

## Modeling *Bythotrephes longimanus* invasions in the Great Lakes basin based on its European distribution

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With 3 figures, 1 table and 1 appendix

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**Abstract:** The predatory cladoceran *Bythotrephes longimanus* LEYDIG has a natural distribution that extends throughout much of the Palearctic region, and an ever increasing distribution in the Great Lakes basin of North America, where it was first observed in 1982. In this study we define characteristics of 55 waterbodies with and without *Bythotrephes* in Europe, and use these distributions to predict the species' occurrence in 49 lakes in the Great Lakes basin of North America. Lakes in Europe that supported *Bythotrephes* were significantly larger, deeper, had higher transparency and lower maximum bottom temperature during summer, and lower total chlorophyll concentration, than those that lacked the species. These patterns also were observed for lakes in North America, although differences between invaded and noninvaded basins were significant only for lake area and maximum depth. A discriminant function model correctly predicted *Bythotrephes* occurrence in 91 % of study lakes in Europe, and was influenced most by Secchi disk transparency and lake surface area. Application of this model to North America correctly predicted occurrence of *Bythotrephes* in 82 % (18 of 22) of lakes in which the species has been recorded. However, the model incorrectly predicted *Bythotrephes* presence in 74 % (20 of 27) of lakes in which the species has not yet been observed. These findings indicate that many of the study lakes in the Great Lakes basin may be vulnerable to invasion by *Bythotrephes*. Human activ-

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ities responsible for *Bythotrephes* dispersal must be curtailed to reduce additional invasions in Europe and the Great Lakes region.

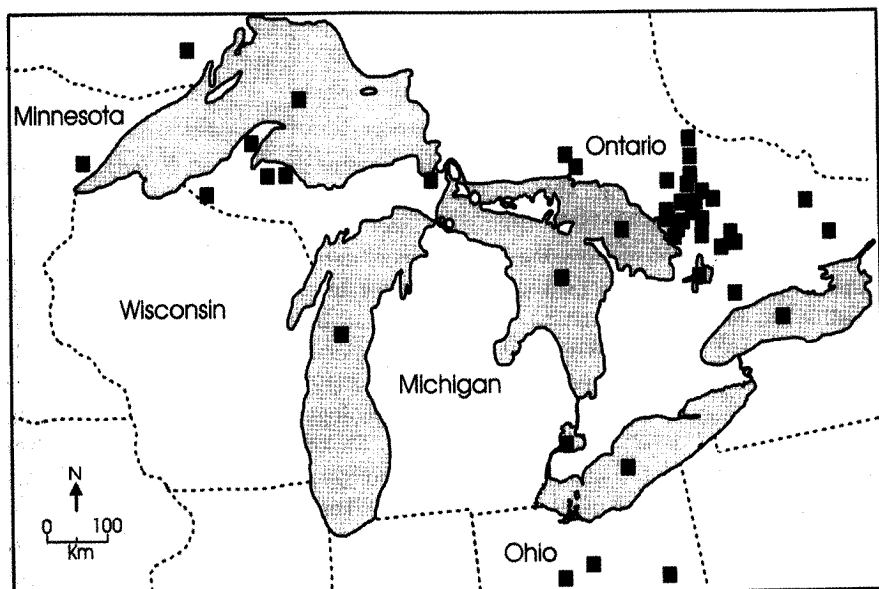
**Key words:** biological invasion, exotic species, zooplankton, invasion models.

## Introduction

Structure and function of planktonic and benthic communities throughout Europe have been dramatically affected by introductions of nonindigenous species. European waterbodies that are subject to intensive human use have been particularly receptive to and affected by introduced species. For example, the River Rhine and Baltic Sea currently support many nonindigenous species, many of which originated in southeast Europe, Asia or North America (TITTI-ZER 1996, KETELAARS et al. 1999, OLENIN & LEPPÄKOSKI 1999).

