Biol Invasions (2011) 13:2423–2432
DOI 10.1007/s10530-011-0069-9

INTRODUCTION

The spread, establishment and impacts of the spiny water flea, *Bythotrephes longimanus,* in temperate North America: a synopsis of the special issue

Norman D. Yan · Brian Leung · Mark A. Lewis · Scott D. Peacor

Received: 10 July 2011 / Accepted: 12 July 2011 / Published online: 12 August 2011

Abstract More than most sub-disciplines of ecology, the study of biological invasions is characterized by breadth rather than by depth. Studies of expanding ranges of invaders are common, as are post-invasion case studies, but we rarely have a deep understanding of the dynamics and regulators of the processes of invasion and resultant ecological transformations. This is unfortunate because such depth may well be needed to develop targeted, knowledge-based, management plans. In this collection we provide this needed depth of study of the key aspects of the invasion process for the spiny water flea, *Bythotrephes longimanus*. We do so by presenting the results of the work conducted by researchers in the Canadian Aquatic Invasive Species Network (CAISN), and several of their American and European collaborators over the past half decade. Given its rapid spread in the Great Lakes basin in North America, and the decreases in pelagic biodiversity that have ensued, the last decade has witnessed a surge of research on *Bythotrephes*. In this collection we learn much about mechanisms and dynamics of its spread, about the key role of humans in that spread, about the importance of Allee effects to establishment and persistence, about choices and parameterization of risk assessment models, about the value of comparing "effects" in native and invaded regions, about complex probable interactions of the invasion with impending changes in the climate, and about the regulators of the invader's abundance and impacts. There should be

N. D. Yan (✉)
Department of Biology, York University, Toronto, ON M3J 1P3, Canada
e-mail: nyan@yorku.ca

N. D. Yan
Dorset Environmental Science Centre, Dorset, ON P0A 1E0, Canada

B. Leung
Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada

M. A. Lewis
Centre for Mathematical Biology Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB T6G 2G1, Canada

M. A. Lewis
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2G1, Canada

S. D. Peacor
Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824-1222, USA

much of interest in the collection for aquatic ecologists and invading species biologists alike.

Keywords *Bythotrephes* · Special issue · Synopsis · Review · Non-indigenous species · Invasive species

Introduction: on the relevance of *Bythotrephes longimanus* to invasion biologists

Most invading species biologists work on the land, or in the littoral regions of lakes and oceans, ecozones that together form roughly a third of the planet's surface. Pelagic ecosystems, both fresh and saline, blanket the remaining two-thirds of the earth, and the key biota that underpin the productivity of these waters are the plankton. Based on their areal coverage alone, it should come as no surprise, then, that the services provided by plankton are important to mankind. A healthy global plankton community supplies humankind with services we either cannot do without, e.g. atmospheric oxygen, or without which our lives would be greatly impoverished, e.g. essential fatty acids (Arts et al. 2001). The provision of these and many other services from the pelagian relies on its continued productivity and function, both of which are underpinned by planktonic biodiversity (Dodson et al. 2000; Cardinale 2011). Thus, any serious anthropogenic threat to the biodiversity of pelagic waters deserves our scrutiny, followed, hopefully, by our enlightened management (Vander Zanden and Olden 2008). Planktonic invaders are now quite common in lakes and oceans (Bollens et al. 2002), and some of these species may pose a serious threat to pelagic biodiversity. Unfortunately these invaders have rarely received much scrutiny, but one exception to this pattern is the spiny water flea, *Bythotrephes longimanus* (Crustacea, Onychopoda, Cercopagidae)—the world's best studied invasive zooplankter (Bollens et al. 2002; Strecker in press). There has been a surge of recent interest in the impacts of *Bythotrephes* on pelagic freshwaters, and we highlight this research in this special issue.

Bythotrephes longimanus (Fig. 1a) was more than likely introduced to North America via ballast water discharged from ships that picked it up in ports in the northwest (Berg et al. 2002), or perhaps other regions (Colautti et al. 2005) of Europe. It was misidentified

