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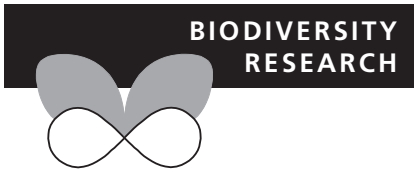
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# Differential short- and long-term effects of an invertebrate predator on zooplankton communities in invaded and native lakes

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## ABSTRACT

**Aim** Forecasting the effects of invasive species remains difficult, because short-term effects may be transitory and theories of long-term effects are poorly developed and rarely tested. Here, we compare zooplankton communities from freshwater lakes in Norway and Canada that differ in their duration of exposure to the invertebrate predator *Bythotrephes longimanus*, to aid in predicting its potential long-term impacts on Canadian zooplankton communities.

**Location** Freshwater lakes in Canada and Norway.

**Methods** We compared differences in zooplankton community structure, richness and occurrence between lakes with and without *Bythotrephes* in Canada and Norway using univariate and multivariate analyses of the incidence of crustacean zooplankton species.

**Results** Correspondence analysis confirmed that zooplankton community composition differed dramatically in lakes with and without *Bythotrephes* in Canada but not in Norway. The short-term exposure of Canadian lakes to *Bythotrephes* led to lower zooplankton diversity, particularly for cladoceran species, whereas in Norway, a greater diversity of zooplankton, particularly for copepod species, occurred in lakes where *Bythotrephes* has been present for long periods. Significantly more species in Norway demonstrated an increase in their frequency of occurrence, while significantly more species in Canada demonstrated a decrease, in lakes containing *Bythotrephes*.

**Main conclusions** *Bythotrephes* can modify zooplankton community structure, diversity, and spatial occurrence across a watershed in a short period (i.e. a few decades) after invasion; however, some species appear to adapt to the presence of *Bythotrephes* over time. We hypothesize the long-term effects of higher diversity in Norwegian lakes is attributed to altered interspecific community interactions, coupled with behavioural adaptations to avoid *Bythotrephes* predation, enabling the remaining species to increase their populations in space and time. If Canadian communities adapt similarly, the long-term effects of *Bythotrephes* invasion in Canada may thus be less severe than those observed in the first few decades of the invasion.

## Keywords

Biological invasions, *Bythotrephes*, Canada, community structure, long-term effects, Norway, zooplankton.

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## INTRODUCTION

Invasions by non-indigenous species are one of the greatest threats to biodiversity in aquatic ecosystems (Wilcove *et al.*, 1998; Sala *et al.*, 2000). Freshwater lakes are particularly susceptible to species invasions, because of the large pool of individuals and species available to be transported beyond their natural range; once introduced, lake and stream networks, reductions in dispersal barriers with canals and locks, and transport of human goods by water facilitate their spread (Lodge *et al.*, 1998). Although the impacts of most introduced species are relatively benign, some invaders have transformed ecosystems, driving native species to extinction and altering community structure and ecosystem function (Ricciardi & Rasmussen, 1999; Mack *et al.*, 2000). On occasion, economic damage has been enormous (Pimentel *et al.*, 2005). Thus, the study of invasive species is vital, not only for its potential to increase our knowledge of the regulators of ecosystem structure and function, but also for the conservation and wise management of freshwater resources.

Crustacean zooplankton are key components of freshwater ecosystems, mediating the energy flow between phytoplankton communities and higher trophic levels, such as fish, in pelagic habitats. Thus, invading species that negatively impact zooplankton biodiversity and community composition have the potential to simultaneously influence the dynamics of multiple trophic levels, from primary producers (Strecker *et al.*, 2011) to top predators (Parker Stetter *et al.*, 2005), with cascading consequences for primary and secondary production (Strecker & Arnott, 2008; Strecker *et al.*, 2011), nutrient cycling and water quality (Fahnenstiel *et al.*, 1995; Barbiero *et al.*, 2006; Turner, 2010), and overall ecosystem functioning (Mack *et al.*, 2000). Given the potential for drastic ecosystem change, studies of invaded zooplankton communities are essential to examine how invaders alter recipient communities and to understand the broader impacts of how invaders alter the operation of complex ecosystems.

The spiny water flea, *Bythotrephes longimanus* (Crustacea, Branchiopoda, Onychopoda), hereafter *Bythotrephes*, is a parthenogenetic invertebrate predator with an extensive natural distribution throughout the Palearctic region (Grigorovich *et al.*, 1998; MacIsaac *et al.*, 2000; Colautti *et al.*, 2005). While it is most commonly found in large, deep, oligotrophic lakes in its native range (MacIsaac *et al.*, 2000), it also tolerates a wide range of salinity, pH, temperature and conductivity and occurs in many alpine lakes and lakes ranging widely in size (Grigorovich *et al.*, 1998; MacIsaac *et al.*, 2000). *Bythotrephes* is a generalist predator that appears to prefer small-bodied, slow, herbivorous cladocerans (Vanderploeg *et al.*, 1993; Grigorovich *et al.*, 1998; Wahlström & Westman, 1999; Yan *et al.*, 2001; Strecker & Arnott, 2010). In turn, *Bythotrephes* is heavily preyed upon by zooplanktivorous fish (Coulas *et al.*, 1998; Straile & Halbach, 2000; Pothoven *et al.*, 2007; Young and Yan, 2008).

*Bythotrephes* was almost certainly introduced to the Great Lakes via ballast water exchange of transoceanic ships returning from the Baltic Sea (Sprules *et al.*, 1990; Mills *et al.*, 1993), although secondary invasions of *Bythotrephes* from other locations in Eurasia are ongoing (Colautti *et al.*, 2005). Since its initial detection in the Great Lakes in the 1980s (Johannsson *et al.*, 1991), *Bythotrephes* has dispersed to > 160 inland lakes in Ontario, Canada (Weisz & Yan, 2010; OFAH unpublished data; Cairns & Yan, 2011), as well as lakes in the mid-western USA (Branstrator *et al.*, 2006; Kerfoot *et al.*, 2011), primarily because of human vectors (MacIsaac *et al.*, 2004; Weisz & Yan, 2010). The invasion of *Bythotrephes* is routinely associated with reductions in native zooplankton abundance, biomass and diversity, particularly of cladocerans (Yan & Pawson, 1997; Dumitru *et al.*, 2001; Yan *et al.*, 2002; Boudreau & Yan, 2003; Barbiero & Tuchman, 2004; Strecker *et al.*, 2006), alterations in the behaviour of zooplankton (Pangle *et al.*, 2007; Young and Yan, 2008; Bourdeau *et al.*, 2011) and the displacement of some common, native predatory invertebrates (Foster & Sprules, 2010; Weisz & Yan, 2011). Additionally, *Bythotrephes* invasion may exert strong effects on zooplankton size structure (Manca & Ruggiu, 1998; Yan & Pawson, 1998) and indirectly impact biomass of lower trophic levels (e.g. rotifers: Hovius *et al.*, 2007; phytoplankton: Strecker *et al.*, 2011).

Given its rapid spread throughout Ontario, Canada, and its potential to invade a large number of lakes across North America (MacIsaac *et al.*, 2004; Weisz & Yan, 2010; Gertzen & Leung, 2011), there is currently great interest in predicting the eventual impacts of *Bythotrephes* on native biodiversity and ecosystem processes (Yan *et al.*, 2011). Invading species frequently play a more devastating role in recently invaded ecosystems compared with systems where they have co-adapted to, and co-existed with, the natural communities for long periods (cf. Sax *et al.*, 2005). However, forecasting the effects of invasive species in freshwater ecosystems remains difficult, as it is unknown how such effects will change through time (e.g. Strayer & Malcom, 2006; Pace *et al.*, 2010), because little theory and empirical data currently exist to support accurate predictions (Strayer *et al.*, 2006). The long-term effects of invasion may differ, if behavioural adaptations or evolutionary changes in the invader alter how it interacts with species in the community or with other temporally changing variables that control the ecosystem, while changes in the species composition of the invaded community may shift towards species insensitive to the invader (Strayer, 2010). Comparative studies of an invading species among similar ecosystems that differ in the length of time since invasion would provide greater insight into the mechanisms by which invasive species can dominate recipient communities and accelerate understanding of how effects of invading species change through time.