In North America, the Laurentian Great Lakes have been invaded by a large number of species (>140; MILLS et al. 1993). Release of ballast water by inter-continental ships is the predominant mechanism responsible for species introductions to the Great Lakes for the latter half of the twentieth century (MILLS et al. 1993). Seventy percent of the animal taxa that have been introduced to, and have established in, the Great Lakes over the past fifteen years are endemic to the Ponto-Caspian region (RICCIARDI & MACISAAC 2000). These invasions appear to be linked to deballasting of water collected at European ports. Very few ships travel in ballast directly from Ponto-Caspian ports to the Great Lakes (LOCKE et al. 1991), thus many of these introductions have apparently occurred as secondary invasions from western or northern European waterways that were previously invaded by Ponto-Caspian taxa. Ports on the Baltic Sea and lower River Rhine appear to be among the most important waterways linked to invasions of Eurasian species to the Great Lakes. Allozyme patterns of North American populations of *Bythotrephes* are very similar to those from the Baltic Sea – Lake Ladoga corridor (D. BERG, unpubl. data), corroborating SPRULES et al.'s (1990) speculation that this region was the most likely source of Great Lakes' populations.

*Bythotrephes* has an extensive natural distribution throughout the Palearctic region (e.g. ISCHREYT 1930, PATALAS & PATALAS 1966, KETELAARS & GILLE 1994, GRIGOROVICH et al. 1998). The species also has an invasion history in Europe and Asia (see KETELAARS & VAN BREEMEN 1993, KETELAARS & GILLE 1994). For example, beginning in 1987 *Bythotrephes longimanus* was first observed in the Biesbosch reservoirs in the Netherlands (KETELAARS & GILLE 1994). It also has been introduced to other basins in the Netherlands, Belgium and Germany (KETELAARS & GILLE 1994, KETELAARS, unpubl. data). *Bythotrephes* was first observed in North America in Lake Ontario in



**Fig. 1.** Occurrence of *Bythotrephes* in lakes and reservoirs in North America. As of summer 1999, the species had been reported in 42 basins.

1982, and soon thereafter in Lakes Huron and Erie (BUR et al. 1986, LANGE & CAP 1986, JOHANSSON et al. 1991). Subsequent to colonization of the remaining Great Lakes, *Bythotrephes* invaded inland basins in Ontario, Michigan, Minnesota and Ohio (YAN et al. 1992, K. FERRY, R. WRIGHT, L. NEUWAHL & T. JARNAGIN, pers. comm.). As of summer 1999, *Bythotrephes* has been identified in forty-two basins in North America (Fig. 1).

*Bythotrephes* may exert strong effects on zooplankton community species composition and size structure (YAN & PAWSON 1997, MANCA & RUGGIU 1998), thus it is important to understand factors that influence its natural and human-assisted dispersal. Ecosystem managers currently lack this information and have been unable to erect effective defenses against further invasions in consequence. In this study we attempt to predict the distribution of *Bythotrephes* in North American lakes based on the species' European distribution. Specific objectives include an examination of limnological characteristics of lakes that support or lack *Bythotrephes* in Europe and in North America, and construction of a discriminant function model to describe characteristics of lakes in which the species does and does not occur in Europe. We then apply the model to lakes in the Great Lakes drainage to forecast lake vulnerability to invasion.

