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INTRODUCTION

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

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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 much of interest in the collection for

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aquatic ecologists and invading species biologists alike.

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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

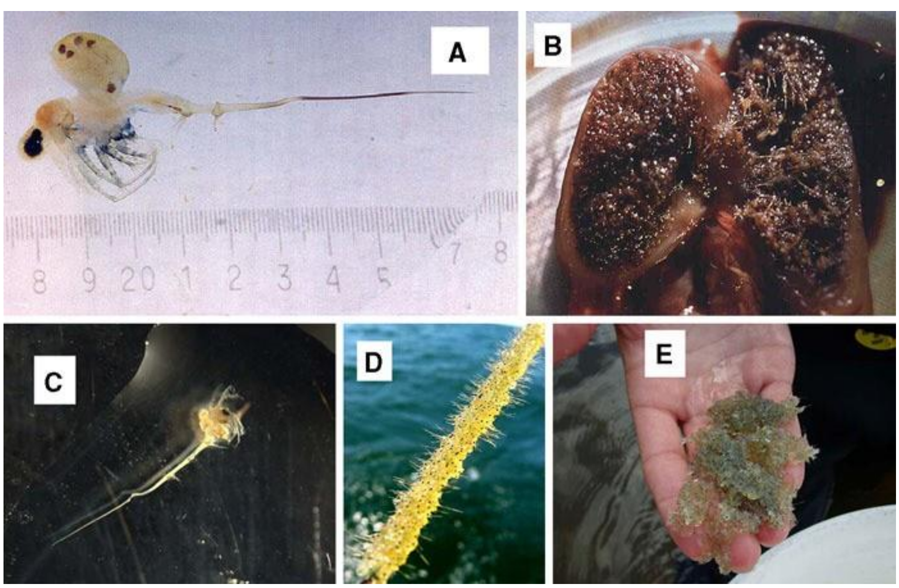

Fig. 1 a Photograph of a mature *Bythotrephes* with 5 late-stage embryos in her brood pouch. Animal was collected from Harp Lake, in Muskoka, Ont, Canada (photograph by Bill O'Neill), b photograph of *Bythotrephes* collected from the ballast tank of a ship in transit in the Great Lakes (photograph provided by Hugh MacIsaac, University of Windsor), c thousands of *Bythotrephes* in the stomach of a lake herring (*Coregonus artedi*) from Lake Rosseau, District of Muskoka, Ontario (photograph by Bev Clarke), d 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), and e *Bythotrephes* on a downrigger fishing cable in Lake Erie (photograph by A. Jaeger) 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 phyto-plankton (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 wide-spread 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 1987; 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 north-western 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 et al. 2011, 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

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(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

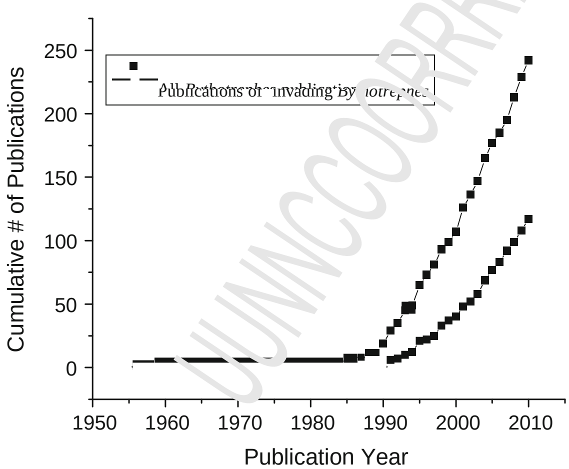

Fig. 2 Growth of the *Bythotrephes* literature, distinguishing all ISI-tracked publications with the keyword *Bythotrephes* from those specifically concerned with *Bythotrephes* as an invading species

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.

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-

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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.

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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*,

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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

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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 of the readers of the journal will benefit from this focused examination of one invader, the spiny water flea, *B. longimanus*.

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