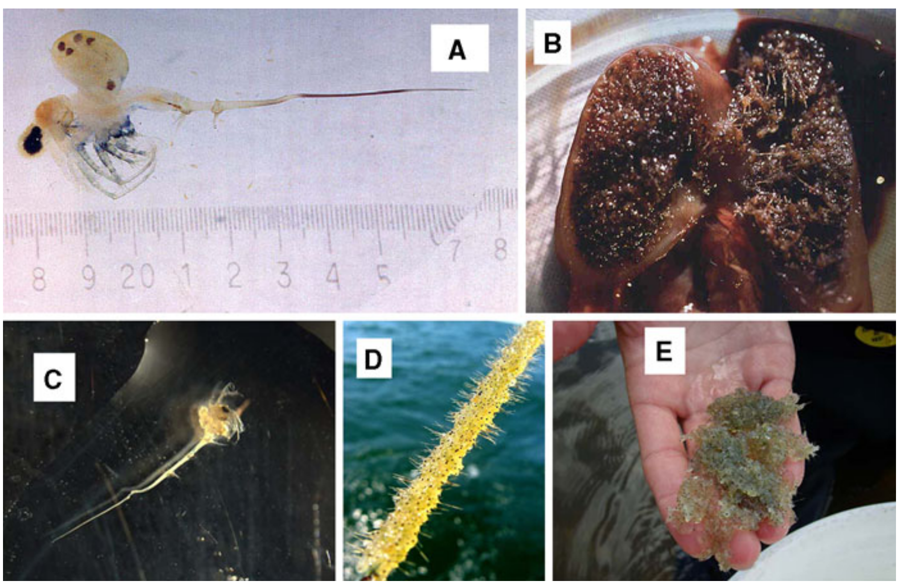

Fig. 1 **a** Photograph of a mature *Bythotrephes* with 5 late-stage embryos in her brood pouch. Animal was collected from Harp Lake, in Muskoka, Ont, Canada (photograph by Bill O'Neill), **b** thousands of *Bythotrephes* in the stomach of a lake herring (*Coregonus artedi*) from Lake Rosseau, District of Muskoka, Ontario (photograph by Bev Clarke), **c** photograph of *Bythotrephes* collected from the ballast tank of a ship in transit in the Great Lakes (photograph provided by Hugh MacIsaac, University of Windsor), **d** *Bythotrephes* on a downrigger fishing cable in Lake Erie (photograph by A. Jaeger) and **e** a handful of *Bythotrephes* collected in a larval fish drift net in the Rainy River in northwestern Ontario, Canada (photograph provided by Ont. Min. Natural Resources)

in the earlier literature as *B. cederstrœmi*, before the great polymorphism of *Bythotrephes* was recognized (Berg and Garton 1994; Therriault et al. 2002), and following prior naming conventions, *B. longimanus* was accepted as the proper binomial. It is a Ponto-Caspian zooplanktivore that has been established for millennia in large, temperate, nutrient-poor lakes in Eurasia (Grigorovich et al. 1998; MacIsaac et al. 2000). By many criteria, it is an important member of its native pelagic ecosystems, for example, inhabiting about 20% of lakes in Norway (Hessen et al. 2011), contributing to salmonid fish diets out of proportion to its contribution to planktonic biomass (Nilsson 1979, and Fig. 1b), and functioning as a key regulator of plankton composition (Manca et al. 2000). While *Bythotrephes* is not considered problematic in Europe, the situation is quite different in North America, where it has proven to be a serious threat to pelagic biodiversity in both large and small lakes (Yan et al. 2002; Barbiero and Tuchman 2004; Strecker et al. 2006). Its damaging effects cascade below its immediate crustacean prey to pelagic rotifers (Hovius et al. 2006), and likely to phytoplankton (Strecker et al. 2011), and also up the food chain to competing macro-invertebrate predators (Foster and Sprules 2009; Weisz and Yan 2011) and fish (Parker-Stetter et al. 2005).

Students of biological invasions can learn much of general value from a deep examination of particular invaders. For example, we have learned much about the mechanisms of spread and establishment of invaders, about their ecological and socio-economic impacts, and about challenges and approaches to their management from focused research on *Caulerpa*, the "killer algae", in the Mediterranean Sea (Meinesz 1999), American comb jelly in the Black Sea (Kideys 2002), zebra mussels in the Laurentian Great Lakes (Claudi and Mackie 1993), and Nile perch in Lake Victoria (Goldschmidt et al. 1993). Many of the key issues of interest to invading species biologists also apply to planktonic invaders, i.e. the mechanisms and dynamics of spread, the regulation of establishment success and post-establishment population growth, the subsequent ecological changes, their site specificity, and their effects on ecological services (e.g. Myers and Bazely 2003; Lockwood et al. 2007). We deal with all of these issues in this collection. Our collective goal is to present to invading species biologists the latest knowledge on the mechanisms and models of the spread, establishment, and impacts of *Bythotrephes* on freshwater ecosystems, principally in eastern, temperate, North America. There are four specific reasons why *Bythotrephes* deserves such attention: (1) the apparent enormous threat it poses to North American pelagic biodiversity; (2) the many gaps in understanding of this threat which recent research can now plug; (3) its rapidity of spread, which lead to its selection by CAISN (the Canadian Aquatic Invading Species Network) as its model pelagic invader, thus providing us the opportunity to compare risk assessment models with different underlying drivers on a common data set; and 4) the need to better inform managers of best options to reduce the spread of this and other pelagic invaders. We consider each of these reasons in the following few paragraphs.

