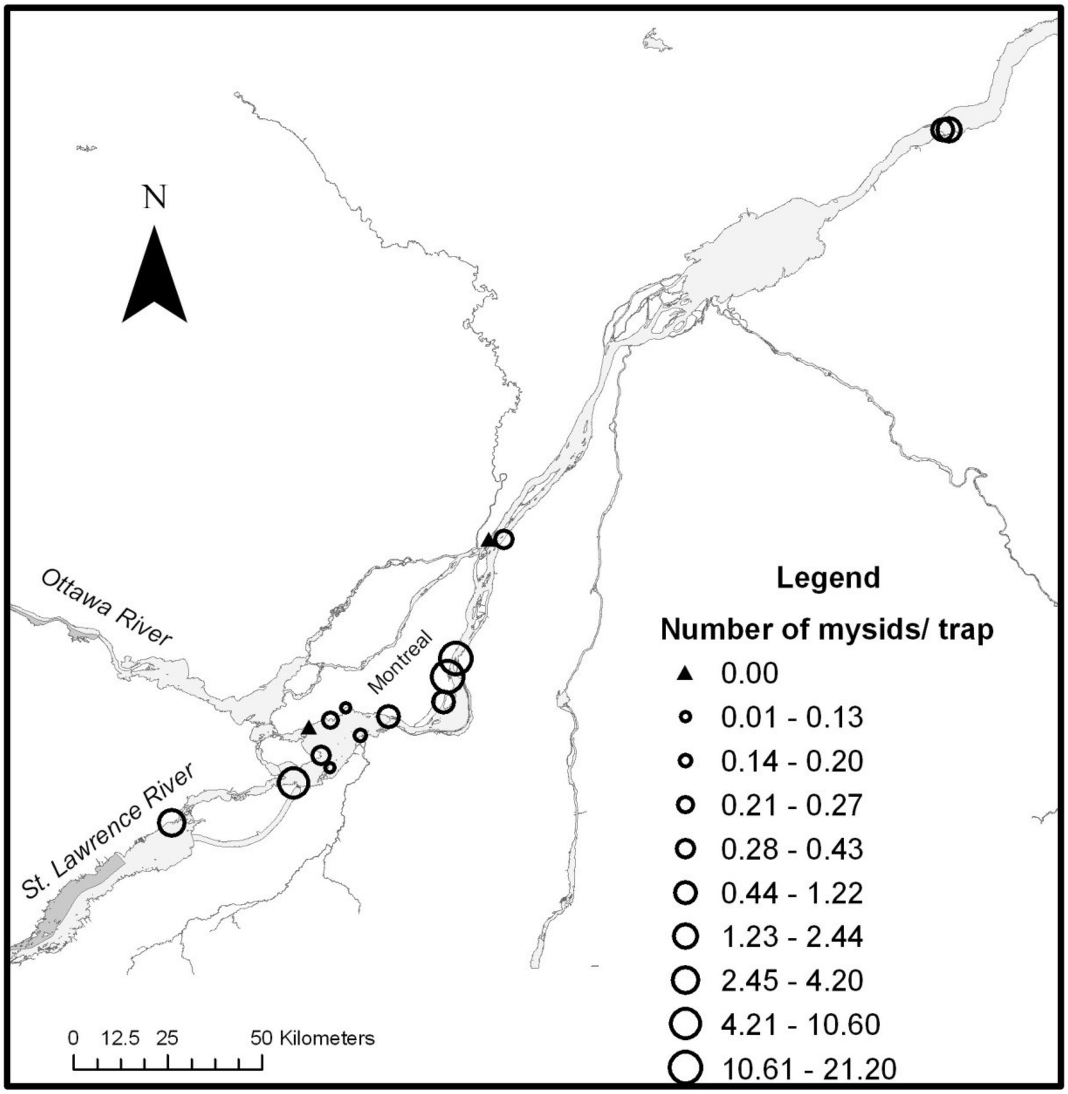

Figure 2.3 Map with mean number of *H. anomala* per trap at each site sampled in 2010.

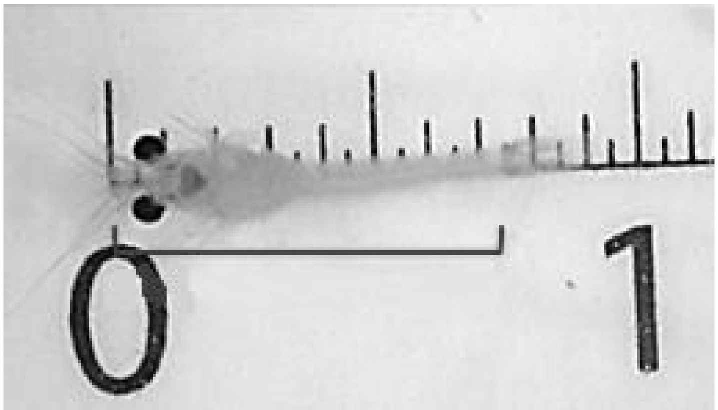

Figure 2.4 Measuring *H. anomala* lengths: from the carapace to the telson.

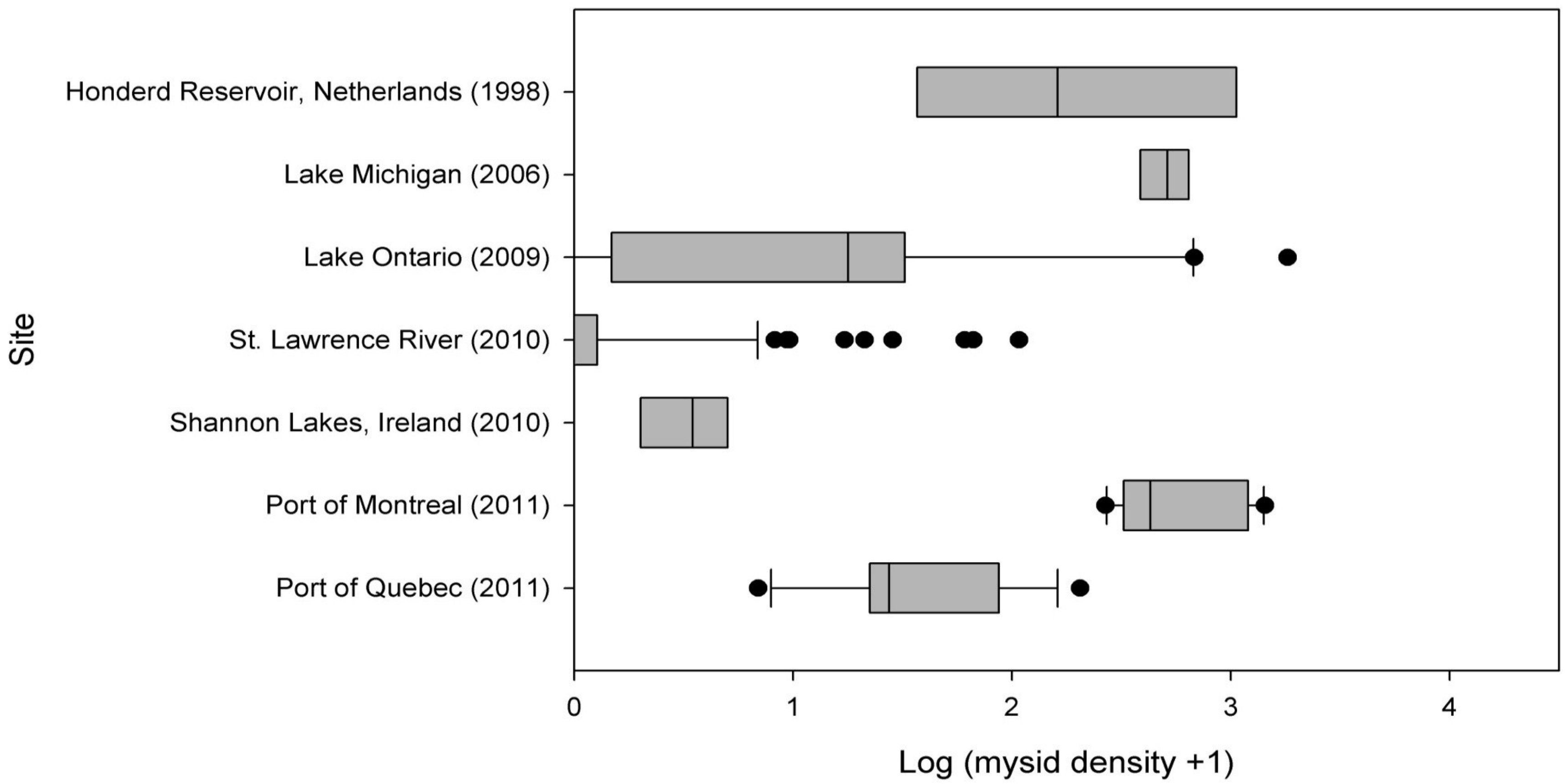

Figure 2.5 Density of *H. anomala* across reported at various sites in Europe and North America. Data sources*:* Honderd Reservoir (Ketelaars et al. 1999); Lake Michigan (Pothoven 2007); Lake Ontario (Taborelli et al, 2011); Shannon Lakes (Minchin and Boelens, 2010).