*Bythotrephes* is a native species in most of Europe (Berg & Garton, 1994) and has likely been present in Norway since the end of the last glaciation. *Bythotrephes* is found in c. 20% of Norwegian lakes where zooplankton has been sampled

(Hessen & Walseng, 2008) and occupies a wide niche, inhabiting lakes with a wide range of elevation, latitudes, lake areas and pH, although it is rare in shallow, eutrophic lakes with cyprinid dominance and the most intensive fish predation pressure (Hessen *et al.*, 2011). Interestingly, while the predatory impact of *Bythotrephes* on the zooplankton prey community has not been directly investigated in Norway, recent observations indicate that zooplankton species richness is greater in Norwegian lakes in the presence of *Bythotrephes* (Hessen *et al.*, 2011). Thus, the long-term impacts of *Bythotrephes* invasion may not be apparent from studies of short-term impacts conducted within its invaded range alone. Fortunately, the majority of freshwater lakes in Norway are similar in many ways (e.g. ionic strength, nutrient status, history of glaciation, connectance, bathymetry and climate) to those in the Canadian Shield region of Ontario, Canada, and contain crustacean zooplankton communities with a high degree of ecological resemblance in geologically comparable settings (Keller & Conlon, 1994; Hessen *et al.*, 1995, 2006; Walseng & Schartau, 2001). Thus, Norwegian lakes provide an ideal space-for-time substitution to study the long-term impacts of *Bythotrephes* invasions on freshwater zooplankton in Canada.

In this study, we examine patterns of zooplankton diversity and community composition from geologically, ecologically and physico-chemically similar freshwater lakes in Norway and Canada that differ in the length of time of exposure to *Bythotrephes*, as a first step in predicting the potential long-term impacts of *Bythotrephes* on zooplankton communities in Canada. In addition, we erect hypotheses that may explain the differences in diversity patterns we observed. Our comparative approach to studying the long-term interactions among invaders and invaded communities provides further insight into the role invasive predators play in shaping community structure and dynamics and extends our understanding of the long-term effects of invaders which may aid in identifying more effective management strategies for freshwater conservation.

## METHODS

### Study areas

Our Canadian dataset was generated from a larger survey of Canadian Shield lakes sampled from the 2EB Watershed of south-central Ontario (Cox, 1978) and covers an area of 5635 km<sup>2</sup> (Cairns *et al.*, 2006). The 2EB watershed was an ideal area for our study, as it represents the North American inland lake region with the longest *Bythotrephes* invasion history (Yan *et al.*, 1992). The region also has the best documented pattern of subsequent spread of the invader (Muirhead & MacIsaac, 2005; Weisz & Yan, 2010; Potapov *et al.*, 2011). As of 2006, when our zooplankton data were generated, the watershed contained 53 lakes known to be invaded by *Bythotrephes* (Cairns *et al.*, 2007). The 311 lakes sampled within the 2EB watershed spanned a wide range in

terms of total phosphorus (TP) (0.6–74.8 µg l<sup>-1</sup>; mean, 9.82; median, 7.80), dissolved organic carbon (DOC) (1.8–33.4 mg l<sup>-1</sup>; mean, 5.86; median, 5.30), conductivity (11.6–661 µS cm<sup>-1</sup>; mean, 38.75; median, 23.3), pH (4.69–8.03; mean, 6.18; median, 6.21), area (0.01–10 km<sup>2</sup>; mean, 0.75; median, 0.25) and elevation (169–495.3 m above sea level; mean, 314.6; median, 312.4), as is typical of Canadian Shield lakes.

Our Norwegian dataset was based on a larger study of 1541 lakes covering the entire mainland of Norway (58°3' to 71°4' N) (Walseng *et al.*, 2006). The lakes ranged widely in conductivity (4.1–2000 µS cm<sup>-1</sup>; mean, 47; median, 24), pH (3.8–9.9; mean, 6.2; median, 6.5), area (0.001–363 km<sup>2</sup>; mean, 214; median, 20) and elevation (1.0–1837 m above sea level; mean, 434; median, 307). While only measured in a limited number of localities, the range of total organic carbon (TOC) (0.2–14.9 mg l<sup>-1</sup>; mean, 3.1; median, 2.1) and TP (0.13–69 µg l<sup>-1</sup>; mean, 17; median, 8) confirmed the low-productivity nature of the majority of these lakes (Walseng *et al.*, 2006). Overall, while the chemistry of sampled lakes in both countries was similar, the Norwegian lakes tended to be somewhat softer, and more nutrient poor, and to have a much larger range in elevation than Canadian Shield lakes. Hence, we selected a subset of the Norwegian lakes used by Walseng *et al.* (2006), to obtain a nearly complete match with the Canadian lake dataset with regards to lake characteristics, to avoid confounding factors because of different lake properties (see below: Lake and species selection).

The crustacean zooplankton communities of Canadian Shield and Norwegian lakes are similar, containing many (apparently) identical species as well as many species in the same genus (Keller & Pitblado, 1989; Walseng & Schartau, 2001). We assume such a high degree of overlap in taxonomic relatedness produces communities with strong ecological resemblance (e.g. Walseng & Schartau, 2001); individuals of the same species and within the same genera and families filling the same niches or functional roles (e.g. herbivores, omnivores and predators) in both Canadian and Norwegian lakes. In addition, both countries have similar species diversity per lake (Arnott *et al.*, 1998; Walseng & Schartau, 2001; Boudreau & Yan, 2003), although Norwegian lakes typically have more species that occur with a low frequency (Hessen & Walseng, 2008) and have a littoral habitat preference (Walseng *et al.*, 2006).

### Zooplankton and water chemistry sampling

The sampling protocol for Canadian Shield lakes is described in detail in Cairns *et al.* (2007). Briefly, zooplankton samples were collected between mid-June and late August (the seasonal period of stable zooplankton communities) in 2005 and 2006. Zooplankton were collected using a conical tow net (30 cm diameter, 63 µm mesh). For lakes early in the invasion sequence, *Bythotrephes* often exhibits dramatic seasonal and interannual variability (e.g. Young *et al.*, 2011); thus, to increase the probability of detecting *Bythotrephes*,

two vertical hauls from 2 m above the lake bottom to the surface were collected and combined into a composite sample at each of five stations along the longest fetch of the lake. To account for potential spatial variation in *Bythotrephes* because of wind-induced movement, an additional horizontal haul was taken from the downwind area of the lake (Cairns *et al.*, 2007). Samples were preserved in 5.5% buffered sugar formalin and examined in their entirety for the presence and abundance of *Bythotrephes*. The composite sample taken from the deepest location along the fetch in each lake was processed for zooplankton species following the protocol of Yan *et al.* (2008). A variety of water chemistry samples were generated in each lake at the same deepest station from an epilimnetic + metalimnetic composite sample. These were subsequently analysed at the chemistry laboratory of the Ontario Ministry of the Environment's Dorset Environmental Science Centre (Dorset, Ontario) following the methods of the Ontario Ministry of the Environment (1983).