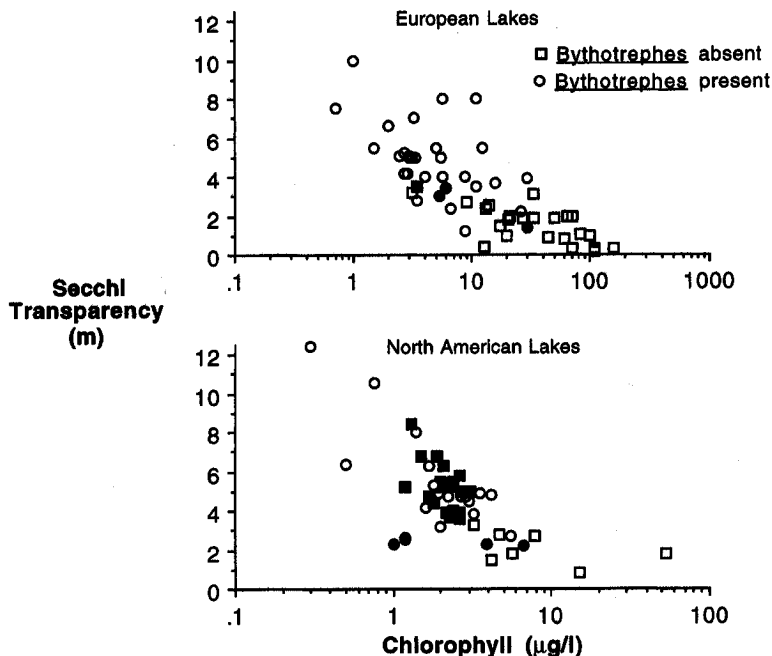
## Materials and methods

### *Bythotrephes* systematics

In this study we make no attempt to distinguish basins that support *B. longimanus* or *B. cederstroemi*. The nature of morphological variation in these 'species' has long troubled ecologists (see BUR et al. 1986). NILSSON (1979) and others support the original classification of the group based on differences in body size and caudal appendage shape, and argued that the taxa are indeed separate species. However, ecological, breeding and genetic studies indicate that these taxa are likely conspecific. MORDUKHAI-BOLTOVOSKOI & RIVIER (1987) suggested that *B. cederstroemi* is a product of thermally-induced cyclomorphosis in *B. longimanus*. EVANS (1988) provided some support for this hypothesis, observing a seasonal shift in morphology of animals in Lake Michigan from 'longimanus' type to 'cederstroemi' type. MORDUKHAI-BOLTOVSKAYA (1959) questioned the utility of caudal appendage morphology to delineate *Bythotrephes* species, and the very existence of *B. cederstroemi*, based on laboratory studies of offspring produced by parthenogenetic females (with mature broods) from Rybinsk Reservoir, Russia. A small fraction of females of both 'species' produced young of the other 'species' and some females produced mixed broods of both 'species'. MORDUKHAI-BOLTOVSKAYA (1959) also noted that *B. longimanus* dominated populations in the reservoir during June, while the *cederstroemi* form of *B. longimanus* usually dominated during warmer months. Finally, the genetic distance of sympatric populations of the two 'species' from Finland was less than that of allopatric European populations of either *B. cederstroemi* or of *B. longimanus* (BERG & GARTON 1994, D. BERG, unpubl. data). Emerging evidence, therefore, points toward a single, polymorphic species of *B. longimanus*.

### Univariate and multivariate analyses

We initially developed a database of European and Asian lakes to assess distribution patterns of *Bythotrephes* (MACISAAC et al., unpubl. data). The database represents an expanded version of that employed by RAMCHARAN et al. (1992) to assess occurrence of *Dreissena polymorpha* in European lakes. In total, *Bythotrephes* was reported present in 510 and absent in 130 waterbodies. The initial database included forty-three physical, chemical and biological characteristics of these basins. However, because we were unable to obtain comprehensive limnological data for many of the lakes, this dataset was reduced to five commonly measured variables. The variables selected – lake surface area, maximum depth, Secchi disk depth, and total chlorophyll and total phosphorus concentrations – represent characterizations of waterbodies of importance to, and commonly measured by limnologists, fisheries managers and ecologists. For example, lake area and depth have been correlated with crustacean zooplankton diversity (DODSON 1992, ARNOTT et al. 1998), while Secchi disk transparency, chlorophyll concentration and total phosphorus concentration are typically related to lake trophic status (e.g. MOLOT & DILLON 1991, SCHANZ 1994, HÅKANSON 1995, Fig. 2). One limitation of our data is the lack of standardized planktivory measures. Intensity of planktivory is an obvious factor that may influence the spatial distribution and temporal abun-



**Fig. 2.** Relationship between Secchi disk transparency and total chlorophyll concentration in European and North American lakes. Open symbols represent field records of *Bythotrephes* presence (circle) or absence (box). Lakes lacking *Bythotrephes* which the discriminant function model predicted would support the species are indicated by solid boxes, while lakes supporting the species that are predicted to lack it are indicated by solid circles. Note that scales differ on the x-axis in the two panels.

dance of large zooplankton like *Bythotrephes* (e.g. see LANGELAND 1972, STENSON 1979, DE BERNARDI et al. 1987, BERGSTRAND 1990, JEPPESEN et al. 1996).