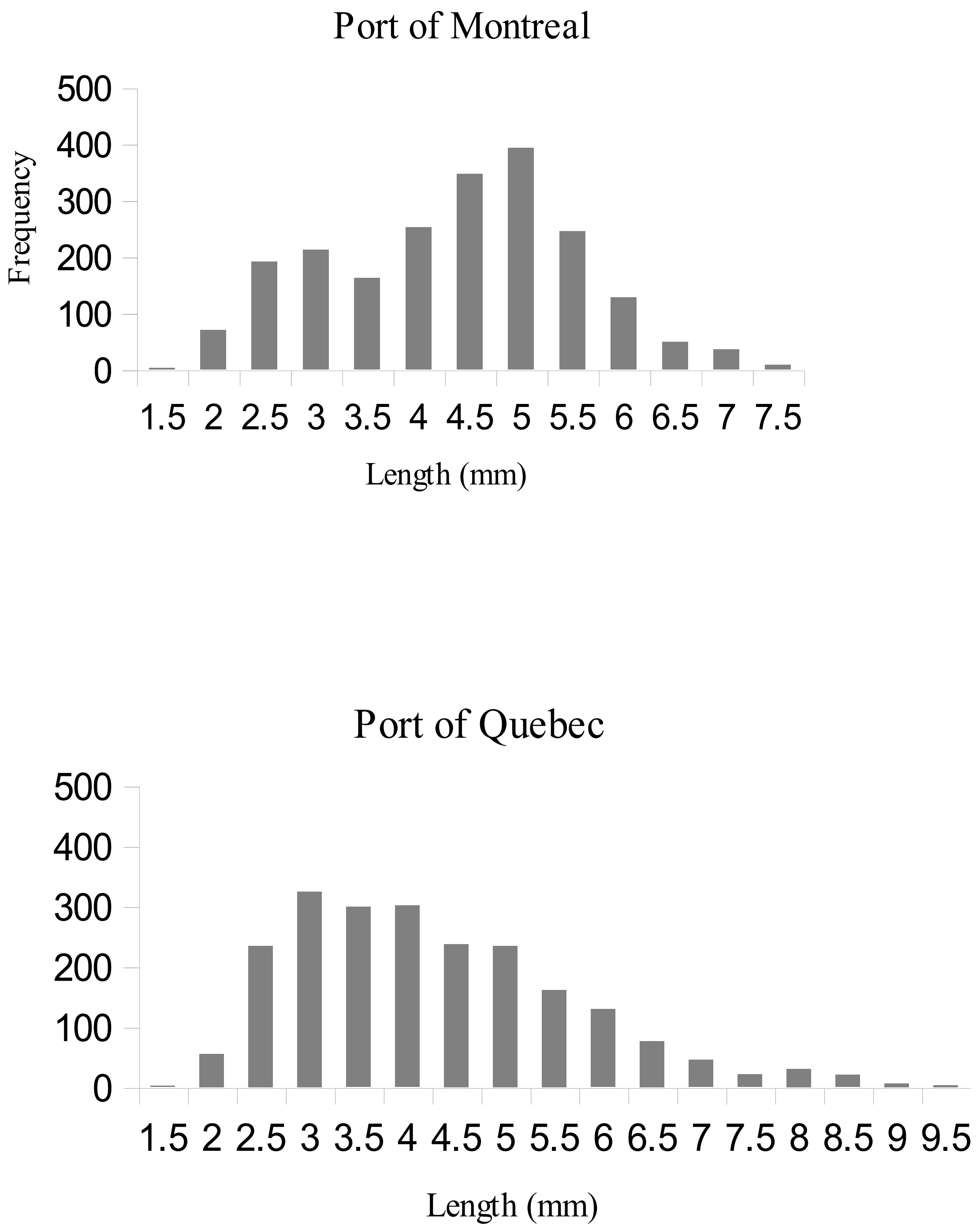

Figure 2.6 Length-frequency distribution of *H. anomala* at Port of Quebec and Port of Montreal in November 2011.

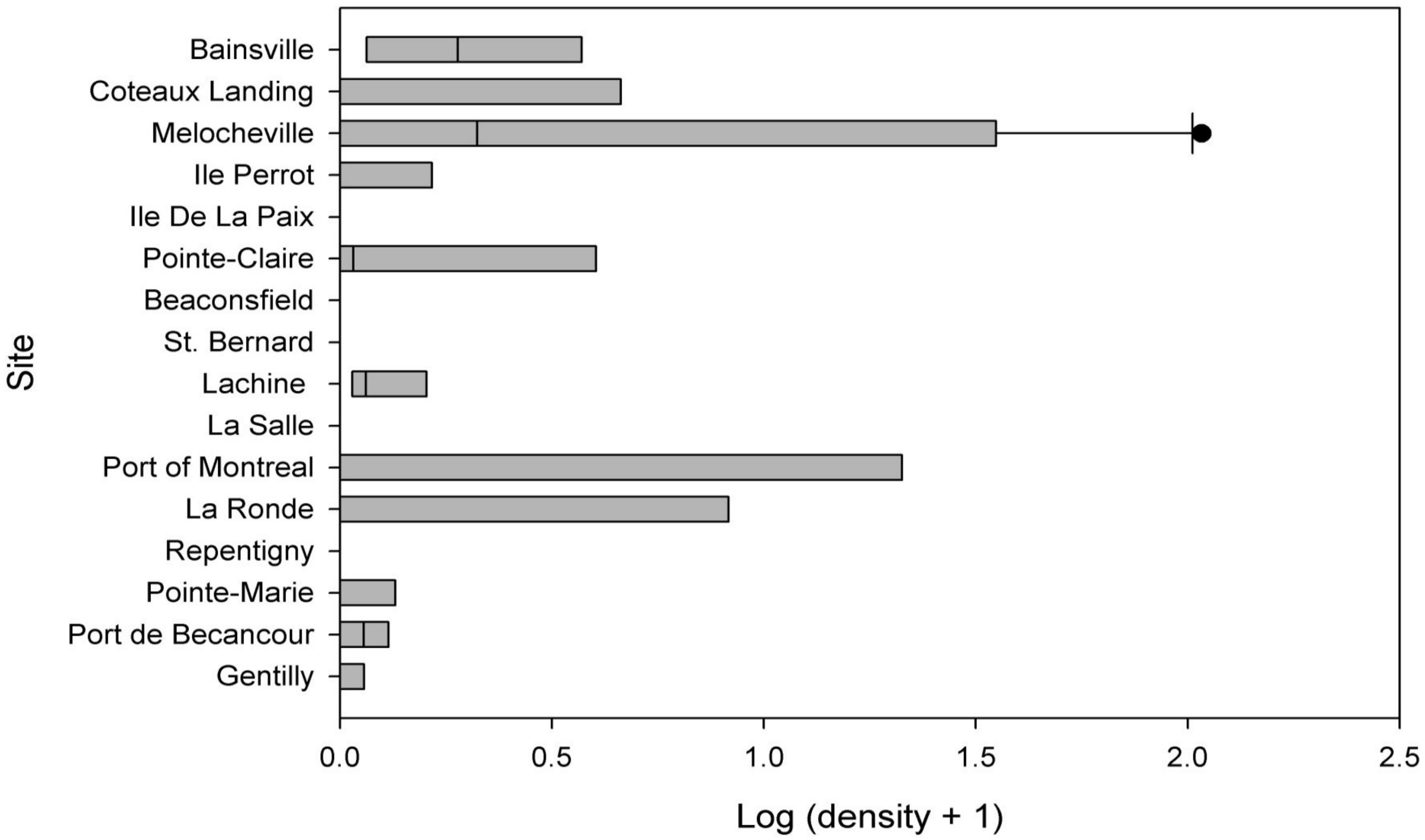

Figure 2.7 Density of *H. anomala* (estimated from net hauls) across sites in the St. Lawrence River. Sites, listed from top to bottom, are in order of increasing distance from Lake Ontario.

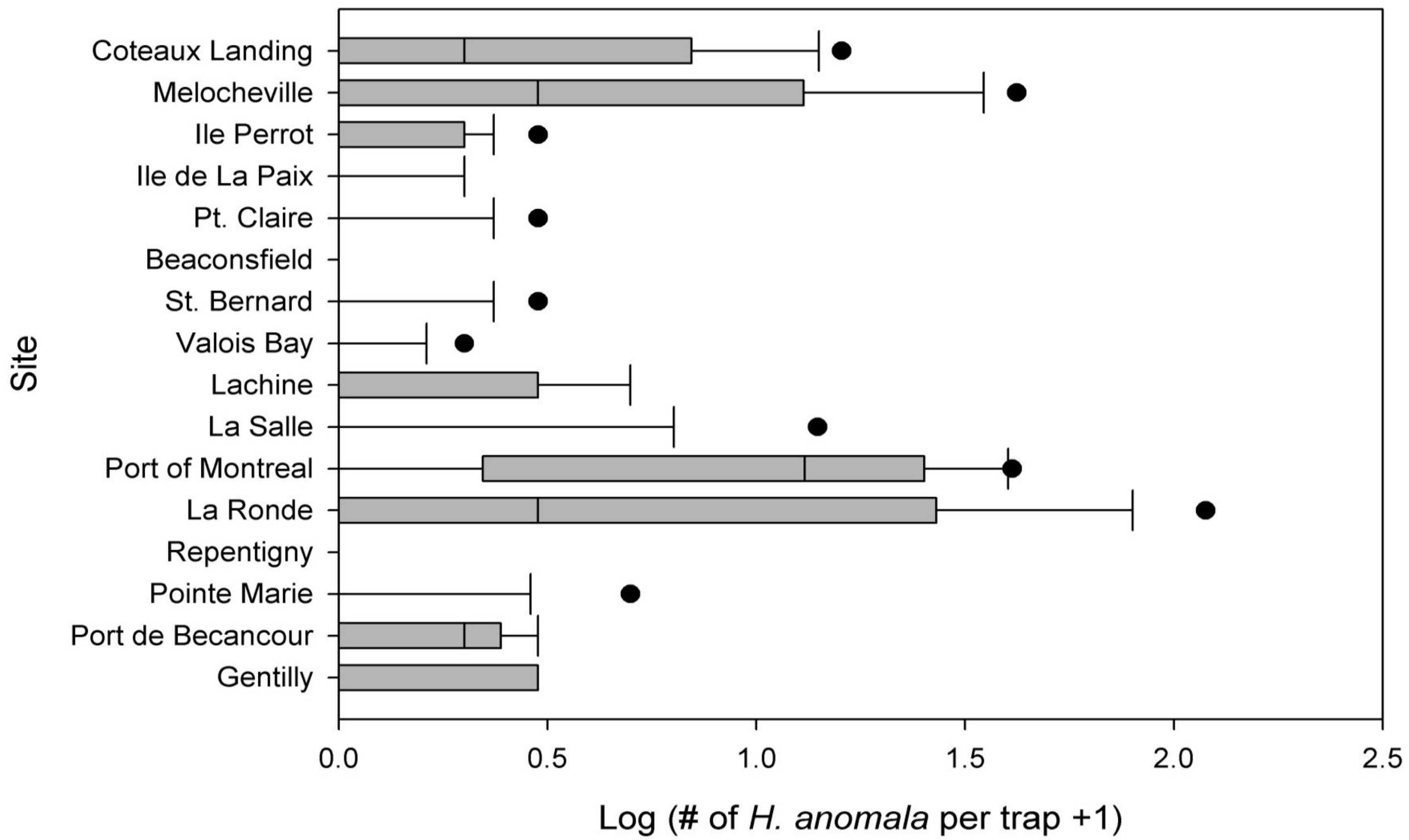

Figure 2.8 Relative abundances of *H. anomala* (determined from trap samples) across sites in the St. Lawrence River. Sites, listed from top to bottom, are in order of increasing distance from Lake Ontario.