Norwegian zooplankton were sampled once in each lake between late June and early September (the seasonal period of stable zooplankton communities) in the period from 1970 to 2000. Zooplankton were collected in a vertical haul using a 27.5–30 cm diameter, 90- $\mu$ m mesh net, taken from the bottom to the surface at the deepest part (at least > 10 m) of each lake. Samples were preserved in formalin or Lugol's iodine. This standard method ensured a high number of individuals and an almost complete species list (Walseng *et al.*, 2006; Hessen *et al.*, 2011). All crustaceans were identified to species, as described in Walseng *et al.* (2006). Samples for lake water chemistry were obtained either from c. 0.5 m depth in the central part of the lake or from the outlet, by filling 1 l acid-washed plastic bottles by hand.

### Lake and species selection

For our analyses, we selected a subset of lakes from within the larger lake datasets available from each country to reduce any potential bias in diversity measures as a result of factors other than *Bythotrephes* invasion. First, we excluded lakes with pH < 6 to remove the well-known effect of decreased biodiversity at low pH (Havens *et al.*, 1993; Walseng & Schartau, 2001). Second, we included only lakes that had been sampled once in the summer in only 1 year. For the Canadian dataset, where lakes were sampled in both 2005 and 2006 ( $n = 41$  lakes), we included only the most recent 2006 sample. Third, we removed lakes from each dataset where no species were recorded ( $n = 3$  lakes in Norway) and removed species that were not identified past the genus level, with two exceptions: (1) there were no other representatives of that genus identified to species within the dataset, and (2) *Holopedium*, whose naming conventions are currently under revision (e.g. Rowe *et al.*, 2007). Last, for the Norwegian dataset only, we included only lakes with a surface area between 0.01 and 10 km<sup>2</sup> (1–1000 ha), to correspond to the range observed in the Canadian dataset.

In selecting lakes for our analysis, we also tried to ensure that morphometric and water quality variables in both countries did not differ between lakes where *Bythotrephes* was present or absent. Of the six lake variables (lake area, pH, Secchi disc depth, calcium concentration, conductivity and lake depth) examined in both the Canadian and Norwegian datasets, none of the six in Norway, nor calcium concentrations, conductivity and depth in Canada, differed between lake invasion categories (*Bythotrephes* present vs. absent), respectively (see Table S1 in Supporting Information). However, in Canada, lake area, pH and Secchi disc depth differed between the two groups of lakes (see Table S1 in Supporting Information), which is unsurprising given that *Bythotrephes* is frequently found in deeper, more oligotrophic lakes in North America (MacIsaac *et al.*, 2000; Weisz & Yan, 2011). Linear regression (N.E.K., data not shown) confirmed only weak (lake area, for the *Bythotrephes* absent lake category only) or non-significant relationships (pH and Secchi disc depth for both *Bythotrephes* lake categories) of zooplankton species richness with these variables and thus are not expected to unduly influence diversity comparisons between lake invasion categories.

Given our sampling protocol, incidence (presence–absence) can be more accurately assessed in our datasets than can abundance. In addition, the use of incidence data allows us to examine changes in zooplankton community structure but not changes in density or biomass with invasion. The relative occurrence of rare species, particularly singletons, is likely under-estimated across our datasets, which may unduly influence any subsequent diversity analyses. To create a quantitative definition of species occurrence, we examined rank-occurrence distributions of zooplankton communities from Canada and Norway. We identified discontinuities in the log<sub>10</sub>(occurrence) vs. ranked species relationship to define the frequency of species occurrence (frequent, common and rare) (see Fig. S1 in Supporting Information). For the Norwegian zooplankton community, definitions of frequent, common and rare species determined herein exactly matched definitions assigned to the same species based on a larger study of Norwegian lakes (Walseng *et al.*, 2006). For both countries, only species defined as frequent and common were used in all further analyses (Table 1).

The end result of these selection criteria was a set of 212 lakes and 33 species (including *Bythotrephes*) for our Canadian dataset (with 26 invaded lakes), and 342 lakes and 27 species (including *Bythotrephes*) comprising our Norwegian dataset (with *Bythotrephes* present in 57 lakes) (Table 1).

### Data analysis

To examine patterns of zooplankton diversity and community composition in lakes with and without *Bythotrephes*, we employed both univariate and multivariate statistical analyses conducted on the incidence of zooplankton species in both Canada and Norway. All statistical analyses were conducted

**Table 1** Numerical codes (used in Fig. 4), abbreviations (used in Fig. S1 in Supporting Information), scientific names and frequency of occurrence in all lakes for Canadian and Norwegian zooplankton species. Per cent frequency of occurrence determined by species' presence in all lakes within a dataset (Canada, 212 lakes; Norway, 342 lakes).