First, we believe *Bythotrephes* represents a widespread threat to pelagic biodiversity in temperate North America. It is spreading rapidly and widely, and severely damaging at least its planktonic prey. *Bythotrephes* was first identified in North America in Lake Ontario in the early 1980s (Johannsson et al. 1991). It has since spread rapidly colonizing all of the Laurentian Great Lakes by the end of the 1980s (Bur et al. 1986; Lange and Cap 1986; Lehman 1988; Evans 1988; Cullis and Johnson 1988), likely moved in ballast among the lakes by the Great Lakes shipping fleet (Fig. 1c). By the late 1980s and early 1990s, the invader appeared in a few inland lakes in Michigan, USA, and more than a dozen inland lakes in Ontario, Canada (Yan et al. 1992). During the 1990s it spread rapidly in Ontario, especially among recreational lakes in the District of Muskoka, a few hours north of Toronto (Yan and Pawson 1997; Therriault et al. 2002; Muirhead and MacIsaac 2005; Weisz and Yan 2010). By 2010, there were 150 known invaded lakes spread over a 1,300 km range from south-central to northwestern Ontario, and in Canada the invader had spread beyond the Great Lakes watershed into the Hudson Bay drainage. During the same time period, many invasions were also documented in lakes and reservoirs in Michigan, Minnesota, Wisconsin, Ohio and New York (Branstrator et al. 2006; Johnson et al. 2008; Strecker in press, and Fig. 1 in Kerfoot et al. 2011). Given the similar climates and water chemistry of Shield lakes in Canada and northern Europe, the 20% prevalence of *Bythotrephes* in lakes in Norway (Hessen et al. 2011), and its rapid recent spread

(Kerfoot et al. 2011), we hypothesize that many thousands of lakes in temperate North America will eventually come to support this invader. As planktonic crustacean species richness typically falls by some 20% after North American *Bythotrephes* invasions (Lehman and Caceres 1993; Schulz and Yurista 1999; Yan et al. 2002; Barbiero and Tuchman 2004; Strecker et al. 2006), we believe the eventual impacts of *Bythotrephes* on zooplankton biodiversity in N. America will be enormous, assuming the initial impacts are long-lasting, which, to date, they appear to be (Yan et al. 2008).

Our second reason for assembling this special issue on *Bythotrephes* was that the work of a large number of researchers that entered the field in the last decade was nearing completion, and its collective publication could build the deep knowledge that the field needs. There is a reasonably large body of published *Bythotrephes* research on which to build (Fig. 2), but predictably, much of the early North American work is limited to reports of range expansions (e.g. Yan et al. 1992), and descriptive case studies (e.g. Yan and Pawson 1997), or what we might term first generation models of spread, which are not mechanistically-based (MacIsaac et al. 2000), nor built on data derived from probability-based surveys (Muirhead and MacIsaac 2005). However, since 2005, much has changed, especially with the Canadian Aquatic Invasive Species Network (CAISN) adopting *Bythotrephes* as their model pelagic invader. CAISN recognized the need for in depth analysis of model systems to identify key issues underlying the mechanisms of spread, establishment and impact of biological invaders. *Bythotrephes* was an obvious choice given their detrimental effects, the current concerns with respect to their spread, and the background research that had already been completed that would facilitate more general advances in invasive species knowledge. Finally, CAISN together with the Ontario Ministry of the Environment hosted an international *Bythotrephes* workshop in Dorset, Ontario, Canada, in the fall of 2009, to bring together CAISN researchers and their North American and European colleagues, resulting in the development of this special issue. Here, we fill several fundamental holes in understanding about *Bythotrephes*. In terms of population and community dynamics, Brown and Branstrator (2011) and Wittmann et al. (2011) demonstrate the role of the resting egg biology of *Bythotrephes* on its invasion success, while Pichlová-Ptáčníková and Vanderploeg (2011), Bourdeau et al. (2011), and Young et al. (2011), respectively, consider how differences in prey avoidance abilities, migration tendencies, and spring abundances can explain the invader's abundance, and its differential impacts on specific taxa. Hessen et al. (2011) and Jokela et al. (2011) compare the invader's interactions with native macro-invertebrate, holoplanktonic predators in Norway and Canada; Kerfoot et al. (2011) prove the role of fish in its dispersal; while Rennie et al. (2011) document the overall changes in trophic structuring of food webs that follow invasion.

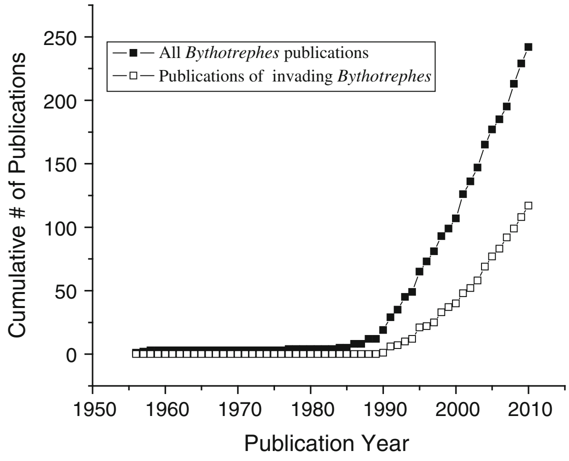

Fig. 2 Growth of the *Bythotrephes* literature, distinguishing all Web of Science-tracked publications with the keyword *Bythotrephes* from those specifically concerned with *Bythotrephes* as an invading species

Our third reason for assembling this special issue is that *Bythotrephes* provides an excellent model for the study of the secondary spread of invaders. The CAISN initiative produced a common data set, which yielded the opportunity to compare alternative formulations of models of spread, produced by independent labs. Such comparisons are rarely possible, but are very useful for consideration of the consequences of subtle differences in model structure (i.e., analysis of model uncertainty), for identification of the potential importance of different underlying invasion processes, and for testing alternative hypotheses when multiple processes or model structures yield similar fits to the data. We assemble that research here, with four papers focused on modeling the growth and spread of the invader on the south-central Canadian Shield (Gertzen and Leung 2011; Muirhead and MacIsaac 2011; Potapov et al. 2011; Wang and Jackson 2011). Combined, this work provides insight into where potential colonists are going, how quickly they are moving, and which sites will allow them to survive and prosper, information crucial to understanding and managing secondary spread.