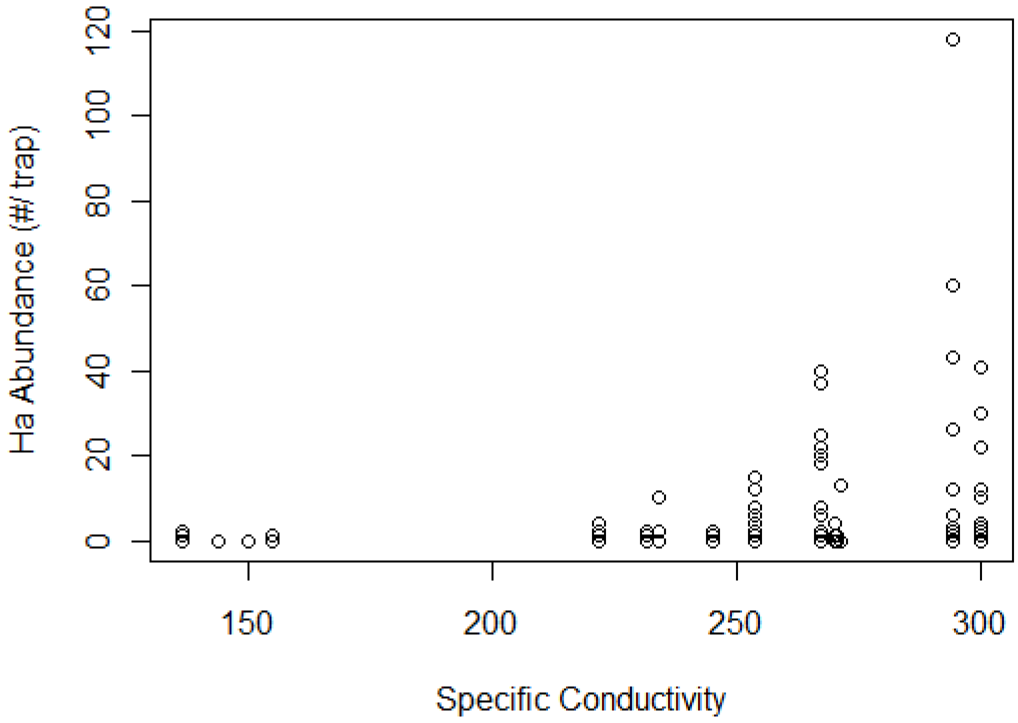

Figure 2.9 Relative abundances of *H. anomala* in traps plotted versus Specific Conductivity (µS/cm)

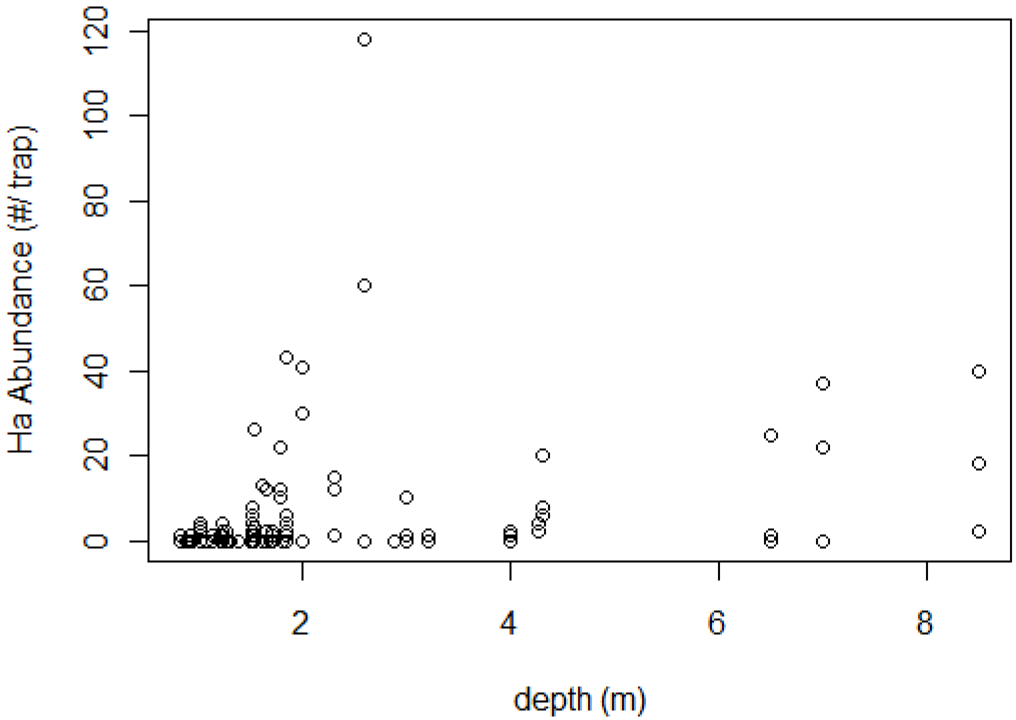

Figure 2.10 Relative abundances of *H. anomala* in traps plotted versus depth (m).

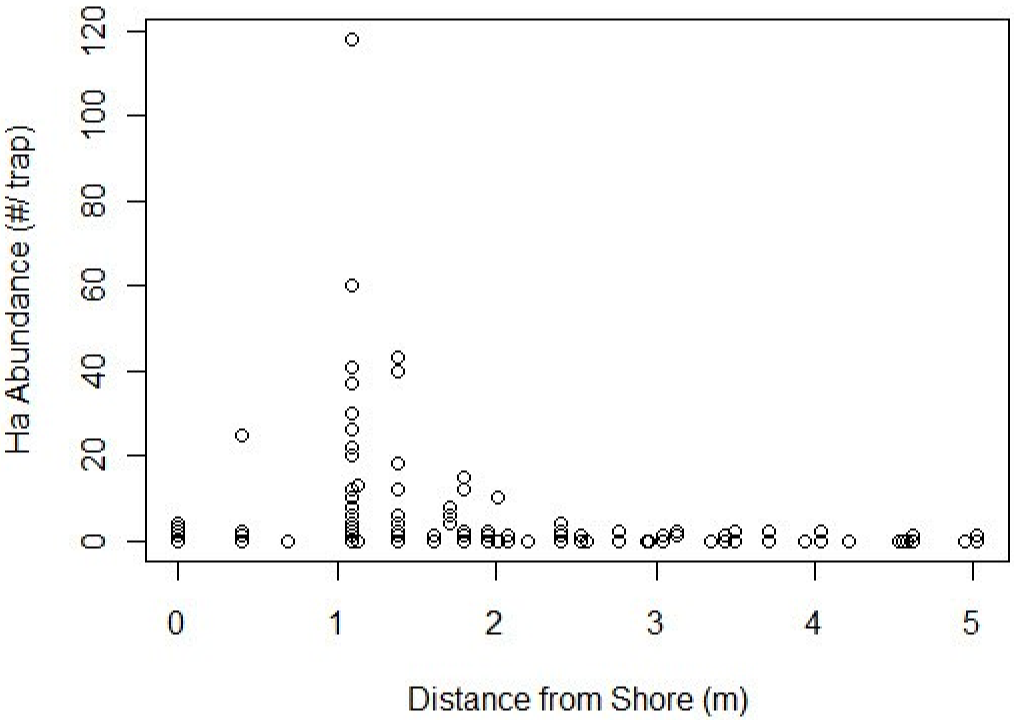

Figure 2.11 Relative abundances of *H. anomala* in traps plotted versus distance from Shore (m).

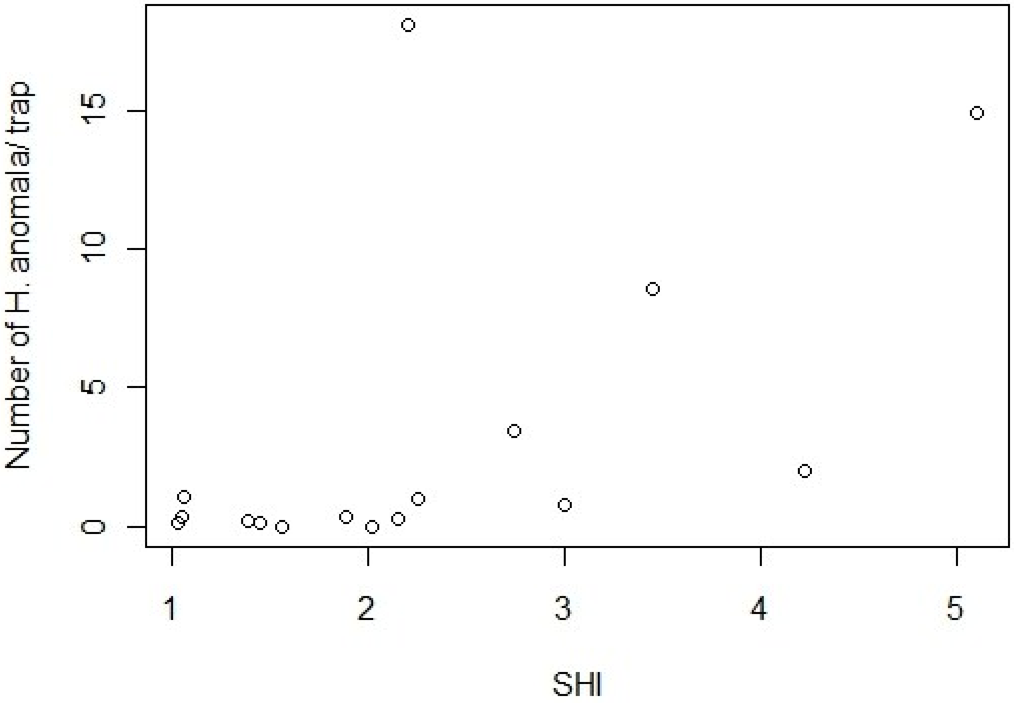

Figure 2.12 Relative abundances of *H. anomala* plotted versus Shoreline Heterogeneity Index score.