We were able to obtain limnological data for 24 and 31 European lakes in which *Bythotrephes* was reported absent or present, respectively (Appendix 1). Selected lakes occur throughout *Bythotrephes*' distribution range on the European continent. In cases where multiple years of physical, chemical and biological data were available, we selected the most recent year. Values for summer months were averaged when intra-annual data were available. Sources of physical, chemical and biological information for European and North American lakes is provided in Appendix 1. Occurrence of *Bythotrephes* was based on literature reports and personal communications with aquatic biologists familiar with the basins. We sought personal corroboration of cases in which *Bythotrephes* was not reported as a component of the zooplankton community in published reports. In three instances, lakes that once supported *Bythotrephes* were classified as non-*Bythotrephes* lakes. Lake Haussee, Germany, was reported to contain *B. longimanus* in 1957 but not when the basin was resampled in recent years (FLÖSSNER 1972, P. KASPRZAK, pers. comm.). Lake Ringsjön, Sweden, was also reported to support the species in 1883 but not when it was resampled in 1973 and 1982 (BERGSTRAND

1990). *Bythotrephes* was historically found in Esthwaite Water, England, though the species is now missing from the lake (SMYLY 1972). These changes stand in contrast to the three Biesbosch reservoirs, Netherlands, and other waterbodies in the lowlands of western Europe which have been invaded by *Bythotrephes* in recent years (KETELAARS et al. 1995).

Differences in water quality and basin parameters between European lakes with and without *Bythotrephes* were examined using *t*-tests with Bonferroni probability adjustments (experiment-wise  $\alpha = 0.05$ ). Similar tests were conducted on data for invaded and noninvaded lakes from the Great Lakes basin. Tests were limited to common limnological parameters and those that have been reported to influence *Bythotrephes* distributions (e.g. water temperature) because Bonferroni-adjusted probabilities become increasingly conservative with increasing numbers of tests performed. We also compared characteristics of lakes without *Bythotrephes* in Europe and North America using *t*-tests with Bonferroni probability adjustments. To minimize the influence of exceptionally large basins (e.g. Great Lakes, Lake Ladoga) on analyses, all data were  $\ln(x+1)$  transformed prior to *t*-test analyses.

We conducted Multivariate Analysis of Variance (MANOVA) on the five limnological parameters, using presence/absence of *Bythotrephes* in European lakes as the independent, categorical variable, to identify the primary differences between lakes with and without the cercopagid. This analysis indicated significant differences ( $P < 0.001$ ) between lakes with and without *Bythotrephes* for lake area, maximum depth, Secchi disk transparency and chlorophyll concentration, but not total phosphorus concentration ( $P = 0.098$ ). We then used the four significant lake variables to construct a discriminant function (DF) to define the model that best separated European waterbodies with and without *Bythotrephes*. DF analysis has been used in a similar manner to distinguish lakes with and without *Dreissena* (RAMCHARAN et al. 1992). Lake area was  $\ln(x+1)$  transformed prior to estimation of the MANOVA and DF models because it varied by more than four orders of magnitude. The error rate of the DF model was cross-validated using a jackknife procedure, wherein lakes are individually eliminated from the dataset. Models are recalculated and predicted occurrence of the species in the deleted lake is calculated. Variation between original and cross-validated data sets was 0% for lakes lacking *Bythotrephes* and 3.3% for lakes with it.