Code	Abbreviation	Species name	Occurrence (%)	Code	Abbreviation	Species name	Occurrence (%)
Canada				Norway			
Cladocera				Cladocera			
		<i>Acantholeberis curvirostris</i> *	1.4	acr.har		<i>Acroperus harpae</i> *	0.9
		<i>A. harpae</i> *	0.9	aln.exc		<i>Alonella excisa</i> *	0.3
1	alo.sp	<i>Alona</i> sp.	6.6	aln.nan		<i>Alonella nana</i> *	0.9
2	bos.fre	<i>Bosmina freyi</i>	66.5	alo.aff		<i>Alona affinis</i> *	0.3
3	bos.lie	<i>Bosmina liederi</i>	25.0	alo.gut		<i>Alona guttata</i> *	0.3
4	cer.lac	<i>Ceriodaphnia lacustris</i>	17.9	alp.elo		<i>Alonopsis elongata</i> *	0.9
	bytho	<i>Bythotrephes longimanus</i>	12.3	1	bos.cor	<i>Bosmina coregoni</i>	5.6
5	chy.sph	<i>Chydorus sphaericus</i>	19.3	2	bos.gir	<i>Bosmina longirostris</i>	12.6
6	dap.amb	<i>Daphnia ambigua</i>	19.8	3	bos.spi	<i>Bosmina longispina</i>	87.4
7	dap.cat	<i>Daphnia catawba</i>	50.9		bytho	<i>B. longimanus</i>	16.7
8	dap.dub	<i>Daphnia dubia</i>	13.7		cer.pul	<i>Ceriodaphnia pulchella</i> *	1.2
9	dap.gal	<i>Daphnia galeata</i>	44.8	4	cer.qua	<i>Ceriodaphnia quadrangula</i>	2.9
10	dap.gir	<i>Daphnia longiremis</i>	29.7	5	chy.sph	<i>C. sphaericus</i>	5.3
		<i>Daphnia minnehaha</i> *	0.5	6	dap.cri	<i>Daphnia cristata</i>	20.5
11	dap.pul	<i>Daphnia pulicaria</i>	9.9	7	dap.cuc	<i>Daphnia cucullata</i>	5.6
12	dap.ret	<i>Daphnia retrocurva</i>	21.2	8	dap.gal	<i>D. galeata</i>	32.5
13	dip.bir	<i>Diaphanosoma birgei</i>	80.7		dap.gir	<i>D. longiremis</i> *	0.9
		<i>Disparalona acutirostris</i> *	1.4	9	dap.hya	<i>Daphnia hyalina</i>	7.3
14	eub.lon	<i>Eubosmina longispina</i>	25.5	10	dap.spi	<i>Daphnia longispina</i>	45.3
15	eub.tub	<i>Eubosmina tubicen</i>	37.3	11	dia.bra	<i>Diaphanosoma brachyurum</i>	18.7
		<i>Eurycercus lamellatus</i> *	0.9		eur.lam	<i>E. lamellatus</i> *	1.2
16	holoped	<i>Holopedium</i>	82.5	12	holoped	<i>Holopedium</i>	65.8
17	ily.spi	<i>Ilyocryptus spinifer</i>	3.3	13	lep.kin	<i>Leptodora kindtii</i>	16.4
		<i>Latona setifera</i> *	0.5	14	lim.fro	<i>Limnospira frontosa</i>	4.4
18	lep.kin	<i>L. kindtii</i>	65.6		oph.gra	<i>Ophryoxus gracilis</i> *	0.3
		<i>O. gracilis</i> *	0.5	15	pol.ped	<i>Polyphemus pediculus</i>	12.6
19	pol.ped	<i>P. pediculus</i>	7.5		rhy.fal	<i>Rhynchotalona falcata</i> *	0.3
		<i>Scapholeberis kingi</i> *	1.9		sid.cry	<i>Sida crystallina</i> *	1.5
20	sid.cry	<i>S. crystallina</i>	5.2				
Copepoda				Copepoda			
		<i>Acanthocyclops robustus</i> *	0.5	16	aca.den	<i>Acanthodiptomus denticornis</i>	28.1
		<i>Acanthocyclops vernalis</i>	1.4		aca.rob	<i>A. robustus</i> *	0.3
		complex*					
		<i>Aglaodiptomus leptopus</i> *	0.9		aca.ver	<i>A. vernalis</i> *	0.3
21	cyc.scu	<i>Cyclops scutifer</i>	28.3	17	arc.lat	<i>Arctodiptomus laticeps</i>	14.6
22	dia.bth	<i>Diacyclops bicuspidatus thomasi</i>	40.6	18	cyc.aby	<i>Cyclops abyssorum</i>	2.9
23	epi.lac	<i>Epischura lacustris</i>	37.7	19	cyc.scu	<i>C. scutifer</i>	55.3
24	euc.agi	<i>Eucyclops agilis</i>	15.6		cyc.str	<i>Cyclops strenuus</i> *	0.9
25	euc.ele	<i>Eucyclops elegans</i>	4.2		cyc.vic	<i>Cyclops vicinus</i> *	0.3
26	let.min	<i>Leptodiptomus minutus</i>	68.9		euc.ser	<i>Eucyclops serrulatus</i> *	1.5
		<i>Leptodiptomus sicilis</i> *	0.9	20	eud.des	<i>Eudiptomus graciloides</i>	4.7
		<i>Macrocyclus albidus</i> *	1.4	21	eud.gra	<i>Eudiptomus gracilis</i>	22.2
27	mes.eda	<i>Mesocyclops edax</i>	80.2		eut.lac	<i>Eurytemora lacustris</i> *	0.3
28	ort.mod	<i>Orthocyclops modestus</i>	14.6		eut.vel	<i>Eurytemora velox</i> *	0.3
		<i>Paracyclops poppei</i> *	0.5	22	het.app	<i>Heterocope appendiculata</i>	15.5
29	sen.cal	<i>Senecella calanoides</i>	3.3	23	het.sal	<i>Heterocope saliens</i>	26.6
30	ski.ore	<i>Skistodiptomus oregonensis</i>	51.9		mac.alb	<i>Macrocyclus albidus</i> *	0.6
31	ski.rei	<i>Skistodiptomus reighardi</i>	4.7		meg.gig	<i>Megacyclops gigas</i> *	1.5
32	tro.ext	<i>Tropocyclops extensus</i>	87.3		meg.vir	<i>Megacyclops viridis</i> *	0.3
				24	mes.leu	<i>Mesocyclops leuckarti</i>	7.9
				25	mix.lac	<i>Mixodiptomus laciniatus</i>	7.0
				26	the.oit	<i>Thermocyclops oithonoides</i>	6.1

\*Species were considered rare based on analysis of rank-occurrence distributions (see Fig. S1 in Supporting Information) and were not considered further in any analyses.

using the software package R (v 2.14.1; R Development Core Team, 2011).

We used a multivariate ordination technique to examine zooplankton community-level differences between lakes with and without *Bythotrephes* in Canada and Norway. Correspondence analysis (CA) was conducted separately for each country, using a zooplankton community that included *Bythotrephes*, with the community ecology package *vegan* (v 1.17-0) (Oksanen *et al.*, 2010). To test whether the zooplankton communities in lakes with, differed from lakes without, *Bythotrephes*, we compared the distribution of CA axis I and II scores for lakes with and without *Bythotrephes* in Canada and Norway using a Wilcoxon rank-sum test. We used a nonparametric test to avoid the problems associated with the heavily skewed distribution of, and heterogeneous variances observed for, the CA site scores on both axes for both countries.

To test for differences in zooplankton diversity in both countries, we compared total crustacean zooplankton, cladoceran, and copepod species richness between lakes where *Bythotrephes* was present and absent in both Canada and Norway, respectively. Species richness was defined as the total number of crustacean zooplankton species, cladocerans, or copepods detected in our samples in each lake. To test for differences in the mean species richness between the two categories (*Bythotrephes* presence-absence) in each country, comparisons were made using a two-tailed Student's *t*-test for independent samples. We used the unequal variances assumption for comparisons with heterogeneous variances, as indicated by significant Bartlett's tests. *Bythotrephes* was excluded from the richness counts.

We explored differences in the frequency of zooplankton species occurrence between lakes with and without *Bythotrephes* in both countries. Frequency of species occurrence was calculated as the number of occurrences of species *a* in all lakes where *Bythotrephes* was present ( $F_{BP}$ ) or absent ( $F_{BA}$ ) expressed as a per cent. We fit a linear major axis regression to the  $F_{BP}-F_{BA}$  relationship in each country and tested whether the slopes of each regression differed from one (using a maximum likelihood ratio test), using the (standardized) major axis estimation and testing routines package *SMATR* (v 3.2.6) (Warton *et al.*, 2012). Prior to analysis,  $F_{BP}$  and  $F_{BA}$  values were arcsine transformed to approximate the assumptions of bivariate normality and homogeneity of error variances. In this context, the slope of the  $F_{BP}-F_{BA}$  regression represents the average change in frequency of occurrence of species across the zooplankton community in the presence of *Bythotrephes*. Slope values significantly different than one indicate an overall change in the spatial distribution of zooplankton species with *Bythotrephes* presence.

Finally, we examined the response of individual zooplankton species to the presence of *Bythotrephes* in both countries. First, we calculated the change in the per cent frequency of species occurrence between lakes with and without *Bythotrephes*. Per cent change in occurrence ( $PF_C$ ) of species *a* was

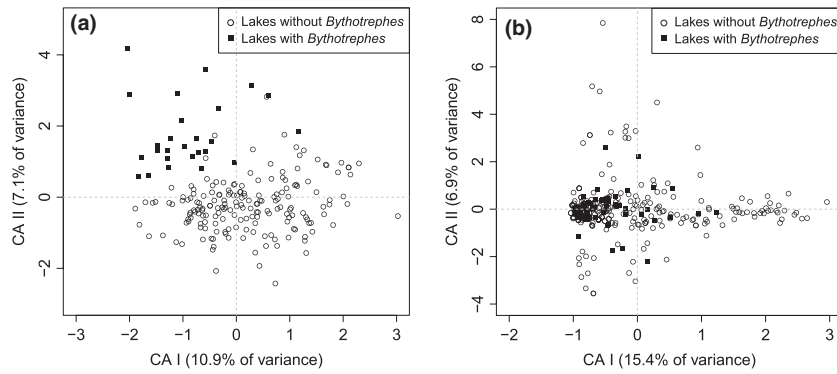
calculated as the difference between  $F_{BP}$  minus  $F_{BA}$ , divided by  $F_{BA}$ , expressed as a per cent. We used permutation tests (after Legendre & Legendre, 1998) to examine whether  $PF_C$  differed significantly from zero for each species in each country. Species presence was randomized across all lakes (i.e. across both *Bythotrephes* present and absent categories) within a dataset, and  $PF_C$  recalculated. The randomization was repeated 9999 times to generate a permutation distribution of  $PF_C$  values. A *P* value was calculated based on the number of values in the  $PF_C$  permutation distribution as extreme as or more extreme to the original  $PF_C$  value. On the basis of  $PF_C$  permutation results, we then assigned a response to each species in the Canadian and Norwegian datasets, that is, a positive, neutral or negative response to the presence of *Bythotrephes*. To examine whether the pattern of species responses to the presence of *Bythotrephes* differed from a random pattern, we conducted chi-square goodness-of-fit tests on the response categories within each country ('within country' tests), expecting equal observations across the three response categories if the pattern was random. We then conducted a chi-square two-sample test for differences in the pattern of species responses to the presence of *Bythotrephes* between Canada and Norway ('between countries' test).