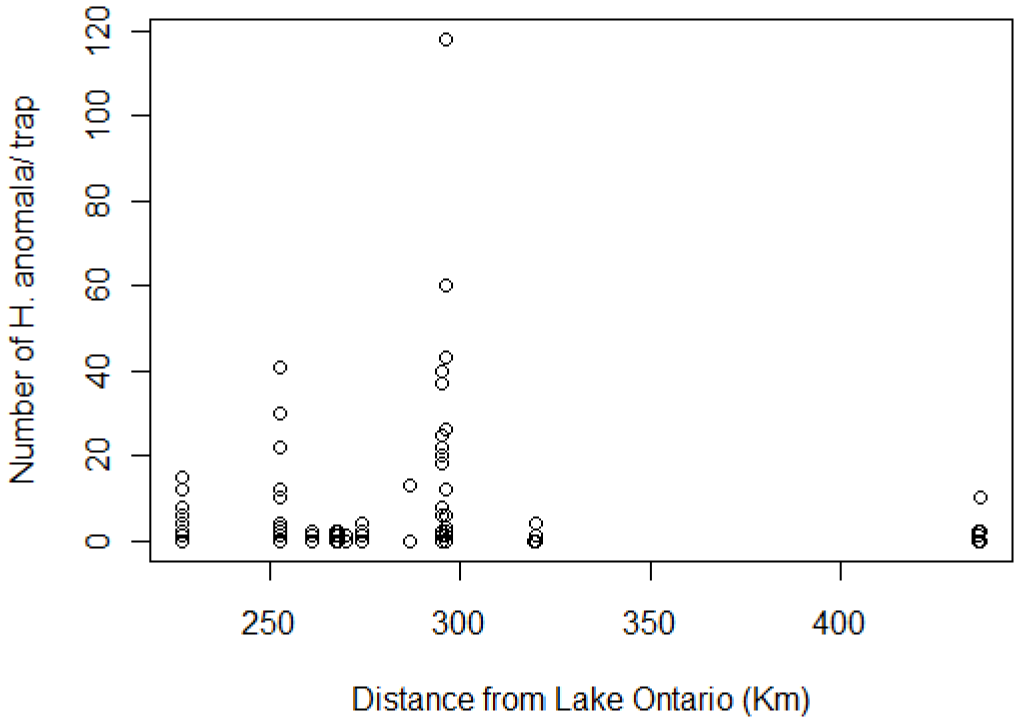

Figure 2.13 Relative abundances of *H. anomala* plotted versus distance from Lake Ontario (in km).

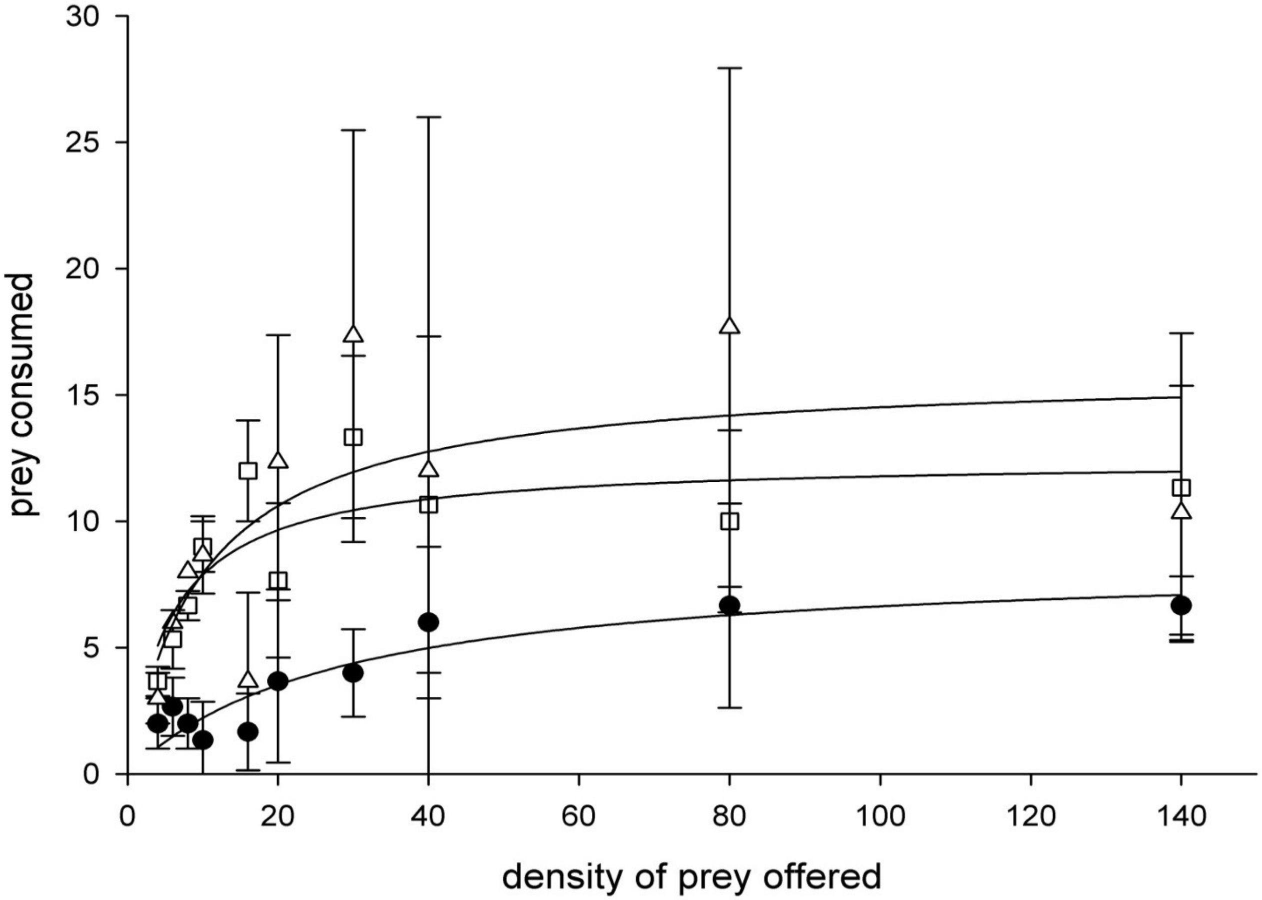

Figure 2.14 Functional Response of *H. anomala* as measured across three levels of conductivity (● 110µS/cm , □ 214µS/cm and Δ 307µS/cm)

General Conclusion

There is a lot of evidence that *H. anomala* has the potential to negatively affect invaded ecosystems. Studies comparing invertebrate communities pre and post-*H. anomala* invasion indicate changes in zooplankton species composition and relative abundance after introduction of the mysid (Ketelaars et al 1999); experimental comparisons of functional responses between *H. anomala* and other highly disruptive invasive freshwater mysids show that *H. anomala* has higher predation rates (Dick et al, in review), and recent surveys found the mysid in high densities in areas of prime Lake Trout spawning habitat where it is likely to compete for resources with juvenile fish (Claramunt et al 2012).

If we hope to develop successful management strategies to prevent or minimize *H. anomala* impacts, it is essential to have an effective surveillance programme (Britton et al 2011). Ideally, we should be able to detect *H. anomala* before it establishes self-sustaining populations (Nunn and Cowx 2012) because once a dense population is established, they spread quickly to other sites (Claramunt et al. 2012), aided by flow regimes in lotic habitats, where spread upwards of 71 km/year has been recorded.

Monitoring should be conducted with an appropriate gear type for the particular habitat being sampled (e.g. benthic traps rather than nets in shallow or macrophyte-covered sites) to avoid underestimating invader abundances due to gear biases. Sites for monitoring and the location sampled within each site must be selected with care. Based on our current knowledge, monitoring in large rivers should be prioritized at sites with the following characteristics: high Shoreline

Heterogeneity Index, where *H. anomala* is likely to become entrained, and where the specific conductivity of the water is above 200 µS/cm. Within the sites, sampling should be concentrated close to shore (within 2 m), and in sections of the shoreline that are deepest. Considering the rapid spread of *H. anomala* throughout the Great Lakes and into the St. Lawrence River, sampling programs should be put in place in areas vulnerable to spread. For example, the Illinois River, which flows out of Lake Michigan and into the Mississippi River, should be monitored, as it has a good probability of being the next river to be colonized.

Finally, the results of this study are just the groundwork for building the predictive models necessary to successfully manage freshwater mysid invasions. Other parameters should be studied and assessed for inclusion in a more comprehensive model, particularly studies of biotic effects on *H. anomala* abundance, which have been scarce thus far. Moreover, it would be wise to develop models predicting relative abundance and occurrence specific to other mysids, like Limnomysis benedeni (Ricciardi 1998), which have the potential to arrive into North American watersheds.

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Appendix 1. Raw data from trap samples.