We then applied the European DF model to data for North American lakes to determine whether invasion patterns are consistent between the continents, and to assess vulnerability of lakes in the Great Lakes basin to invasion. In total we were able to evaluate the model using 22 lakes that contained *Bythotrephes* and 27 lakes that lacked it. Lakes with *Bythotrephes* included one from Minnesota, sixteen from Ontario, plus all of the Great Lakes (Appendix 1). Lakes without *Bythotrephes* included two from Minnesota and twenty-five from Ontario's Muskoka region (Appendix 1). Lakes without *Bythotrephes* were selected from the same watersheds as those with *Bythotrephes* to preclude confounding by gross differences in dispersal opportunities or limnological characteristics of the waterbodies. Plankton samples from Ontario lakes have been collected since 1996 by members of the public using conical, 30 cm-diameter, 63  $\mu\text{m}$ -mesh nets, and preserved in 70% ethanol (OFAH 1998; Appendix 1). Two vertical hauls were collected from the deepest region of each basin in each lake, with within-basin contents pooled. Lakes were sampled once between July and September, encom-

passing the time periods when *Bythotrephes* is typically reported from inland lakes in Ontario. Additional zooplankton samples were collected from Ontario lakes during 1995 with a single haul of a 0.75 m-diameter, 500- $\mu$ m mesh net, and preserved in 6% sugar-formalin. Sources of limnological data for these lakes are provided in Appendix 1. Chlorophyll concentration data was not available for six Ontario Lakes, and was estimated using a chlorophyll to total phosphorus regression model developed for central Ontario lakes (MOLOT & DILLON 1991). Two of the North American basins categorized as non-*Bythotrephes* basins (Boulder and Fish lakes, Minnesota) were initially reported to contain the species by sport fishermen, although recent attempts to collect the species have proven unsuccessful (YAN et al. 1992, M. R. FORMAN, pers. comm.). We tested the observed vs. predicted (from the DF model) occurrence of *Bythotrephes* in North American lakes using  $\chi^2$  contingency analysis. All statistical analyses were conducted using Systat 8.0 software.

## Results

### European Lakes

European lakes with and without *Bythotrephes* differed in many ways. For example, lakes that contained *Bythotrephes* had drainage basins that were, on average, more than thirty times larger than those that lacked the species (Table 1). These lakes also had significantly greater surface areas, mean and maximum depths, and tended to flush at lower rates than basins that lacked *Bythotrephes* (Table 1). Maximum and mean depths of the shallowest basin reported to support *Bythotrephes* were 15.0 and 4.9 m, respectively. Lakes with *Bythotrephes* also had significantly lower maximum bottom temperature during summer (5.7 vs. 12.2 °C) and slightly lower maximum surface temperature (19.8 vs. 21.3 °C). Mean minimum oxygen concentration in benthic waters during summer was similar in both lake classes (Table 1).

Concentrations of major nutrients including total phosphorus and nitrate nitrogen tended to be higher in lakes that lacked *Bythotrephes*, although variation within lake classes was extensive (Table 1). Chlorophyll concentration was significantly higher in lakes lacking *Bythotrephes* (Table 1; Fig. 2 a). Chlorophyll concentration was inversely related to Secchi disk transparency in both European and North American lakes (Fig. 2). Lakes lacking *Bythotrephes* also tended to support higher mean algal biomass (5.5 vs. 2.3 mg/l) and higher mean primary productivity (1.40 vs. 0.53 g C m<sup>-2</sup> d<sup>-1</sup>) than lakes without *Bythotrephes*. Water transparency averaged almost three times higher in lakes with *Bythotrephes*. Thus, even though *Bythotrephes* has been reported from small, shallow basins in northern Europe and Asia, its distribution in this study was confined primarily to large, deep, clear basins with relatively low benthic water temperature during summer.

**Table 1.** Mean ( $\pm$ SE) morphometric and limnological characteristics of lakes with and without *Bythotrephes* in Europe and North America. All statistical comparisons are between means of lake groups within continents. \*  $p < 0.05$ ; NS =  $P > 0.10$ , following Bonferroni multiple comparison adjustment; NT = not tested; NA = not available. Data were  $\ln(x+1)$  transformed prior to statistical analysis. Median values are presented for pH. Only a subset of key limnological and morphometric variables were tested owing to the increasingly conservative nature of Bonferroni-adjusted  $t$ -test probabilities with increasing numbers of tests conducted.