## RESULTS

CA ordination confirmed that all but three Canadian lakes with *Bythotrephes* were assigned to one quadrant of the ordination, demonstrating that the zooplankton communities within these lakes have a different composition compared to non-*Bythotrephes* lakes (Fig. 1a). Such a gradient was not found for Norwegian lakes containing *Bythotrephes* (Fig. 1b). In addition, CA axis I and II scores were significantly different between lake categories in Canada, but not in Norway (Table 2, Fig. 2). Together, these results suggest that the presence of *Bythotrephes* alters zooplankton community composition in Canada, but not in Norway.

Diversity of zooplankton, measured as mean species richness per lake, was significantly lower in Canada and significantly higher in Norway in lakes where *Bythotrephes* was present, when compared to lakes where *Bythotrephes* was absent (Table 3, Fig. 3). Cladoceran richness was significantly lower in the presence of *Bythotrephes* in Canada, while there was no significant difference in Norway. In contrast, copepod richness was significantly higher in Norway in lakes with *Bythotrephes* than without, but there was no difference in Canada (Table 3, Fig. 3).

The configuration of percent frequency of species occurrence with and without *Bythotrephes* differed between countries (Fig. 4). In Norway, *Bythotrephes* appears to negatively impact only common species (< 20% frequency of occurrence), whereas in Canada both common and frequently encountered species were negatively impacted by the presence of *Bythotrephes* (Fig. 4). There was a positive linear regression between  $F_{BP}$  and  $F_{BA}$  in both Canada



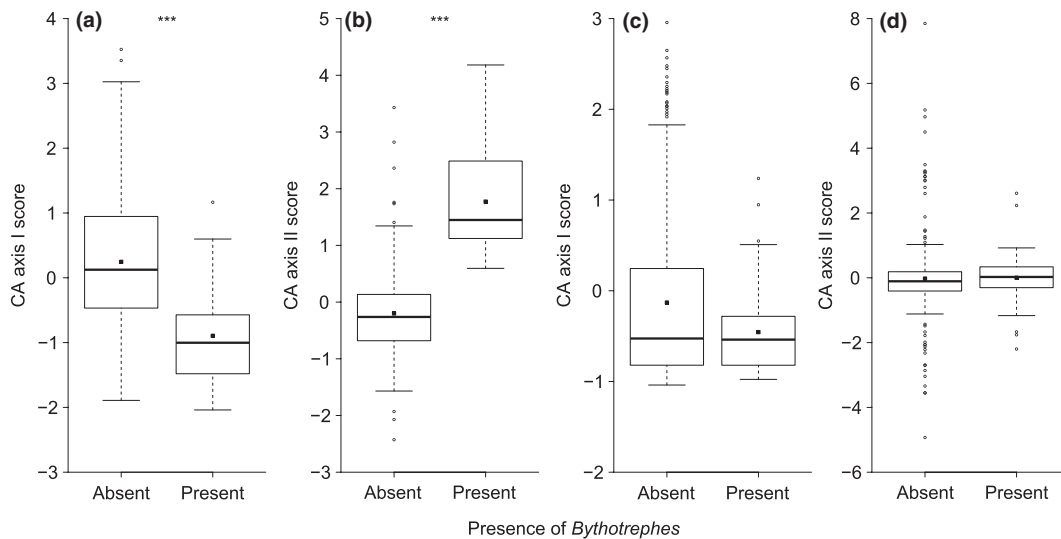
**Figure 1** Correspondence analysis ordination displaying site scores of the zooplankton communities from lakes in (a) Canada and (b) Norway. *Bythotrephes* was included as a member of the zooplankton community in both countries.

**Table 2** Results of Wilcoxon rank-sum tests comparing correspondence analysis (CA) axis I and II scores between lakes where *Bythotrephes* is present (P) or absent (A) in Canada and Norway.

Country	Metric	<i>Bythotrephes</i> lake status		W value	P value
		Mean			
Canada	CA	P	-0.89	3993	< <b>0.0001</b>
	Axis I	A	0.246		
	CA	P	1.77	192	< <b>0.0001</b>
	Axis II	A	-0.20		
Norway	CA	P	-0.456	9047	0.161
	Axis I	A	-0.129		
	CA	P	0.003	7175	0.176
	Axis II	A	-0.022		

Values in bold indicate significant differences at  $P < 0.05$ .

(FBP =  $-10.2 + 1.18 \cdot \text{FBA}$ ,  $R^2 = 0.64$ ,  $P < 0.0001$ ) and Norway (FBP =  $-14.8 + 1.65 \cdot \text{FBA}$ ,  $R^2 = 0.87$ ,  $P < 0.0001$ ). However, in Canada, the slope was not significantly different from one ( $r = 0.215$ , d.f. = 30,  $P = 0.237$ ), indicating the presence of species that both increased and decreased their population distributions in the presence of *Bythotrephes*. In contrast for Norway, the slope was significantly greater than one ( $r = 0.729$ , d.f. = 24,  $P < 0.0001$ ), indicating more species, on average, increased their population distributions in lakes when *Bythotrephes* was present. There was a markedly different pattern in the per cent change in frequency of species occurrence ( $\text{PF}_C$ ) with *Bythotrephes* presence in Canada vs. Norway. In Canada and Norway, the  $\text{PF}_C$  of 22 and 16 species, respectively, were significantly affected by the presence of *Bythotrephes* ( $P < 0.1$ ) (Table 4). In both Canada and Norway, the distributions of species with positive,



**Figure 2** Correspondence analysis (CA) scores for axes I and II in lakes from (a, b) Canada and (c, d) Norway characterized by the presence–absence of *Bythotrephes*. The rectangle shows the interquartile range (IQR; 25th to 75th percentile), the solid black line represents the median and the black square represents the mean. Whiskers represent the minimum and maximum values or 1.5\*IQR from the first or third quartile, whichever is less. Open circles indicate values larger or smaller than 1.5\*IQR. Significant differences in mean CA axis scores between lakes with and without *Bythotrephes* are indicated ( $***P < 0.001$ ).