Finally, there is a clear need to develop effective management strategies for this and other aquatic invaders, and we believe the large body of recent research on *Bythotrephes* can lead to sound advice for managers. We hope the research we have assembled on: (1) the comparison of different models to estimate secondary spread, (2) the parameterization of these models, (3) the comparative importance of propagule pressure of natural and human origin, (4) the occurrence of Allee effects, and (5) the effects on *Bythotrephes* establishment of local climatic and chemical factors and food-web interactions, will all contribute to the wiser management of aquatic invasive species, including *Bythotrepehes*.

Synthesizing *Bythotrephes* knowledge—highlights of the special issue

The impacts of *Bythotrephes* on pelagic ecosystems in North America have been dramatic and fairly repeatable. In lakes of all sizes, the diversity of crustacean zooplankton, particularly its cladoceran component, has fallen (Lehman and Caceres 1993; Schulz and Yurista 1999; Yan and Pawson 1997; Yan et al. 2001, 2002; Barbiero and Tuchman 2004; Strecker et al. 2006), both because *Bythotrephes* consumes a very large fraction of total zooplankton production (Dumitru et al. 2001; Strecker and Arnott 2008), and indirectly because *Bythotrephes* induces downward migration of its prey into deeper cooler waters that lower their growth rates (Pangle et al. 2007; Bourdeau et al. 2011). The impacts of the invader also cascade beyond their immediate crustacean prey, down the food chain to rotifers, which apparently benefit from competitive release (Hovius et al. 2006, 2007), and likely to phytoplankton (Strecker et al. 2011). Effects also are felt up the food chain to competing macro-invertebrate predators, at least one of which (*Leptodora*) suffers dramatic losses (Foster and Sprules 2009; Weisz and Yan 2011), and to fish, whose behaviour and diet changes (Mills et al. 1992; Parker Stetter et al. 2005).

This special issue advances our understanding of *Bythotrephes* in many ways:

1. its rapid ongoing spread in North America,
2. the contributions of propagule pressure and habitat conditions to this spread,
3. the site specificity of factors influencing spread,
4. the complex influence of temperature on the invader's current and future threat,
5. the role of resting egg production, and
6. Allee effects in population establishment and persistence,
7. the importance of indirect, trait-mediated effects of the invader on its prey,
8. the effects of the invader on overall pelagic trophic structure,
9. the effects of inter-specific differences in prey swimming speeds as the cause of community-wide patterns of change,
10. the performance of different approaches to risk assessment modeling, and
11. features of the spread and impacts of this invasion that may inform management.

1. *Bythotrephes* incidence is increasing in lakes on the south-central Canadian Shield (Weisz and Yan 2010), and the modeling efforts of Potapov et al. (2011), Muirhead and MacIsaac (2011) and Gertzen and Leung (2011) in this collection were built on that growing data set. However, Kerfoot et al. (2011) add their own survey data to other recent American survey data (e.g. Branstrator et al. 2006) to provide strong evidence that *Bythotrephes* is spreading west of the Great Lakes in the USA in a latitudinal band consistence with the current incidences in Ontario. Intriguingly, the distributional data suggest temperature-limited establishment success, i.e. the invader does not appear to prosper in lakes south of the 27–30° isocline of maximum surface air temperatures (Kerfoot et al. 2011). Because this observation is consistent with lab-derived thermal limits for the invader (e.g. Yurista 1999; Kim and Yan 2010), we hypothesize that many lakes in the USA will be too warm for *Bythotrephes*, and there may well be both latitudinal and altitudinal regulators of North American spread.