Site	Sub-Site	Trap replicate	Abundance of Adults	Total Abundance	Conductivity (µS/cm)	SHI	Macrophyte cover	Sediment size (phi value)	Distance from shore (m)	Depth (m)	Flow (m/s)	Shoreline slope	Artificial structure	Distance from L. Ontario (km)
beaconsfield	bet1	bet1a	0	0	144.06	1.557	4	-7.48	15	1.5	0.8017	1	0	267.4
beaconsfield	bet1	bet1b	0	0	144.06	1.557	4	-7.48	15	1.5	0.8017	1	0	267.4
beaconsfield	bet1	bet1c	0	0	144.06	1.557	4	-7.48	15	1.5	0.8017	1	0	267.4
beaconsfield	bet2	bet2a	0	0	144.06	1.557	4	-7.48	18	1.5	0.4031	0	0	267.4
beaconsfield	bet2	bet2b	0	0	144.06	1.557	4	-7.48	18	1.5	0.4031	0	0	267.4
beaconsfield	bet2	bet2c	0	0	144.06	1.557	4	-7.48	18	1.5	0.4031	0	0	267.4
beaconsfield	bet3	bet3a	0	0	144.06	1.557	4	-7.48	4	1.6	0.9189	1	0	267.4
beaconsfield	bet3	bet3b	0	0	144.06	1.557	4	-7.48	4	1.6	0.9189	1	0	267.4
beaconsfield	bet3	bet3c	0	0	144.06	1.557	4	-7.48	4	1.6	0.9189	1	0	267.4
beaconsfield	bet4	bet4a	0	0	144.06	1.557	4	-7.48	5	1.8	0.3964	1	0	267.4
beaconsfield	bet4	bet4b	0	0	144.06	1.557	4	-7.48	5	1.8	0.3964	1	0	267.4
beaconsfield	bet4	bet4c	0	0	144.06	1.557	4	-7.48	5	1.8	0.3964	1	0	267.4
beaconsfield	bet5	bet5a	0	0	144.06	1.557	4	-7.48	10	1.8	0.2026	1	0	267.4
beaconsfield	bet5	bet5b	0	0	144.06	1.557	4	-7.48	10	1.8	0.2026	1	0	267.4
beaconsfield	bet5	bet5c	0	0	144.06	1.557	4	-7.48	10	1.8	0.2026	1	0	267.4
coteauxlanding	clt1	clt1a	1	6	253.94	2.7407	4	9	4.5	1.5	0.0656	1	1	226.7
coteauxlanding	clt1	clt1b	2	8	253.94	2.7407	4	9	4.5	1.5	0.0656	1	1	226.7
coteauxlanding	clt1	clt1c	2	4	253.94	2.7407	4	9	4.5	1.5	0.0656	1	1	226.7

coteauxlanding	clt2	clt2a	4	12	253.94	2.7407	2	9	5	2.29	0.0703	3	1	226.7
coteauxlanding	clt2	clt2b	3	15	253.94	2.7407	2	9	5	2.29	0.0703	3	1	226.7
coteauxlanding	clt2	clt2c	0	1	253.94	2.7407	2	9	5	2.29	0.0703	3	1	226.7
coteauxlanding	clt3	clt3a	0	0	253.94	2.7407	2	-0.04	6	1.22	0.0221	1	1	226.7
coteauxlanding	clt3	clt3b	1	1	253.94	2.7407	2	-0.04	6	1.22	0.0221	1	1	226.7
coteauxlanding	clt3	clt3c	0	2	253.94	2.7407	2	-0.04	6	1.22	0.0221	1	1	226.7
coteauxlanding	clt4	clt4a	0	0	253.94	2.7407	0	-0.04	15	1.25	0.033	3	1	226.7
coteauxlanding	clt4	clt4b	1	2	253.94	2.7407	0	-0.04	15	1.25	0.033	3	1	226.7
coteauxlanding	clt4	clt4c	0	0	253.94	2.7407	0	-0.04	15	1.25	0.033	3	1	226.7
coteauxlanding	clt5	clt5a	0	0	253.94	2.7407	2	-10.67	15	1.13	0.0224	3	1	226.7
coteauxlanding	clt5	clt5b	0	0	253.94	2.7407	2	-10.67	15	1.13	0.0224	3	1	226.7
coteauxlanding	clt5	clt5c	0	0	253.94	2.7407	2	-10.67	15	1.13	0.0224	3	1	226.7
gentillypp	gt1	gt1a	0	0	233.97	4.2174	0	-3.1699	5	1.5	2	1	1	436.7
gentillypp	gt1	gt1b	1	2	233.97	4.2174	0	-3.1699	5	1.5	2	1	1	436.7
gentillypp	gt1	gt1c	0	2	233.97	4.2174	0	-3.1699	5	1.5	2	1	1	436.7
gentillypp	gt2	gt2a	NA	NA	233.97	4.2174	4	-3.1699	50	1.5	0.8	0	0	436.7
gentillypp	gt2	gt2b	0	0	233.97	4.2174	4	-3.1699	50	1.5	0.8	0	0	436.7
gentillypp	gt2	gt2c	0	0	233.97	4.2174	4	-3.1699	50	1.5	0.8	0	0	436.7
gentillypp	gt3	gt3a	3	10	233.97	4.2174	3	9	6.5	3	2.59	0	1	436.7
gentillypp	gt3	gt3b	0	0	233.97	4.2174	3	9	6.5	3	2.59	0	1	436.7

gentillypp	gt3	gt3c	NA	NA	233.97	4.2174	3	9	6.5	3	2.59	0	1	436.7
iledelapaix	ipt1	ipt1a	0	0	270.5	1.0345	4	4.91	100	1.2	0	0	0	261
iledelapaix	ipt1	ipt1b	0	0	270.5	1.0345	4	4.91	100	1.2	0	0	0	261
iledelapaix	ipt1	ipt1c	0	0	270.5	1.0345	4	4.91	100	1.2	0	0	0	261
iledelapaix	ipt2	ipt2a	0	0	270.5	1.0345	4	4.91	100	1.3	1.1079	0	0	261
iledelapaix	ipt2	ipt2b	0	0	270.5	1.0345	4	4.91	100	1.3	1.1079	0	0	261
iledelapaix	ipt2	ipt2c	0	0	270.5	1.0345	4	4.91	100	1.3	1.1079	0	0	261
iledelapaix	ipt3	ipt3a	0	0	270.5	1.0345	4	4.91	100	1.2	0.0134	0	0	261
iledelapaix	ipt3	ipt3b	1	1	270.5	1.0345	4	4.91	100	1.2	0.0134	0	0	261
iledelapaix	ipt3	ipt3c	0	0	270.5	1.0345	4	4.91	100	1.2	0.0134	0	0	261
iledelapaix	ipt4	ipt4a	0	0	270.5	1.0345	4	4.91	150	1.6	0.1792	0	0	261
iledelapaix	ipt4	ipt4b	0	0	270.5	1.0345	4	4.91	150	1.6	0.1792	0	0	261
iledelapaix	ipt4	ipt4c	0	0	270.5	1.0345	4	4.91	150	1.6	0.1792	0	0	261
iledelapaix	ipt5	ipt5a	0	0	270.5	1.0345	4	4.91	100	1.5	0.933	0	0	261
iledelapaix	ipt5	ipt5b	0	0	270.5	1.0345	4	4.91	100	1.5	0.933	0	0	261
iledelapaix	ipt5	ipt5c	1	1	270.5	1.0345	4	4.91	100	1.5	0.933	0	0	261
ileperrot	pet1	pet1a	0	0	245	1.8788	4	4.91	20	3.2	1.0477	1	0	260.6
ileperrot	pet1	pet1b	0	1	245	1.8788	4	4.91	20	3.2	1.0477	1	0	260.6
ileperrot	pet1	pet1c	0	0	245	1.8788	4	4.91	20	3.2	1.0477	1	0	260.6
ileperrot	pet2	pet2a	0	0	245	1.8788	1	-10.67	10	1.71	0.1822	1	0	260.6
ileperrot	pet2	pet2b	0	2	245	1.8788	1	-10.67	10	1.71	0.1822	1	0	260.6
ileperrot	pet2	pet2c	0	1	245	1.8788	1	-10.67	10	1.71	0.1822	1	0	260.6
ileperrot	pet3	pet3a	0	0	245	1.8788	1	-7.48	8	1.52	1.0477	1	0	260.6

ileperrot	pet3	pet3b	0	0	245	1.8788	1	-7.48	8	1.52	1.0477	1	0	260.6
ileperrot	pet3	pet3c	0	0	245	1.8788	1	-7.48	8	1.52	1.0477	1	0	260.6
ileperrot	pet4	pet4a	0	0	245	1.8788	1	-10.67	5	1.83	0.7883	0	0	260.6
ileperrot	pet4	pet4b	0	0	245	1.8788	1	-10.67	5	1.83	0.7883	0	0	260.6
ileperrot	pet4	pet4c	1	1	245	1.8788	1	-10.67	5	1.83	0.7883	0	0	260.6
ileperrot	pet5	pet5a	0	0	245	1.8788	2	-0.04	15	1.52	0.963	1	0	260.6
ileperrot	pet5	pet5b	0	0	245	1.8788	2	-0.04	15	1.52	0.963	1	0	260.6
ileperrot	pet5	pet5c	0	0	245	1.8788	2	-0.04	15	1.52	0.963	1	0	260.6
lachine	lct1	lct1a	1	1	221.92	2.2545	4	-0.04	30	0.82	0.0592	1	0	274
lachine	lct1	lct1b	0	0	221.92	2.2545	4	-0.04	30	0.82	0.0592	1	0	274
lachine	lct1	lct1c	0	0	221.92	2.2545	4	-0.04	30	0.82	0.0592	1	0	274
lachine	lct2	lct2a	0	0	221.92	2.2545	3	-0.04	0	0.91	0.1408	3	0	274
lachine	lct2	lct2b	0	0	221.92	2.2545	3	-0.04	0	0.91	0.1408	3	0	274
lachine	lct2	lct2c	1	1	221.92	2.2545	3	-0.04	0	0.91	0.1408	3	0	274
lachine	lct3	lct3a	0	4	221.92	2.2545	0	-12.67	2	4.27	2	3	0	274
lachine	lct3	lct3b	0	2	221.92	2.2545	0	-12.67	2	4.27	2	3	0	274
lachine	lct3	lct3c	1	2	221.92	2.2545	0	-12.67	2	4.27	2	3	0	274
lachine	lct4	lct4a	0	0	221.92	2.2545	0	-6.36	3	1.83	2	1	1	274
lachine	lct4	lct4b	0	1	221.92	2.2545	0	-6.36	3	1.83	2	1	1	274
lachine	lct4	lct4c	3	4	221.92	2.2545	0	-6.36	3	1.83	2	1	1	274