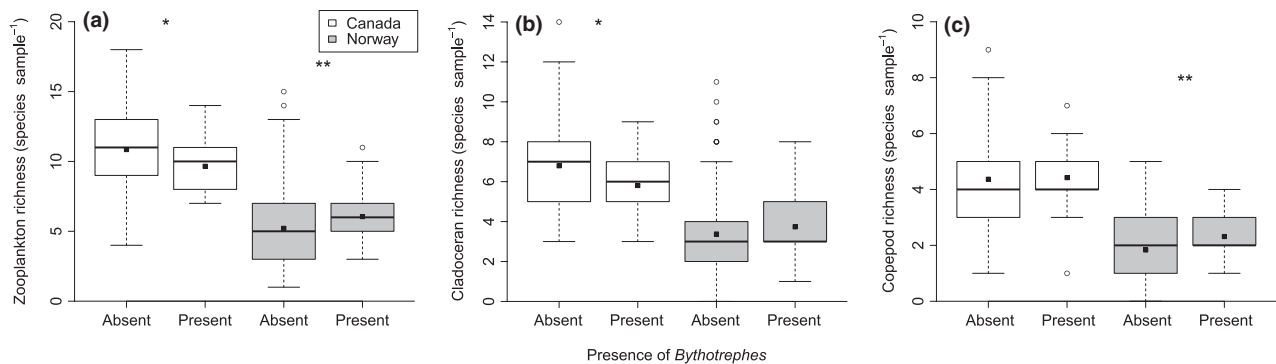


**Table 3** Results of Student's *t*-tests for independent samples comparing zooplankton, cladocera, and copepod richness, respectively, between lakes where *Bythotrephes* is present (P) or absent (A) in Canada and Norway.

Country	Metric	<i>Bythotrephes</i> lake status	Mean	<i>t</i> value	d.f.	<i>P</i> value
Canada	Zooplankton	P	9.65	2.59	39.34*	<b>0.013</b>
		A	10.9			
	Cladocera	P	5.81	2.50	210	<b>0.013</b>
		A	6.80			
Norway	Zooplankton	P	4.42	-0.184	210	0.855
		A	4.37			
	Cladocera	P	6.05	-3.18	113.9*	<b>0.002</b>
		A	5.19			
Copepoda	P	3.74	-1.68	96.76*	0.092	
	A	3.36				
Copepoda	P	2.32	-3.33	94.45*	<b>0.001</b>	
	A	1.83				

Values in bold indicate significant differences at  $P < 0.05$ .

\*Degrees of freedom (d.f.) adjusted for unequal variances.



**Figure 3** (a) Zooplankton, (b) cladoceran, and (c) copepod species richness (species per sample) in lakes from Canada and Norway characterized by the presence–absence of *Bythotrephes*. Components of boxes, whiskers, and circles defined as in Fig. 2. Significant differences in mean richness between lakes with and without *Bythotrephes* are indicated by an asterisk (\* $P < 0.05$ ; \*\* $P < 0.01$ ). *Bythotrephes* was excluded from the richness calculations.

neutral and negative responses to the presence of *Bythotrephes* were not random ( $P < 0.05$ ), and the distribution of species responses differed significantly between the two countries ( $P < 0.001$ ) (Table 5). Significantly more species in Norway demonstrated a positive response, while significantly more species in Canada demonstrated a negative response, to the presence of *Bythotrephes* (Table 5).

Of the six species found in both Canada and Norway, both *Chydorus sphaericus* and *Daphnia galeata* had a neutral and positive response to the presence of *Bythotrephes*, respectively, in both countries (Table 4). The remaining 4 species (*Holopedium*, *Leptodora kindtii*, *Polyphemus pediculus* and *Cyclops scutifer*) exhibited differing responses to the presence of *Bythotrephes*. *Holopedium*, *P. pediculus* and *C. scutifer* had positive responses in Norway but neutral or negative ones in Canada. *Leptodora kindtii* had a negative response to *Bythotrephes* presence in Canada but a neutral one in Norway (Table 4).

## DISCUSSION

Comparing the impacts of the invertebrate predator *Bythotrephes* in lakes in Canada and Norway has revealed differential impacts on zooplankton biodiversity and community structure over time that could not be predicted from analysis of short-term impacts observed within the invaded range alone. Short-term impacts of *Bythotrephes*, as observed in Canadian Shield lakes, led to lower zooplankton diversity, particularly for cladocerans, a pattern which has been observed multiple times following *Bythotrephes* invasion into other North American lakes (Boudreau & Yan, 2003; Barbiero & Tuchman, 2004; Strecker *et al.*, 2006). In addition, zooplankton community composition differed dramatically in lakes with and without *Bythotrephes*. Species occurrence decreased at the individual species level, but not at the overall community level, suggesting the redistribution of species across the watershed because of *Bythotrephes* invasion has not yet

**Table 4** Per cent change in species frequency of occurrence (PFC) due to the presence of *Bythotrephes*. Each species was tested whether it deviated from a null hypothesis of ‘zero per cent change’ using permutation tests. Response of species to the presence of *Bythotrephes* is based on results of the permutation tests and classified as negative (species disappeared or decreased), positive (species increased) or neutral (no significant change).

Species name	% Change	Response	Species name	% Change	Response
Canada			Norway		
<i>Alona</i> sp.	−100***	Negative	<i>Bosmina coregoni</i>	−100***	Negative
<i>Bosmina freyi</i>	−14.8	Neutral	<i>Bosmina longirostris</i>	−48.7	Neutral
<i>Bosmina liederii</i>	−57.1*	Negative	<i>Bosmina longispina</i>	12.7**	Positive
<i>Ceriodaphnia lacustris</i>	−80.7**	Negative	<i>Ceriodaphnia quadrangula</i>	114.3*	Positive
<i>Daphnia ambigua</i>	−100***	Negative	<i>Daphnia cristata</i>	−26.2	Neutral
<i>Daphnia catawba</i>	−35.0*	Negative	<i>Daphnia cucullata</i>	−100***	Negative
<i>Daphnia dubia</i>	−74.5*	Negative	<i>Daphnia hyalina</i>	57.9	Neutral
<i>Daphnia longiremis</i>	35.0	Neutral	<i>D. longispina</i>	45.8**	Positive
<i>Daphnia pulicaria</i>	68.3*	Positive	<i>Diaphanosoma brachyurum</i>	−66.7**	Negative
<i>Daphnia retrocurva</i>	−48.9	Neutral	<i>Limnospida frontosa</i>	−64.3	Neutral
<i>Diaphanosoma birgei</i>	−36.2***	Negative	<i>Acatodiaptomus denticornis</i>	40.0*	Positive
<i>Eubosmina longispina</i>	126.8***	Positive	<i>Arctodiaptomus laticeps</i>	114.3**	Positive
<i>Eubosmina tubicen</i>	−61.8**	Negative	<i>Cyclops abyssorum</i>	−100***	Negative
<i>Ilyocryptus spinifer</i>	186.2*	Positive	<i>Eudiaptomus graciloides</i>	−28.6	Neutral
<i>Sida crystallina</i>	−28.5	Neutral	<i>Eudiaptomus gracilis</i>	−6.3	Neutral
<i>Diacyclops bicuspidatus thomasi</i>	102.9***	Positive	<i>Heterocope appendiculata</i>	62.5*	Positive
<i>Epischura lacustris</i>	65.1**	Positive	<i>Heterocope saliens</i>	31.9*	Positive
<i>Eucyclops agilis</i>	−77.6**	Negative	<i>Mesocyclops leuckarti</i>	−80.8*	Negative
<i>Eucyclops elegans</i>	472.3*	Positive	<i>Mixodiaptomus laciniatus</i>	31.6	Neutral
<i>Leptodiaptomus minutus</i>	20.2	Neutral	<i>Thermocyclops oithonoides</i>	−47.4	Neutral
<i>Mesocyclops edax</i>	−30.8**	Negative			
<i>Orthocyclops modestus</i>	−23.4	Neutral			
<i>Senecella calanoides</i>	186.2*	Positive			
<i>Skistodiaptomus oregonensis</i>	−43.9*	Negative			
<i>Skistodiaptomus reighardi</i>	−100***	Negative			
<i>Tropocyclops extensus</i>	−3.4	Neutral			
Found in both countries					
<i>Chydorus sphaericus</i>	−0.6	Neutral	<i>C. sphaericus</i>	−37.5	Neutral
<i>Daphnia galeata</i>	55.9*	Positive	<i>D. galeata</i>	85.2***	Positive
<i>Holopedium</i>	8.2	Neutral	<i>Holopedium</i>	18.1*	Positive
<i>Leptodora kindtii</i>	−38.5**	Negative	<i>L. kindtii</i>	−4.3	Neutral
<i>Polyphemus pediculus</i>	−100***	Negative	<i>P. pediculus</i>	93.5*	Positive
<i>Cyclops scutifer</i>	−35.0*	Negative	<i>C. scutifer</i>	42.9***	Positive