2. Propagule pressure, linked to human recreational activity including fishing (Jarnagin et al. 1999), is likely the major determinant of the spread of *Bythotrephes* (e.g. Muirhead and MacIsaac 2005; Weisz and Yan 2010, e.g. Fig. 1d), but habitat quality may also affect establishment success of propagules (MacIsaac et al. 2000). Research in this collection dramatically enriches this understanding. In independent modeling efforts, Potapov et al. (2011); Gertzen and Leung (2011), and Muirhead and MacIsaac (2011) all demonstrate the central role of propagule pressure in explaining the current pattern of *Bythotrephes* presence on the Canadian Shield. Further Gertzen and Leung (2011) prove that the component of propagule pressure contributed by stream connections in this landscape is so low it can be practically ignored, while it certainly can be high in much larger rivers (e.g. Fig. 1e). Wang and Jackson (2011) and Potapov et al. (2011) demonstrate that habitat information can improve predictions of invader prevalence, with consideration, respectively, of sport fish composition and habitat acidity, while Jokela et al. (2011) prove that interactions with numerous native macro-invertebrate predators will not slow the spread of the invader.
3. The collection proves that the regulators of establishment of *Bythotrephes* may vary from place to place in North America. On the Canadian Shield, lake connections in landscapes do not appear to influence the spread of the invader (Gertzen and Leung 2011), suggesting *Bythotrephes* does not move between lakes in water masses. In Lake Superior, in contrast, Kerfoot et al. (2011) prove that currents may well control spread along coastlines and into embayments, while local temperature regimes may well control persistence.
4. There is a growing interest in the effects of climatic change on the spread of invaders. For *Bythotrephes*, it appears that present and future water temperatures may have a complex effect on the spread of *Bythotrephes*. Wittmann et al. (2011) predict that small increases in temperature should increase the probability of establishment of *Bythotrephes* by increasing rates of population growth of founding propagules to Allee effect thresholds that will lead to establishment. However, *Bythotrephes* is a cool-water species, dying at temperatures just above 25°C (Grigorovich et al. 1998; Yurista 1999; Kim and Yan 2010); hence, climate warming should eventually alter the invader's spread and its eventual distribution.
5. Brown and Branstrator (2011) provide strong evidence that early seasonal introductions and large propagule sizes promote establishment of *Bythotrephes*, because the over-wintering survival of its resting eggs can be surprisingly low, and turnover of resting eggs within a year can be surprising high. Persistence may well be dependent on the production of a great many resting eggs.
6. We learn much about Allee effects in this collection. Potapov et al. (2011), Wittmann et al. (2011), and Brown and Branstrator (2011) all provide evidence for a strong Allee effect influencing *Bythotrephes* establishment success, (see also Gertzen et al. 2011). Underlying mechanisms of Allee effects were also identified, in particular bottom-up control and starvation (Young et al. 2011) controlling summer population size, the rapid turnover and relative low survival rate of resting eggs (Brown and Branstrator 2011), and temperature-limited growth (Wittmann et al. 2011), below thermal thresholds. Even relatively well established populations may fail in particularly hot years (Kerfoot et al. 2011).
7. *Bythotrephes* are planktivorous, and influence prey populations directly by increasing their death rates, but they are also known to influence at least their daphniid prey indirectly, by altering their migratory behaviour and subsequent growth rates (Pangle et al. 2007). In this collection we learn more about such indirect effects. Jokela et al. (2011) demonstrate alterations in the vertical distributions of the invader's macro-invertebrate competitors, while Bourdeau et al. (2011) used chemical cues from the invader to induce alterations in the diel vertical distribution of copepods in Lake Michigan waters.
8. Much of the published work on the effects of *Bythotrepehes* has been focused on alterations

in pelagic structure, with limited work on function (Strecker and Arnott 2008), or on the determinants of *Bythotrephes* population size. In this collection, we learn that *Bythotrephes*, by reducing abundances of herbivorous Cladocera, alters trophic positioning of the entire pelagic assemblage (Rennie et al. 2011). We learn from an examination of Norwegian lakes that the ongoing replacement of *Leptodora* by *Bythotrephes* in North America (Foster and Sprules 2009; Weisz and Yan 2011) might well have been predicted from their co-occurrence patterns in Europe (Hessen et al. 2011). Finally, we learn that spring prey abundance may well be the prime determinant of *Bythotrephes* population size (Young et al. 2011), and perhaps, establishment success, given the large Allee effect.

9. Of the many species of *Daphnia* found in North American Lakes, only *D. mendotae* appears to thrive in the presence of *Bythotrephes*. In this collection, Hessen et al. (2011) demonstrate that the related *D. galeata* is one of few species that is actually positively associated with *Bythotrephes* in Norway. Pichlová-Ptácníková and Vanderploeg (2011) provide compelling evidence to explain this persistence of *D. mendotae* in Lake Michigan with their demonstration that *D. mendotae* has much faster escape responses to the invader than other daphniids, allowing it to prosper from the increased availability of resources left behind by its slower competitors.
10. Much has also been learned about modeling the risk of spread and establishment of invaders in this body of work (see especially point 2 above). There are methodological advances, regarding the maximal usage of incomplete spatial and temporal information (Gertzen and Leung 2011), and the influence of the underlying structure of gravity models on their predictive ability. Production-contrained gravity models may well be the best overall choice (Muirhead and MacIsaac 2011). More fundamentally we learn that the ongoing invasion of CAISN's key 1600-lake watershed is actually slowing, despite increased discovery rates, likely because of saturation of optimal sites (Gertzen and Leung 2011).
11. Beyond efforts to educate the public, there is currently no management directed specifically at *Bythotrephes*; hence, there is no article on *Bythotrephes* management in this collection. Nonetheless, there are many implications for management in the knowledge assembled in this collection. First, with a single sampling of 300 of the 1600 lakes in an invaded watershed, it was possible to produce risk assessment models of several types that had a high probability of predicting the pattern of occurrence of *Bythotrephes* in a landscape. Clearly, such models can be developed from incomplete data sets for this invader, and likely for other invaders with similar life histories, such as *Cercopagis* (Panov et al. 2007). Propagule pressure from humans emerged as the single best predictor of spread on the Shield in the work of Muirhead and MacIsaac (2011), Potapov et al. (2011), Gertzen and Leung (2011), and Kerfoot et al. (2011). This strongly suggests that management efforts are best directed at recreational lake users, especially boaters and anglers that are moving from invaded to non-invaded lakes. The recognition of strong Allee effects in several papers in this collection (and in Gertzen et al. 2011) counters earlier suggestions that only a few *Bythotrephes* colonists might found permanent populations (Drake et al. 2006), and clearly indicates that efforts to reduce propagule size and number, at least via public communication programs are justified,. We also learn from the collection that long-term establishment is not guaranteed, even if initial colonization success appears high, e.g. Portage Lake (Kerfoot et al. 2011). Hence, managers should endeavour to reduce propagule supply to lakes even after establishment, especially for relatively shallow lakes that suffer occasional hot summers that may decimate the established population of invaders.