lachine	lct5	lct5a	0	0	221.92	2.2545	4	9	6	0.94	0.05	3	1	274
lachine	lct5	lct5b	0	0	221.92	2.2545	4	9	6	0.94	0.05	3	1	274
lachine	lct5	lct5c	0	0	221.92	2.2545	4	9	6	0.94	0.05	3	1	274
laronde	lrt1	lrt1a	0	0	294.46	2.197	3	4.91	3	1.65	0.2595	1	0	295.9
laronde	lrt1	lrt1b	3	12	294.46	2.197	3	4.91	3	1.65	0.2595	1	0	295.9
laronde	lrt1	lrt1c	1	2	294.46	2.197	3	4.91	3	1.65	0.2595	1	0	295.9
laronde	lrt2	lrt2a	11	26	294.46	2.197	4	4.91	2	1.52	0.5236	1	0	295.9
laronde	lrt2	lrt2b	1	3	294.46	2.197	4	4.91	2	1.52	0.5236	1	0	295.9
laronde	lrt2	lrt2c	1	1	294.46	2.197	4	4.91	2	1.52	0.5236	1	0	295.9
laronde	lrt3	lrt3a	0	0	294.46	2.197	4	-6.36	1	1.52	0.1112	1	0	295.9
laronde	lrt3	lrt3b	0	0	294.46	2.197	4	-6.36	1	1.52	0.1112	1	0	295.9
laronde	lrt3	lrt3c	0	0	294.46	2.197	4	-6.36	1	1.52	0.1112	1	0	295.9
laronde	lrt4	lrt4a	18	60	294.46	2.197	0	-6.36	2	2.59	3.1883	1	0	295.9
laronde	lrt4	lrt4b	85	118	294.46	2.197	0	-6.36	2	2.59	3.1883	1	0	295.9
laronde	lrt4	lrt4c	0	0	294.46	2.197	0	-6.36	2	2.59	3.1883	1	0	295.9
laronde	lrt5	lrt5a	0	0	294.46	2.197	0	-10.67	3	1.83	3.1883	1	0	295.9
laronde	lrt5	lrt5b	4	6	294.46	2.197	0	-10.67	3	1.83	3.1883	1	0	295.9
laronde	lrt5	lrt5c	9	43	294.46	2.197	0	-10.67	3	1.83	3.1883	1	0	295.9
lasalle	lst1	lst1a	NA	NA	271.26	1.0596	4	-7.48	80	2	2.6235	1	0	286.8
lasalle	lst1	lst1b	NA	NA	271.26	1.0596	4	-7.48	80	2	2.6235	1	0	286.8
lasalle	lst1	lst1c	NA	NA	271.26	1.0596	4	-7.48	80	2	2.6235	1	0	286.8
lasalle	lst2	lst2a	0	0	271.26	1.0596	4	-10.67	6	1.5	1.5197	1	0	286.8
lasalle	lst2	lst2b	0	0	271.26	1.0596	4	-10.67	6	1.5	1.5197	1	0	286.8

lasalle	lst2	lst2c	0	0	271.26	1.0596	4	-10.67	6	1.5	1.5197	1	0	286.8
lasalle	lst3	lst3a	0	13	271.26	1.0596	3	-10.67	2.1	1.6	0.3725	1	0	286.8
lasalle	lst3	lst3b	0	0	271.26	1.0596	3	-10.67	2.1	1.6	0.3725	1	0	286.8
lasalle	lst3	lst3c	0	0	271.26	1.0596	3	-10.67	2.1	1.6	0.3725	1	0	286.8
lasalle	lst4	lst4a	0	0	271.26	1.0596	2	-6.36	2	2	0.4773	3	0	286.8
lasalle	lst4	lst4b	0	0	271.26	1.0596	2	-6.36	2	2	0.4773	3	0	286.8
lasalle	lst4	lst4c	0	0	271.26	1.0596	2	-6.36	2	2	0.4773	3	0	286.8
lasalle	lst5	lst5a	0	0	271.26	1.0596	1	-6.36	6	2.87	2.1802	1	0	286.8
lasalle	lst5	lst5b	0	0	271.26	1.0596	1	-6.36	6	2.87	2.1802	1	0	286.8
lasalle	lst5	lst5c	0	0	271.26	1.0596	1	-6.36	6	2.87	2.1802	1	0	286.8
melocheville	mt1	mt1a	0	1	300.2	3.45	2	4.91	0.5	1.7	0.0256	3	0	252.6
melocheville	mt1	mt1b	0	2	300.2	3.45	2	4.91	0.5	1.7	0.0256	3	0	252.6
melocheville	mt1	mt1c	0	0	300.2	3.45	2	4.91	0.5	1.7	0.0256	3	0	252.6
melocheville	mt2	mt2a	0	3	300.2	3.45	0	-10.67	0	1	0.0168	3	0	252.6
melocheville	mt2	mt2b	0	2	300.2	3.45	0	-10.67	0	1	0.0168	3	0	252.6
melocheville	mt2	mt2c	0	4	300.2	3.45	0	-10.67	0	1	0.0168	3	0	252.6
melocheville	mt3	mt3a	0	0	300.2	3.45	0	-6.36	4	1.83	1.5287	1	0	252.6
melocheville	mt3	mt3b	0	0	300.2	3.45	0	-6.36	4	1.83	1.5287	1	0	252.6
melocheville	mt3	mt3c	0	1	300.2	3.45	0	-6.36	4	1.83	1.5287	1	0	252.6
melocheville	mt4	mt4a	1	22	300.2	3.45	2	-6.36	2	1.77	2.852	2	0	252.6

melocheville	mt4	mt4b	4	10	300.2	3.45	2	-6.36	2	1.77	2.852	2	0	252.6
melocheville	mt4	mt4c	0	12	300.2	3.45	2	-6.36	2	1.77	2.852	2	0	252.6
melocheville	mt5	mt5a	0	0	300.2	3.45	0	-6.36	2	2	2.4142	2	0	252.6
melocheville	mt5	mt5b	20	41	300.2	3.45	0	-6.36	2	2	2.4142	2	0	252.6
melocheville	mt5	mt5c	13	30	300.2	3.45	0	-6.36	2	2	2.4142	2	0	252.6
pointemarie	mat1	mat1a	0	0	270.14	1.05	1	9	10	1.22	0.9406	1	0	320
pointemarie	mat1	mat1b	0	4	270.14	1.05	1	9	10	1.22	0.9406	1	0	320
pointemarie	mat1	mat1c	0	0	270.14	1.05	1	9	10	1.22	0.9406	1	0	320
pointemarie	mat2	mat2a	0	0	270.14	1.05	1	9	10	1.28	1.9859	1	0	320
pointemarie	mat2	mat2b	0	0	270.14	1.05	1	9	10	1.28	1.9859	1	0	320
pointemarie	mat2	mat2c	0	0	270.14	1.05	1	9	10	1.28	1.9859	1	0	320
pointemarie	mat3	mat3a	0	0	270.14	1.05	1	9	7	1.83	6.8353	0	0	320
pointemarie	mat3	mat3b	0	0	270.14	1.05	1	9	7	1.83	6.8353	0	0	320
pointemarie	mat3	mat3c	0	0	270.14	1.05	1	9	7	1.83	6.8353	0	0	320
pointemarie	mat4	mat4a	0	0	270.14	1.05	0	9	7	1.13	2.1635	1	0	320
pointemarie	mat4	mat4b	0	1	270.14	1.05	0	9	7	1.13	2.1635	1	0	320
pointemarie	mat4	mat4c	0	0	270.14	1.05	0	9	7	1.13	2.1635	1	0	320
pointemarie	mat5	mat5a	0	0	270.14	1.05	0	9	3	1	4.4864	0	0	320
pointemarie	mat5	mat5b	0	0	270.14	1.05	0	9	3	1	4.4864	0	0	320
pointemarie	mat5	mat5c	0	0	270.14	1.05	0	9	3	1	4.4864	0	0	320
portdebecancour	pbt1	pbt1a	0	0	231.57	3	0	9	11.5	3	0.066	2	1	436
portdebecancour	pbt1	pbt1b	1	1	231.57	3	0	9	11.5	3	0.066	2	1	436
portdebecancour	pbt1	pbt1c	0	0	231.57	3	0	9	11.5	3	0.066	2	1	436