\* $P < 0.1$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

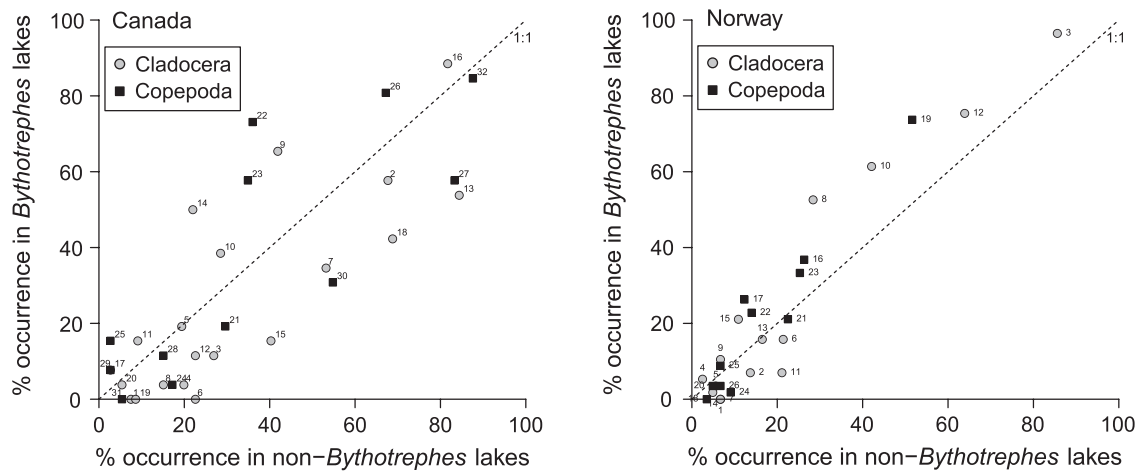
**Table 5** Results of contingency table analysis for the response of species occurrence to the presence of *Bythotrephes*. Within country test: chi-square goodness-of-fit tests for difference in pattern of species responses to *Bythotrephes* from a random pattern (i.e. expected frequencies across three classes = 33.33); between countries test: chi-square two-sample test for difference in pattern of species responses to *Bythotrephes* between Canada and Norway. Species response categories defined as in Table 4.

Test	Country	Response to <i>Bythotrephes</i> (%)			$\chi^2$	d.f.	P
		Positive	Neutral	Negative			
Within country	Canada	25.0	28.1	46.9	8.398	2	<b>0.015</b>
	Norway	42.3	38.5	19.2	9.205	2	<b>0.010</b>
Between countries	Canada–Norway				17.315	2	<b>0.0002</b>

Values in bold indicate significant differences at  $P < 0.05$ .

reached equilibrium. In contrast, in Norway, a greater diversity of zooplankton, particularly for copepod species, occurred in lakes where *Bythotrephes* has been present for

long periods. This pattern of greater zooplankton species diversity with *Bythotrephes* presence confirms observations made by Hessen *et al.* (2011) for a different Norwegian



**Figure 4** Per cent frequency of occurrence of zooplankton species in lakes from Canada and Norway in the presence–absence of *Bythotrephes*. Numerical codes representing species are listed in Table 1. Species falling below the 1:1 line have a lower per cent occurrence in the presence of *Bythotrephes*.

dataset of lakes that span a greater range of physicochemical properties. In addition, Norwegian zooplankton community composition could not be distinguished among lakes based on the presence–absence of *Bythotrephes*. Species occurrences increased over both the community and individual species level, suggesting *Bythotrephes* presence increases the population distributions of zooplankton on regional scales. Overall, our analyses suggest that *Bythotrephes* can modify zooplankton community structure, diversity and incidence of species in a short period (i.e. a few decades) after invasion but also that zooplankton can adapt to the presence of *Bythotrephes* over time.

The differential effect of *Bythotrephes* on zooplankton biodiversity between the two countries appears to be driven by the specific incidence level of species impacted within the recipient communities. In Norway, *Bythotrephes* negatively impacted only the less common species, while both common and frequently occurring species were negatively impacted in Canada. As there were few common or frequently encountered species that were negatively affected in Norway in *Bythotrephes* presence, diversity on average increased. In contrast, in Canadian lakes, a greater number of common and frequently encountered species were negatively, rather than positively, affected by *Bythotrephes* presence; thus, diversity on average decreased.

Several different hypotheses may explain the differential impacts of *Bythotrephes* on zooplankton occurrence, diversity and community structure. First, the morphological form of *Bythotrephes* that invaded Canada may be different from the form that currently exists in Norway, with Canada having inherited a more voracious predator and superior competitor than the variant in Norway, resulting in a negative impact on zooplankton in Canada but not Norway. Second, *Bythotrephes* may reduce zooplankton diversity in Canada through direct predation on species that possess ineffective morphological, behavioural and/or physiological anti-predator

defences, because of the lack of a shared evolutionary history with *Bythotrephes*. In contrast, over thousands of years, Norwegian species have adapted to avoid or withstand *Bythotrephes* predation, and thus diversity eventually recovers. Third, *Bythotrephes* presence may indirectly alter interspecific interactions (e.g. competition, predation) within the zooplankton community, promoting greater species co-existence in Norway, but not in Canada. And fourth, *Bythotrephes* presence in Norway may complement the number of existing planktivorous predators per lake, creating more niches in which zooplankton species can co-exist, resulting in higher species diversity. Alternatively, *Bythotrephes* invasion in Canada has overburdened the ecosystem with too many planktivorous predators, resulting in a decline in prey diversity.

The observed differences in zooplankton occurrence, diversity and community structure between Canada and Norway are unlikely to be attributed to differences in the morphological form of *Bythotrephes* between the two countries. Historically, *Bythotrephes* in North America was classified as *B. cederstroemi*, because of the considerable plasticity observed in its body size and tail spine morphology (Burkhardt, 1994; Straile & Halbich, 2000; Branstrator, 2005). However, subsequent morphological and genetic investigations have shown that these various ‘forms’ represent a single polymorphic species, *B. longimanus* (Berg & Garton, 1994; Martin & Cash-Clark, 1995; Therriault *et al.*, 2002; Colautti *et al.*, 2005). The mean female body size of *Bythotrephes*, which excludes the length of the abdominal process, ranges from 1.0 to 4.0 mm in Canadian Shield lakes (Yan & Pawsen, 1998; Young, 2008) and 1.2 to 3.0 mm in Norway (Flössner, 2000). As the total range in body size of *Bythotrephes* between the two countries overlaps strongly, one would expect the physiological demands and prey size preferences to be similar. In addition, *Bythotrephes* has been shown to be the superior competitor with other carnivorous cladocerans, particularly *L. kindtii*, in both countries (Branstrator, 2005;

Hessen *et al.*, 2011; Weisz & Yan, 2011), suggesting little differentiation in the ecological attributes of *Bythotrephes* between Canada and Norway.