In summary, the research contained in this collection has taught us that, despite complex dynamics and interactions, the North American *Bythotrephes* establishment, spread and impacts, can be understood in terms of key drivers. These drivers are the essential determinants of invasion outcomes. Establishment depends crucially upon dispersal at a level sufficient to overcome Allee effects. These Allee effects are, in turn, dependent upon local environmental conditions such as temperature. Once Allee effects are overcome, spread is quite predictable over broad spatial scales, determined first by anthropogenic dispersal in Shield lakes, or anthropogenic dispersal coupled with water mass movements in the Great Lakes, and second by local environmental conditions. As with many invading species, impacts on biodiversity are fundamentally different in endemic and invaded ranges; hence, we take insights from work in endemic ranges, but not necessarily specific predictions of impacts. The impacts of the invader scale with its abundance, and the key driver that influences the invader's abundance and phenology in many, newly invaded North American lakes appears to be vernal prey density. The impacts may also be site-specific influenced by the capacity of native residents to avoid the predator either by changing their diel migratory behaviour, or, for a few taxa, having inherent escape abilities good enough to avoid capture. The regulation of impact is thus complex, including both direct, predatory drivers, and indirect behavioural drivers that differ among the invader, its prey, and likely its predators. A full unraveling of the food web interactions that govern these impacts is, perhaps unsurprisingly, not yet available. Much has been learned, as the collection demonstrates. The threat to pelagic biodiversity that *Bythotrephes* represents should motivate continued research. We advise plankton ecologists and fisheries biologists that work in temperate lakes in North America to watch for *Bythotrephes* in their plankton and fish diet samples, given the rapid spread of this invader, and the damage to pelagic ecosystems that it causes. Importantly, many of these key drivers and issues are applicable to planktonic invaders in general. To the extent that a deep knowledge of one invader can inform the study and management of others, we hope that the readers of the journal will benefit from this focused examination of one invader, the spiny water flea, *B. longimanus*.

Acknowledgments We thank the NSERC Canadian Aquatic Invading Species Network and the Ontario Ministry of the Environment for their support of *Bythotrephes* research in Canada, and for funding the 2009 *Bythotrephes* workshop at Dorset, Ontario, at which the majority of the authors of this special issue compared their *Bythotrephes* research, and at which the idea for this special issue blossomed. We thank Julia Dewing for her secretarial, administrative, and organizational work. The co-editors' work was greatly simplified by her competence, hard work and joyful spirit. MAL gratefully acknowledges a Canada Research Chair, and BL, NDY and MAL acknowledge NSERC Discovery Grants for support.

References

Arts MT, Ackman RG, Holub BJ (2001) Essential fatty acids in aquatic ecosystems: a crucial link between diet and human health and evolution. Can J Fish Aquat Sci 58:122–137

Barbiero RP, Tuchman ML (2004) Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. Can J Fish Aquat Sci 61:2111–2125

Berg DJ, Garton DW (1994) Genetic differentiation in North American and European populations of the cladoceran *Bythotrephes*. Limnol Oceanogr 39:1503–1516

Berg DJ, Garton DW, MacIsaac HJ, Panov VE, Telesh IV (2002) Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga, Russia. Freshw Biol 47:275–282

Bollens SM, Cordell JR, Avent S, Hooff R (2002) Zooplankton invasions: a brief review, plus two case studies from the northeast Pacific. Hydrobiol 480:87–110

Bourdeau PE, Pangle KL, Peacor SD (2011) The invasive predator *Bythotrephes* induces vertical migration in native copepods of Lake Michigan. Biol Invasions (this issue)

Branstrator DK, Brown ME, Shannon LJ, Thabes M, Heimgartner K (2006) Range expansion of *Bythotrephes longimanus* in North America: evaluating habitat characteristics in the spread of an exotic zooplankter. Biol Invasions 8:1367–1379

Brown M, Branstrator D (2011) Patterns in the abundance, phenology and hatching of the resting egg stage of the invasive zooplankton *Bythotrephes longimanus*. Biol Invasions (this issue)

Bur MT, Klarer DM, Krieger KA (1986) First records of a European cladoceran, *Bythotrephes cederstroemi*, in lakes Erie and Huron. J Great Lakes Res 12:144–146

Cardinale BJ (2011) Biodiversity improves water quality through niche partitioning. Nature 472:86–89

Claudi R, Mackie GL (1993) Practical manual for zebra mussel monitoring and control. Lewis, London, pp 227

Colautti RI, Manca M, Viljanen M, Ketelaars HAM, Burgi HR, MacIsaac HJ, Heath DH (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. Mol Ecol 14:1869