portdebecancour	pbt2	pbt2a	2	2	231.57	3	0	-10.67	22	4	0.0269	2	1	436
portdebecancour	pbt2	pbt2b	1	1	231.57	3	0	-10.67	22	4	0.0269	2	1	436
portdebecancour	pbt2	pbt2c	0	1	231.57	3	0	-10.67	22	4	0.0269	2	1	436
portdebecancour	pbt3	pbt3a	0	2	231.57	3	0	-10.67	32	4	0.1113	2	1	436
portdebecancour	pbt3	pbt3b	0	0	231.57	3	0	-10.67	32	4	0.1113	2	1	436
portdebecancour	pbt3	pbt3c	0	0	231.57	3	0	-10.67	32	4	0.1113	2	1	436
portofmontreal	pmt1	pmt1a	37	40	267.5	5.1	0	4.91	3	8.5	0.0642	3	1	295.1
portofmontreal	pmt1	pmt1b	18	18	267.5	5.1	0	4.91	3	8.5	0.0642	3	1	295.1
portofmontreal	pmt1	pmt1c	1	2	267.5	5.1	0	4.91	3	8.5	0.0642	3	1	295.1
portofmontreal	pmt2	pmt2a	21	22	267.5	5.1	0	4.91	2	7	0	3	1	295.1
portofmontreal	pmt2	pmt2b	28	37	267.5	5.1	0	4.91	2	7	0	3	1	295.1
portofmontreal	pmt2	pmt2c	0	0	267.5	5.1	0	4.91	2	7	0	3	1	295.1
portofmontreal	pmt3	pmt3a	5	6	267.5	5.1	0	4.91	2	4.3	0	3	1	295.1
portofmontreal	pmt3	pmt3b	20	20	267.5	5.1	0	4.91	2	4.3	0	3	1	295.1
portofmontreal	pmt3	pmt3c	7	8	267.5	5.1	0	4.91	2	4.3	0	3	1	295.1
portofmontreal	pmt4	pmt4a	1	1	267.5	5.1	0	-12.67	0.5	6.5	0	3	1	295.1
portofmontreal	pmt4	pmt4b	24	25	267.5	5.1	0	-12.67	0.5	6.5	0	3	1	295.1
portofmontreal	pmt4	pmt4c	0	0	267.5	5.1	0	-12.67	0.5	6.5	0	3	1	295.1
ptclaire	pct1	pct1a	0	0	136.64	2.1461	3	-10.67	12	0.88	0.1622	3	0	267.3
ptclaire	pct1	pct1b	0	0	136.64	2.1461	3	-10.67	12	0.88	0.1622	3	0	267.3

ptclaire	pct1	pct1c	0	0	136.64	2.1461	3	-10.67	12	0.88	0.1622	3	0	267.3
ptclaire	pct2	pct2a	0	0	136.64	2.1461	4	-0.04	94	1.07	0.0228	1	0	267.3
ptclaire	pct2	pct2b	0	0	136.64	2.1461	4	-0.04	94	1.07	0.0228	1	0	267.3
ptclaire	pct2	pct2c	0	0	136.64	2.1461	4	-0.04	94	1.07	0.0228	1	0	267.3
ptclaire	pct3	pct3a	0	0	136.64	2.1461	4	-6.36	10	0.88	0.0865	1	0	267.3
ptclaire	pct3	pct3b	0	0	136.64	2.1461	4	-6.36	10	0.88	0.0865	1	0	267.3
ptclaire	pct3	pct3c	0	0	136.64	2.1461	4	-6.36	10	0.88	0.0865	1	0	267.3
ptclaire	pct4	pct4a	0	0	136.64	2.1461	2	4.91	7	1.83	0.0046	1	0	267.3
ptclaire	pct4	pct4b	0	1	136.64	2.1461	2	4.91	7	1.83	0.0046	1	0	267.3
ptclaire	pct4	pct4c	0	1	136.64	2.1461	2	4.91	7	1.83	0.0046	1	0	267.3
ptclaire	pct5	pct5a	1	2	136.64	2.1461	2	-6.36	40	1.83	0.2923	3	0	267.3
ptclaire	pct5	pct5b	0	0	136.64	2.1461	2	-6.36	40	1.83	0.2923	3	0	267.3
ptclaire	pct5	pct5c	0	0	136.64	2.1461	2	-6.36	40	1.83	0.2923	3	0	267.3
repentigny	rt1	rt1a	0	0	150.06	2.0234	2	9	10	1	2.5287	0	0	319
repentigny	rt1	rt1b	0	0	150.06	2.0234	2	9	10	1	2.5287	0	0	319
repentigny	rt1	rt1c	0	0	150.06	2.0234	2	9	10	1	2.5287	0	0	319
repentigny	rt2	rt2a	0	0	150.06	2.0234	3	9	66.35	0.9	2.0111	0	0	319
repentigny	rt2	rt2b	0	0	150.06	2.0234	3	9	66.35	0.9	2.0111	0	0	319
repentigny	rt2	rt2c	0	0	150.06	2.0234	3	9	66.35	0.9	2.0111	0	0	319
repentigny	rt3	rt3a	0	0	150.06	2.0234	2	9	7	1.68	3.2466	1	0	319
repentigny	rt3	rt3b	0	0	150.06	2.0234	2	9	7	1.68	3.2466	1	0	319
repentigny	rt3	rt3c	0	0	150.06	2.0234	2	9	7	1.68	3.2466	1	0	319
repentigny	rt4	rt4a	0	0	150.06	2.0234	0	9	18.288	1.49	0.7715	3	1	319

repentigny	rt4	rt4b	0	0	150.06	2.0234	0	9	18.288	1.49	0.7715	3	1	319
repentigny	rt4	rt4c	0	0	150.06	2.0234	0	9	18.288	1.49	0.7715	3	1	319
repentigny	rt5	rt5a	0	0	150.06	2.0234	1	9	27.432	1.5	6.2675	0	0	319
repentigny	rt5	rt5b	0	0	150.06	2.0234	1	9	27.432	1.5	6.2675	0	0	319
repentigny	rt5	rt5c	0	0	150.06	2.0234	1	9	27.432	1.5	6.2675	0	0	319
stbernard	sbt1	sbt1a	0	0	267.52	1.3909	3	-6.36	96.012	0.91	1.0573	1	0	267.5
stbernard	sbt1	sbt1b	0	0	267.52	1.3909	3	-6.36	96.012	0.91	1.0573	1	0	267.5
stbernard	sbt1	sbt1c	0	0	267.52	1.3909	3	-6.36	96.012	0.91	1.0573	1	0	267.5
stbernard	sbt2	sbt2a	0	0	267.52	1.3909	2	-0.04	55.7784	1.22	0.3234	0	0	267.5
stbernard	sbt2	sbt2b	0	0	267.52	1.3909	2	-0.04	55.7784	1.22	0.3234	0	0	267.5
stbernard	sbt2	sbt2c	0	2	267.52	1.3909	2	-0.04	55.7784	1.22	0.3234	0	0	267.5
stbernard	sbt3	sbt3a	0	0	267.52	1.3909	3	-0.04	91.44	0.91	0.3084	0	0	267.5
stbernard	sbt3	sbt3b	0	0	267.52	1.3909	3	-0.04	91.44	0.91	0.3084	0	0	267.5
stbernard	sbt3	sbt3c	0	0	267.52	1.3909	3	-0.04	91.44	0.91	0.3084	0	0	267.5
stbernard	sbt4	sbt4a	0	1	267.52	1.3909	4	-0.04	150.876	0.91	0.798	0	0	267.5
stbernard	sbt4	sbt4b	0	0	267.52	1.3909	4	-0.04	150.876	0.91	0.798	0	0	267.5
stbernard	sbt4	sbt4c	0	0	267.52	1.3909	4	-0.04	150.876	0.91	0.798	0	0	267.5
stbernard	sbt5	sbt5a	0	0	267.52	1.3909	4	-0.04	139.9032	1.37	0.8654	2	0	267.5
stbernard	sbt5	sbt5b	0	0	267.52	1.3909	4	-0.04	139.9032	1.37	0.8654	2	0	267.5
stbernard	sbt5	sbt5c	0	0	267.52	1.3909	4	-0.04	139.9032	1.37	0.8654	2	0	267.5

valoisbay	vbt1	vbt1a	0	0	155.2	1.445	4	4.91	30	1.5	0	1	0	270
valoisbay	vbt1	vbt1b	0	0	155.2	1.445	4	4.91	30	1.5	0	1	0	270
valoisbay	vbt1	vbt1c	0	0	155.2	1.445	4	4.91	30	1.5	0	1	0	270
valoisbay	vbt2	vbt2a	0	0	155.2	1.445	4	4.91	10	1.5	0	1	0	270
valoisbay	vbt2	vbt2b	1	1	155.2	1.445	4	4.91	10	1.5	0	1	0	270
valoisbay	vbt2	vbt2c	0	0	155.2	1.445	4	4.91	10	1.5	0	1	0	270
valoisbay	vbt3	vbt3a	0	0	155.2	1.445	4	4.91	7	1.5	0	1	0	270
valoisbay	vbt3	vbt3b	0	0	155.2	1.445	4	4.91	7	1.5	0	1	0	270
valoisbay	vbt3	vbt3c	0	0	155.2	1.445	4	4.91	7	1.5	0	1	0	270
valoisbay	vbt4	vbt4a	0	0	155.2	1.445	4	4.91	10	1.5	0	1	0	270
valoisbay	vbt4	vbt4b	0	0	155.2	1.445	4	4.91	10	1.5	0	1	0	270
valoisbay	vbt4	vbt4c	0	0	155.2	1.445	4	4.91	10	1.5	0	1	0	270