Bythotrephes? Lakes Surveyed	Continent						
	Europe			North America			
	Present	n	Absent	Present	n	Absent	
Basin area (km <sup>2</sup> )	22243 (11631)	25	684 (382)*	15	74742 (21433)	7	87 (27)*
Surface area (km <sup>2</sup> )	1428 (666)	31	152 (106)*	24	11152 (5078)	22	14 (4)*
Maximum depth (m)	126.6 (22.7)	31	14.1 (4.2)*	24	94 (22)	22	35 (6)*
Mean depth (m)	50.6 (10.4)	29	5.1 (0.9)*	24	36 (10)	15	12 (2)*
Flushing rate (yr <sup>-1</sup> )	1.0 (0.6)	22	2.1 (0.8) <sup>NT</sup>	18	0.3 (0.2)	7	0.4 (0.1) <sup>NT</sup>
Maximum bottom temperature (°C) (summer)	5.7 (0.4)	17	12.2 (1.6)*	13	6.7 (1)	18	10.0 (1.6) <sup>NS</sup>
Maximum surface temperature (°C) (summer)	19.8 (0.6)	20	21.3 (1.0) <sup>NT</sup>	15	NA	NA	NA
Bottom minimum oxygen (mg/l) (summer)	5.9 (1.0)	13	4.3 (1.2) <sup>NS</sup>	9	NA	NA	NA
Secchi disk transparency (m)	4.7 (0.4)	31	1.6 (0.2)*	24	4.9 (0.6)	22	4.4 (0.3) <sup>NS</sup>
pH	7.5	25	8.3 <sup>NT</sup>	21	7.1	22	7.7 <sup>NT</sup>
Alkalinity (mEq/l)	1.26 (0.31)	10	2.21 (0.77) <sup>NT</sup>	13	2.00 (1.41)	21	3.80 (2.00) <sup>NT</sup>
Total phosphorus (mg/l)	0.093 (0.036)	31	0.403 (0.204) <sup>NS</sup>	24	0.012 (0.004)	22	0.017 (0.002) <sup>NS</sup>
Nitrate nitrogen (mg/l)	0.98 (0.63)	23	2.04 (0.67) <sup>NT</sup>	15	0.22 (0.03)	18	0.06 (0.02) <sup>NT</sup>
Chlorophyll-a (µg/l)	7.5 (1.4)	31	48.0 (8.3)*	24	2.3 (0.4)	17	5.1 (2.0) <sup>NS</sup>

European lakes that supported or lacked *Bythotrephes* differed in several key respects (MANOVA,  $F = 15.1$   $df = 5, 47$ ,  $P < 0.0001$ ), including the aforementioned maximum depth, lake area, Secchi transparency and chlorophyll concentration. Discriminant function (DF) analysis generated a model that successfully described the occurrence of *Bythotrephes* in European lakes. The model correctly predicted 28 of 31 (90%) lakes inhabited by *Bythotrephes*, and 23 of 24 (96%) basins that lacked the species. The model [lake score =  $-1.7650 + (\text{Secchi depth} * 0.4309) + (\ln[\text{lake area} + 1] * 0.1925) - (\text{chlorophyll} * 0.0144) + (Z_{\text{max}} * 0.0004)$ ] was influenced most by water clarity and lake area (Figs. 2–3). Mean DF scores of European lakes with and without *Bythotrephes* were 1.0603 and  $-1.3695$ , respectively.

Lake Paasivesi, Finland was incorrectly predicted to support *Bythotrephes*, while two Dutch reservoirs – Volkerak-Zoom and Petrusplaat – and one Belgian reservoir – Broechem – were incorrectly predicted to lack the species. All four model variables of Lake Paasivesi were more consistent with a lake that supported *Bythotrephes* than one that lacked it. Interestingly, the model correctly predicted that Lakes Haussee, Ringsjön and Esthwaite Water would not support *Bythotrephes*, even though the species was reported in each of these lakes at one time. The model also correctly predicted that two (De Gijster, Honderd en Dertig) of the three Biesbosch reservoirs (excepting Petrusplaat) would support *Bythotrephes*. Broechem, Volkerak-Zoom and Petrusplaat were incorrectly predicted to lack the species because they are relatively small and turbid. Volkerak-Zoom also has a relatively high chlorophyll concentration ( $30 \mu\text{g/l}$ ).