Ecological theory predicts that phylogenetically unique taxa are more likely to become successful invaders. As native taxa have no history of coexistence with the invader, preventing the co-evolution of prey defences and countermeasures, the invader has a greater effect on communities that lack similar species (Ricciardi & Atkinson, 2004; Cox & Lima, 2006). The dramatic decline or disappearance of many less common species (e.g. those found in c. 20% or fewer lakes) in both Norway and Canada in the presence of *Bythotrephes* supports the hypothesis that some zooplankton species are naïve to *Bythotrephes*' predation. The *Bythotrephes* invasion introduced a new predator archetype into the freshwater ecosystems of North America, as *Bythotrephes* is an atypical invertebrate predator in terms of prey choice, hunting and feeding mode (Schulz & Yurista, 1999) and has a strong reliance on visual predation rather than the tactile cues utilized by other common invertebrate predators (Muirhead & Sprules, 2003; Pangle & Peacor, 2009). However, in Canada, many commonly and frequently distributed species also suffered population losses after *Bythotrephes* invasion, whereas this pattern was not observed for Norway, suggesting many zooplankton species suffer population losses when first exposed to *Bythotrephes*, but over time, some species adapt to withstand or avoid predation. In contrast, despite coexisting in Norway for thousands of years, less commonly observed species may never have fully adapted anti-predator defences to *Bythotrephes*, owing to the fact that they have small populations that likely experienced little exposure to this predator and thus did not develop a shared evolutionary history with *Bythotrephes*.

*Bythotrephes* predation may alter interspecific interactions among prey species differently in zooplankton communities in Canada and Norway, resulting in the observed differential effects on zooplankton distributions, biodiversity and community composition. For example, *Bythotrephes* predation on superior competitors could alter the equality of competitive abilities that exist, as well as the resource partitioning among members of the zooplankton community, varying the potential coexistence of any number of prey species (Chase *et al.*, 2002). In addition, less commonly occurring species may be outcompeted by superior competitors who, in response to *Bythotrephes* presence, changed habitat preferences (e.g. induced vertical migrations into different thermal layers; Pangle *et al.*, 2007). Norwegian zooplankton communities are characterized by few frequently and commonly, but many rarely, occurring species (Hessen & Walseng, 2008). Thus, the removal of even one dominant competitor because of *Bythotrephes* predation could result in a positive effect on prey species coexistence in Norway. The removal of a dominant competitor may also explain why omnivorous copepods appear to benefit from *Bythotrephes* predation, as they may be better poised to take advantage of newly available resources, particularly in the lower productivity lakes found

throughout Norway. Interestingly, three (*L. kindtii*, *P. pediculus* and *C. scutifer*) of the four species with differing responses to *Bythotrephes* in Canada and Norway are carnivores, suggesting *Bythotrephes* may alter interspecific interactions within the zooplankton community through competition with other predators. As a result, shifting predatory regimes in lakes where *Bythotrephes* is present would have cascading consequences for the rest of the zooplankton community.

Alternatively, differences between Canada and Norway in the planktivorous fish communities present may also explain the observed differential effects of *Bythotrephes* predation. For example, *Bythotrephes* presence in Norway complements the number of existing planktivorous predators per lake, perhaps creating more niches and greater resource availability in which zooplankton species can co-exist, resulting in higher species diversity. In Norway, *Bythotrephes* is typically absent from lakes with very high predation pressure (e.g. shallow lakes with fish communities dominated by cyprinids) and present in low-predation communities dominated by brown trout, salmonids or coregonids (Hessen *et al.*, 2011). Previous studies suggested that fish predation was not a significant predictor of zooplankton diversity in these lakes (Hessen *et al.*, 1995, 2006), suggesting that *Bythotrephes* may be filling the functional role of a small fish in lakes with low fish predation pressure. Owing to its dependence on light availability rather than hydromechanical cues to detect its prey (Muirhead & Sprules, 2003; Pangle & Peacor, 2009), as well as its ability to consume prey items from a wide size spectrum (Schulz & Yurista, 1999), *Bythotrephes* appears more functionally equivalent to a planktivorous larval fish than an invertebrate size-dependent predator. Further, *Bythotrephes* trophic position has been found to overlap with that of young-of-year fish in Lago Maggiore, Italy (Visconti & Manca, 2011). In contrast, if the addition of *Bythotrephes* to Canadian Shield lakes increases the predation pressure experienced by zooplankton prey beyond some threshold, predation would have very little effect on increasing the diversity of zooplankton prey resources (Chase *et al.*, 2002), leading to a negative effect on prey species coexistence and diversity. On the other hand, *Bythotrephes* is a large, conspicuous zooplankton that is itself preyed upon by planktivorous fish in both countries (de Bernardi *et al.*, 1987; Coulas *et al.*, 1998; Pothoven *et al.*, 2007; Young *et al.*, 2009; Hessen *et al.*, 2011). If *Bythotrephes* replaces other zooplankton as the primary prey species of planktivorous fish, it could also alter interspecific zooplankton interactions, because of the changing predation pressure on both *Bythotrephes* and zooplankton over time. In Norwegian lakes, the long co-occurrence of *Bythotrephes* with its fish predators may cause a greater check on *Bythotrephes* abundance, reducing the top-down pressures on its zooplankton prey and resulting in higher diversity in lakes where *Bythotrephes* is present.

We currently do not have enough information to clearly distinguish which of the above possible hypotheses are responsible for the observed differential effects of *Bythotrephes* predation on zooplankton occurrence, diversity and

community structure in Canada and Norway. However, given our current evidence, we suggest the most plausible hypothesis explaining higher diversity in Norway is attributed to a combination of zooplankton species adapting to withstand or avoid *Bythotrephes* predation, and the alteration of interspecific interactions among the members of the zooplankton community, enabling them to increase their populations in space and time. Experimental manipulations are required to fully elucidate the mechanisms behind *Bythotrephes*' divergent effects on prey spatial distribution, diversity and community structure in the two countries.

The long-term effects of *Bythotrephes* invasion on zooplankton communities may be less severe than those observed earlier in the invasion sequence. Using Norway as a long-term predictor of zooplankton biodiversity, the future of Canadian Shield zooplankton communities may have fewer zooplankton species per lake with a relatively greater number of copepod species and be dominated by species that can avoid, withstand or are insensitive to the predatory effects of *Bythotrephes*. However, invaded Canadian zooplankton communities may not evolve along the same path as Norwegian species given the slight differences in lake abiotic gradients, number of species in the community and the differential responses of select species to *Bythotrephes* presence. With only 20 years of exposure to *Bythotrephes* (Yan *et al.*, 1992), zooplankton communities in Canadian Shield lakes will require a longer period of time to adjust to changes imposed by *Bythotrephes* invasion and for the community to reach a new equilibrium. The time required for such equilibrium to be achieved is unknown, but the ongoing spread of *Bythotrephes* throughout Canadian Shield lakes (Cairns & Yan, 2011) and the temperate lakes of the Midwestern USA (Kerfoot *et al.*, 2011) implies zooplankton community composition over regional scales may be in a state of flux for at least the immediate future.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Rank-occurrence of zooplankton species in Canada and Norway.

**Table S1** Statistical results for lake abiotic variables.

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## BIOSKETCHES

Focus of the research teams: Canadian team – limnology and aquatic ecology, biological invasions, restoration ecology, with a focus on zooplankton (**Noreen E. Kelly** and **Norman D. Yan**).

Norwegian team – aquatic biodiversity and trophic interactions, effects of acidification and eutrophication (**Dag O. Hessen** and **Bjørn Walseng**) and ecological stoichiometry (**Dag O. Hessen**).

Author contributions: N.D.Y., D.O.H. and B.W. conceived the idea; N.D.Y. provided the Canadian data and B.W. assembled most of the Norwegian data; N.E.K. performed analyses and wrote the paper; all authors discussed the results and commented on earlier versions of the manuscript.

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