Appendix 2. Raw data from net haul samples

Site	Sub-site	Abundance of adults	Total abundance	Density (#/m^3)	Conductivity (µS/cm)	SHI	Flow (m/s)	Depth (m)	Distance from shore (m)	Shoreline slope	Artificial structure	Distance from L. Ontario (km)
gentillypp	gh1	0	1	0.77	235.9	4.22	0.25	2.71	123.39	0	0	436.7
gentillypp	gh2	0	0	0.00	235.9	4.22	2.59	2.74	41.67	0	1	436.7
gentillypp	gh3	0	0	0.00	235.9	4.22	3.82	2.74	39.1	0	1	436.7
gentillypp	gh4	0	0	0.00	235.9	4.22	3.13	5.18	37.14	1	1	436.7
portdebecancour	pbh1	1	1	1.06	232.29	3	0.11	1.98	22.39	2	1	436

portdebecancour	pbh2	0	0	0.00	232.29	3	0.67	12.8	28.18	3	1	436
portdebecancour	pbh3	0	1	0.16	232.29	3	0.65	12.8	3.61	3	1	436
portdebecancour	pbh4	1	2	1.72	232.29	3	0.03	2.44	54.04	2	1	436
portdebecancour	pbh5	0	0	0.00	232.29	3	0.07	3.41	15.62	2	1	436
portdebecancour	pbh6	0	1	0.98	232.29	3	0.2	2.13	19.87	2	1	436
pointemarie	mah1	0	0	0.00	269.13	1.05	5.57	4.08	91.72	1	0	320
pointemarie	mah2	1	1	1.14	269.13	1.05	5.57	1.83	61.08	1	0	320
pointemarie	mah3	0	0	0.00	269.13	1.05	4.03	2.8	38.36	0	0	320
pointemarie	mah4	0	3	2.29	269.13	1.05	7.82	2.74	31	1	0	320
pointemarie	mah5	0	0	0.00	269.13	1.05	4.49	2.74	63.4	0	0	320
pointemarie	mah6	0	0	0.00	269.13	1.05	3.46	14.94	218.72	1	0	320
repentigny	rh1	0	0	0.00	149.27	2.02	2.94	4.88	93.26	0	0	319
repentigny	rh2	0	0	0.00	149.27	2.02	2.53	3.05	92.15	0	0	319
repentigny	rh3	0	0	0.00	149.27	2.02	3.32	4.27	69.19	0	0	319
repentigny	rh4	0	0	0.00	149.27	2.02	3.32	1.83	70.91	1	0	319
repentigny	rh5	0	0	0.00	149.27	2.02	0.77	1.83	4.56	2	1	319
repentigny	rh6	0	0	0.00	149.27	2.02	0.77	1.83	13.8	3	1	319
laronde	lrh1	0	0	0.00	294.6	2.2	0.11	1.83	26.62	1	0	295.9
laronde	lrh2	0	0	0.00	294.6	2.2	7.25	1.83	15.63	2	0	295.9
laronde	lrh3	0	0	0.00	294.6	2.2	0.11	1.86	9.74	3	0	295.9

laronde	lrh4	0	0	0.00	294.6	2.2	0.54	3.66	23.44	1	0	295.9
laronde	lrh5	0	1	0.45	294.6	2.2	3.19	4.66	32.56	1	0	295.9
portofmontreal	pmh1	79	136	33.48	266	1.24	0.06	8.5	0.5	3	1	295.1
portofmontreal	pmh2	97	104	29.02	266	1.24	0	7.5	0.5	3	1	295.1
portofmontreal	pmh3	34	75	22.42	266	1.24	0	7	0.5	3	1	295.1
portofmontreal	pmh4	0	0	0.00	266	1.24	0	5	0.5	3	1	295.1
portofmontreal	pmh5	118	166	80.79	266	1.24	0	4.3	0.5	3	1	295.1
portofmontreal	pmh6	700	972	239.31	266	1.24	0	8.5	0.5	3	1	295.1
lasalle	lsh1	0	0	0.00	271.26	1.06	2.18	3.38	13.45	1	0	286.8
lasalle	lsh2	0	0	0.00	271.26	1.06	2.62	2.41	103.02	1	0	286.8
lasalle	lsh3	0	0	0.00	271.26	1.06	1.52	2.96	9.81	1	0	286.8
lasalle	lsh4	0	0	0.00	271.26	1.06	1.52	2.68	21.86	1	0	286.8
lasalle	lsh5	0	0	0.00	271.26	1.06	0.37	2.35	13.28	1	0	286.8
lasalle	lsh6	0	0	0.00	271.26	1.06	0.48	3.66	11.75	3	0	286.8
lachine	lch1	0	0	0.00	210.1	2.25	0.06	2.77	111.88	1	0	274
lachine	lch2	0	0	0.00	210.1	2.25	0.14	1.52	34.29	3	0	274
lachine	lch3	0	0	0.00	210.1	2.25	3	6.58	17.48	2	1	274
lachine	lch4	0	1	0.60	210.1	2.25	0.9	3.47	38.06	1	1	274
lachine	lch5	1	1	0.59	210.1	2.25	0.05	3.57	0.5	3	1	274
lachine	lch6	0	1	0.62	210.1	2.25	0.01	3.38	0.5	3	1	274
lachine	lch7	1	10	4.90	210.1	2.25	1	4.27	0.5	3	0	274
stbernard	sbh1	0	0	0.00	268.75	1.39	0.12	1.83	141.36	0	0	267.5
stbernard	sbh2	0	0	0.00	268.75	1.39	0.26	1.52	179.85	0	0	267.5

stbernard	sbh3	0	0	0.00	268.75	1.39	0.73	1.52	261	0	0	267.5
stbernard	sbh4	0	0	0.00	268.75	1.39	1.2	1.83	114.22	0	0	267.5
stbernard	sbh5	0	0	0.00	268.75	1.39	1.11	1.52	108.41	1	0	267.5
stbernard	sbh6	0	0	0.00	268.75	1.39	0.48	9.75	273.16	1	0	267.5
beaconsfield	beh1	0	0	0.00	141.77	1.56	0.8	3.05	122.08	1	0	267.4
beaconsfield	beh2	0	0	0.00	141.77	1.56	0.8	3.14	197.6	0	0	267.4
beaconsfield	beh3	0	0	0.00	141.77	1.56	0.92	3.35	104.92	1	0	267.4
beaconsfield	beh4	0	0	0.00	141.77	1.56	0.4	2.9	229.56	1	0	267.4
beaconsfield	beh5	0	0	0.00	141.77	1.56	0.92	0.67	278.25	1	0	267.4
beaconsfield	beh6	0	0	0.00	141.77	1.56	0.92	3.05	103.13	1	0	267.4
ptclaire	pch1	0	0	0.00	139.37	2.15	0.29	1.52	1.57	3	0	267.3
ptclaire	pch2	6	7	12.01	139.37	2.15	0.29	1.22	1.49	2	0	267.3
ptclaire	pch3	0	1	0.62	139.37	2.15	0.02	3.35	121.06	3	0	267.3
ptclaire	pch4	0	0	0.00	139.37	2.15	0.04	2.38	88.82	1	0	267.3
ptclaire	pch5	0	0	0.00	139.37	2.15	0.04	1.83	55.02	1	0	267.3
ptclaire	pch6	5	9	12.39	139.37	2.15	0.04	1.52	46.1	1	0	267.3
iledelapaix	iph1	0	0	0.00	270.5	1.03	0.8	1.52	652.61	0	0	261
iledelapaix	iph2	0	0	0.00	270.5	1.03	0.8	1.46	933.1	0	0	261
iledelapaix	iph3	0	0	0.00	270.5	1.03	0.05	1.52	66.94	2	1	261
iledelapaix	iph4	0	0	0.00	270.5	1.03	0.05	1.52	64.32	3	1	261

iledelapaix	iph5	0	0	0.00	270.5	1.03	0.8	1.74	745.76	0	0	261
ileperrot	peh1	0	3	2.61	245.47	1.88	1.33	2.41	39.76	1	0	260.6
ileperrot	peh2	0	0	0.00	245.47	1.88	0.29	1.83	287.58	1	0	260.6
ileperrot	peh3	0	0	0.00	245.47	1.88	0.51	1.83	129.18	1	0	260.6
ileperrot	peh4	0	2	2.33	245.47	1.88	0.39	1.8	59.76	1	0	260.6
ileperrot	peh5	0	0	0.00	245.47	1.88	0.29	2.26	83.77	0	0	260.6
ileperrot	peh6	0	0	0.00	245.47	1.88	0.93	2.13	52.09	0	0	260.6
melocheville	mh1	221	1148	262.86	300.2	3.45	2.41	9.14	15.4	2	0	252.6
melocheville	mh2	822	1263	427.01	300.2	3.45	2.41	6.19	23.61	2	0	252.6
melocheville	mh3	17	34	6.19	300.2	3.45	2.85	11.49	17.64	2	0	252.6
melocheville	mh4	1	1	0.59	300.2	3.45	0.02	3.57	17.66	1	0	252.6
melocheville	mh5	0	2	2.99	300.2	3.45	0.02	1.4	6.6	2	1	252.6
melocheville	mh6	0	0	0.00	300.2	3.45	0.03	2.13	26.1	3	0	252.6
melocheville	mh7	0	0	0.00	300.2	3.45	0.03	3.05	0.5	3	0	252.6
melocheville	mh8	305	611	110.14	300.2	3.45	2.41	11.61	8.9	3	0	252.6
melocheville	mh9	46	68	15.06	300.2	3.45	2.41	9.45	14.95	2	0	252.6
melocheville	mh10	0	0	0.00	300.2	3.45	2.85	12.71	107.77	1	0	252.6
coteauxlanding	clh1	0	0	0.00	253.95	2.74	0.07	2.99	127.54	2	1	226.7
coteauxlanding	clh2	54	85	64.92	253.95	2.74	0.12	2.74	2.38	2	1	226.7
coteauxlanding	clh3	1	2	0.92	253.95	2.74	0.07	4.57	19.87	3	1	226.7
coteauxlanding	clh4	0	0	0.00	253.95	2.74	0.09	1.83	9.08	2	1	226.7
coteauxlanding	clh5	0	0	0.00	253.95	2.74	0.29	3.05	13.86	1	1	226.7
coteauxlanding	clh6	0	0	0.00	253.95	2.74	0.01	3.35	16.14	3	1	226.7

bainsville	bah1	0	2	2.25	426.06	2.87	0.55	1.86	74.75	1	0	200
bainsville	bah2	21	30	34.31	426.06	2.87	0.37	1.83	237.6	2	0	200
bainsville	bah3	6	6	5.21	426.06	2.87	1.02	2.41	22.96	2	1	200
bainsville	bah4	2	6	6.86	426.06	2.87	0.02	1.83	226.69	0	0	200
bainsville	bah5	0	1	0.86	426.06	2.87	0.34	2.44	72.28	2	1	200
bainsville	bah6	0	0	0.00	426.06	2.87	0.02	2.13	24.03	0	1	200