### North American vs. European lakes

Patterns of *Bythotrephes* occurrence in North American lakes were generally consistent with those observed in Europe. For example, with the exception of chlorophyll and total phosphorus concentrations, patterns of physical, chemical and biological differences between invaded and noninvaded lakes were in general agreement with those observed in Europe (Table 1). Maximum and mean depths of the shallowest North American basins reported to support *Bythotrephes* were 17.0 and 3.3 m, respectively. Excluding the Great Lakes, many of the invaded basins in North America were smaller and shallower than those in Europe where *Bythotrephes* was reported as resident. For example, median values of maximum and mean depth were lower in North America (44.0 and 14.1 m) than in Europe (68.0 m and 27.0 m). Likewise, median surface area of *Bythotrephes* lakes was only  $15.5 \text{ km}^2$  for North America vs.  $71.1 \text{ km}^2$  in Europe. Even very small ( $< 1 \text{ km}^2$ ) basins on both continents have been colonized by *Bythotrephes*.

Lakes containing *Bythotrephes* in North America had significantly lower chlorophyll levels than European lakes (mean of 2.3 vs. 7.5  $\mu\text{g/l}$ ;  $t$ -test,  $P < 0.01$ ), while mean total phosphorus concentration was only 13.2% of that of European lakes.

North American lakes lacking *Bythotrephes* were significantly deeper and more transparent than comparable lakes in Europe ( $t$ -tests,  $P < 0.01$ ). These North American lakes also had significantly lower chlorophyll and total phosphorus concentrations than their European counterparts ( $t$ -tests,  $P \leq 0.05$ ).

Application of the discriminant function model to North America yielded mixed results. The model correctly predicted *Bythotrephes* occurrence in 18 of 22 (81.8%) invaded lakes, including all of the Great Lakes (Fig. 3 b). How-

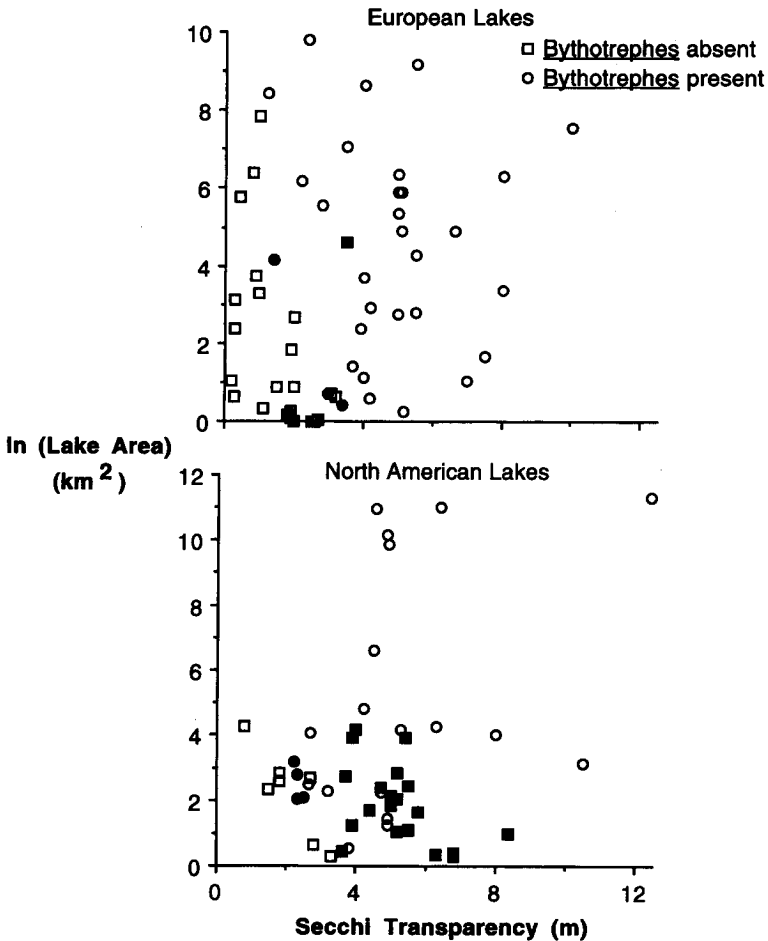


Fig. 3. Relationship between transformed lake area and Secchi disk transparency for North American and European lakes. Symbols as per Fig. 2.