Cullis KI, Johnson GE (1988) First evidence of the cladoceran *Bythotrephes cederstroemi* Schoedler in lake Superior. J Great Lakes Res 14:524–525

Dodson SI, Arnott SE, Cottingham KL (2000) The relationship in lake communities between primary productivity and species richness. Ecology 81:2662–2679

Drake JM, Drury KLS, Lodge DM, Blukacz A, Yan ND, Dwyer G (2006) Demographic stochasticity, environmental variability, and windows of invasion risk for *Bythotrephes longimanus* in North America. Biol Invasions 8:843–861

Dumitru C, Sprules WG, Yan ND (2001) Impact of *Bythotrephes cederstroemi* on zooplankton assemblages of Harp Lake, Canada: an assessment based on predator consumption and prey production. Freshw Biol 46:241–251

Evans MS (1988) *Bythotrephes cederstrœmi*: its new appearance in Lake Michigan. J Great Lakes Res 14:234–240

Foster SE, Sprules WG (2009) Effects of the *Bythotrephes* invasion on native predatory invertebrates. Limnol Oceanogr 54:757–769

Gertzen E, Leung B (2011) Predicting the spread of invasive species in an uncertain world: accommodating multiple vectors and gaps in temporal and spatial data for *Bythotrephes longimanus*. Biol Invasions (this issue)

Gertzen E, Leung B, Yan ND (2011) Propagule pressure, stochasticity, and Allee effects in relation to the probability of establishment of invasive species: an enclosure study and population model of *Bythotrephes longimanus*. Ecosphere 2(3):art30. doi:10.1890/ES10-00170.1

Goldschmidt T, Witte F, Wanink J (1993) Cascading effects of the introduced nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of lake Victoria. Conserv Biol 7:686–700

Grigorovich IA, Pashkova OV, Gromoca YF, van Overdijk CDA (1998) *Bythotrephes longimanus* in the commonwealth of independent states: variability, distribution and ecology. Hydrobiol 379:183–198

Hessen D, Bakkestuen V, Walseng B (2011) Ecological niches of *Bythotrephes* and *Leptodora*: lessons for predicting long-term effects of invasion. Biol Invasions (this issue)

Hovius J, Beisner B, McCanmn KS (2006) Epilimnetic rotifer community responses to *Bythotrephes longimanus* invasion in Canadian shield lakes. Limnol Oceanogr 51:1004–1012

Hovius JT, Beisner BE, McCann KS, Yan ND (2007) Indirect food web effects of *Bythotrephes* invasion: responses by the rotifer *Conochilus* in Harp Lake, Canada. Biol Invasions 9:233–243

Jarnagin ST, Swan BK, Kerfoot WC (1999) Fish as vectors in the dispersal of *Bythotrephes cederstroemi*: diapausing eggs survive passage through the gut. Freshw Biol 43:579–589

Johannsson OE, Mills EL, O'Gorman R (1991) Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–1988. Can J Fish Aquat Sci 48:1546–1557

Johnson PTJ, Olden JD, Vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. Front Ecol Environ 6:357–363

Jokela A, Arnott S, Beisner B (2011) Patterns of *Bythotrephes longimanus* distribution relative to native macroinvertebrates and zooplankton prey. Biol Invasions (this issue)

Kerfoot WC, Yousef F, Hobmeier M, Maki RP, Jarnagin T, Churchill JH (2011) Temperature, recreational fishing and diapause egg connections: dispersal of spiny water fleas (*Bythotrephes longimanus*). Biol Invasions (this issue)

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. Science 297:1482–1484

Kim N, Yan ND (2010) Methods for rearing the invasive zooplankter *Bythotrephes* in the laboratory. Limnol Oceanogr Methods 8:552–561

Lange C, Cap R (1986) *Bythotrephes cederstrœmi* (Schœdler), (Cercopagidae: Cladocera): a new record for lake Ontario. J Great Lakes Res 12:142–143

Lehman JT (1988) Algae biomass unaltered by food-web changes in Lake Michigan. Nature 332:537–538

Lehman JT, Caceres CE (1993) Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. Limnol Oceanogr 38:879–891

Lockwood JL, Hoopers MF, Marchetti MP (2007) Invasion ecology. Blackwell, Oxford, p 304

MacIsaac HJ, Ketelaars HAM, Grigorovich IA, Ramcharan CW, Yan ND (2000) Modeling *Bythotrephes longimanus* invasions in the great lakes basin based on its European distribution. Arch Hydrobiol 149:1–21

Manca M, Ramoni C, Comollie P (2000) The decline of *Daphnia hyalina galeata* in Lago Maggiore: a comparison of the population dynamics before and after oligotrophication. Aquat Sci 62:142–153

Meinesz A (1999) Killer algae: the true tale of a biological invasion. University of Chicago Press, Chicago, p 360

Mills EL, O'Gorman R, Degisi J, Heberger RF, House RA (1992) Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. Can J Fish Aquat Sci 49:2009–2019

Muirhead JR, MacIsaac HJ (2005) Development of inland lakes as hubs in an invasion network. J Appl Ecol 42:80–90

Muirhead JR, MacIsaac HJ (2011) Evaluation of stochastic gravity model selection for use in estimating non-indigenous species dispersal and establishment. Biol Invasions (this issue)

Myers JH, Bazely DR (2003) Ecology and control of introduced plants. Cambridge University Press, p 313

Nilsson NA (1979) Food and habitat of the fish community of the offshore region of lake Vanern, Sweden. Inst Freshw Res Drottningholm 58:126–139

Pangle KL, Peacor SD, Johannsson O (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412

Panov VE, Rodionova NV, Bolshagin PV, Bychek EA (2007) Invasion biology of Ponto-Caspian onychopod cladocerans (Crustacea: Cladocera: Onychopoda). Hydrobiol 590:3–14

Parker Stetter SL, Witzel LD, Rudstam LG, Einhouse DW, Mills EL (2005) Energetic consequences of diet shifts in lake Erie rainbow smelt (*Osmerus mordax*). Can J Fish Aquat Sci 62:145–152

Pichlová-Ptáčníková R, Vanderploeg HA (2011) The quick and the dead: might differences in escape rates explain the changes in the zooplankton community composition of Lake Michigan after invasion by *Bythotrephes*? Biol Invasions (this issue)

Potapov A, Muirhead J, Yan N, Lele S, Lewis M (2011) Models of lake invasibility by *Bythotrephes longimanus*, a non-indigenous zooplankton. Biol Invasions (this issue)

Rennie MD, Strecker AL, Palmer ME (2011) *Bythotrephes* invasion elevates trophic position of zooplankton and fish: Implications for contaminant biomagnification. Biol Invasions (this issue)

Schulz KL, Yurista PM (1999) Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. Hydrobiol 380:179–193

Strecker AL (In press) An overview of invasive freshwater cladocerans: *Bythotrephes longimanus* as a case study. In: Francis R (ed) Handbook of global freshwater invasive species. Earthscan, London

Strecker AL, Arnott SE (2008) Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in freshwater lakes. Ecosystems 11:490–503

Strecker AL, Arnott SE, Yan ND, Girard R (2006) Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes*. Can J Fish Aquat Sci 63:2126–2136

Strecker AL, Beisner BE, Arnott SE, Paterson AM, Winter JG, Johannsson OE, Yan ND (2011) Direct and indirect effects of an invasive planktonic predator on pelagic food webs. Limnol Oceanogr 56:179–192

Therriault TW, Grigorovich IA, Cristescu ME, Ketelaars HAM, Viljanen M, Heath DD, MacIsaac HJ (2002) Taxonomic resolution of the genus *Bythotrephes* Leydig, using molecular markers and a re-evaluation of its global distribution, with notes on factors affecting dispersal, establishment and abundance. Divers Distrib 8:67–84

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. Can J Fish Aquat Sci 65:1512–1522

Wang L, Jackson DA (2011) Modeling the establishment of invasive species: habitat and biotic interactions influencing the establishment of *Bythotrephes longimanus*. Biol Invasion (this issue)

Weisz EJ, Yan ND (2010) Relative value of limnological, geographic and human use variables as predictors of the presence of *Bythotrephes longimanus* in Canadian shield lakes. Can J Fish Aquat Sci 67:462–472

Weisz EJ, Yan ND (2011) Shifting invertebrate zooplanktivores: watershed-level replacement of the native *Leptodora* by the non-indigenous *Bythotrephes* in Canadian shield lakes. Biol Invasions 13:115–123

Wittmann MJ, Lewis MA, Young JD, Yan ND (2011) Temperature-dependent Allee effects in a stage-structured model for *Bythotrephes* establishment. Biol Invasions (this issue)

Yan ND, Pawson TW (1997) Changes in the crustacean zooplankton community of Harp Lake, Canada, following the invasion by *Bythotrephes cederstrœmi*. Freshw Biol 37:409–425

Yan ND, Dunlop W, Pawson TW, Mackay LE (1992) *Bythotrephes cederstrœmi* (Schœdler) in Muskoka lakes: first records of the European invader in inland lakes in Canada. Can J Fish Aquat Sci 49:422–426

Yan ND, Blukacz A, Sprules WG, Kindy PK, Hackett D, Girard R, Clark BJ (2001) Changes in the zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada. Can J Fish Aquat Sci 58:2341–2350

Yan ND, Girard R, Boudreau S (2002) An introduced predator (*Bythotrephes*) reduces zooplankton species richness. Ecol Lett 5:481–485

Yan ND, Somers KM, Girard RE, Paterson A, Keller B, Ramcharan C, Rusak J, Ingram R, Morgan G, Gunn JM (2008) Long-term changes in crustacean zooplankton communities of Dorset, Ontario lakes: the probable interactive effects of changes in pH, TP, dissolved organic carbon, and predators. Can J Fish Aquat Sci 65:862–877

Young JD, Strecker AL, Yan ND (2011) Increased abundance of the non-indigenous zooplanktivore, *Bythotrephes longimanus*, is strongly correlated with greater spring prey availability in Canadian shield lakes. Biol Invasions (this issue)

Yurista PM (1999) A model for temperature correction of size-dependent respiration in *Bythotrephes cederstrœmi* and *Daphnia middendorfianna*. J Plank Res 21:721–734