ever, the model incorrectly predicted *Bythotrephes* presence in 20 of 27 (74 %) lakes from which it is known to be absent. Overall, the predicted pattern of *Bythotrephes* occurrence in North American lakes differed significantly from the observed pattern ( $\chi^2 = 15.1$ ,  $df = 1$ ,  $P < 0.001$ ). All four of the invaded lakes predicted by the model to lack *Bythotrephes* had low Secchi disk transparency ( $\leq 2.5$  m) and small surface area ( $\leq 11$  km<sup>2</sup>). This group included Island Lake, Minnesota, the only basin in the state that presently supports *Bythotrephes*. The model correctly predicted that the other two Minnesota lakes (Boulder, Fish) would lack *Bythotrephes* even though they were initially colonized by it. The model predicted that even small lakes in the Muskoka region of Ontario can support *Bythotrephes* (e.g. Plastic Lake, 0.32 km<sup>2</sup>).

## Discussion

The European and North American data sets used in this study indicate that *Bythotrephes longimanus* occurs principally in lakes with large surface areas and drainage basins, that are also deep and clear. These lakes also have relatively low chlorophyll concentration and phytoplankton productivity, and have relatively cool bottom waters during summer (Table 1). This suite of features suggests that *Bythotrephes* occurs mainly in large oligo- to mesotrophic lakes, a pattern consistent with its geographic distribution in Byelorussia and elsewhere in Eurasia (see review, GRIGOROVICH et al. 1998). However, the species also occurs in very shallow, fishless ponds, pools and lakes throughout Europe and Asia (e.g. EKMAN 1904, CHUGUNOV 1922, ISCHREYT 1930, FLÖSSNER 1972, MORDUKHAI-BOLTOVOSKOI & RIVIER 1987, VEKHOV 1987).

Our generalizations regarding *Bythotrephes*' distribution are also consistent with the species' temporal abundance sequence in Lago Maggiore, Italy. The species first declined, and later increased in abundance, as the lake experienced eutrophication followed by oligotrophication (MANCA & RUGGIU 1998). Other workers have also noted that *Bythotrephes* declined in, or disappeared from, lakes subject to eutrophication. For example, HABERMAN (1998) reported that *Bythotrephes* disappeared from Lake Võrtsjärv, Estonia, when the lake experienced eutrophication, and SMYLY (1972) noted that the species was present in larger lakes in the English lake district but absent from smaller, more productive ones. NILSSON & PEJLER (1973) also observed *Bythotrephes* only in oligotrophic lakes in Sweden.

Many changes accompany eutrophication of lakes including enhanced concentrations of limiting nutrients and of algal (chlorophyll) and fish biomass, and reduced Secchi transparency (e.g. MOLOT & DILLON 1991, HÅKANSON 1995). While any of these factors could potentially influence zooplankton populations, we propose that the tight correspondence between *Bythotrephes* oc-

currence and Secchi depth (Fig. 2 a) reflects the intensity of planktivory on *Bythotrephes*. *Bythotrephes* is often the largest and most conspicuous member of zooplankton communities, and is a highly preferred food of many species of planktivorous fish (e.g. see NILSSON & PEJLER 1973, GIUSSANI & DE BERNARDI 1977, STENSON 1979, COULAS et al. 1998, MOOKERKI et al. 1998). Abundance of planktivorous fish often increases with cultural eutrophication of lakes, potentially increasing predation pressure on *Bythotrephes* and other large-bodied zooplankton. As evidence, ROGNERUD & KJELLBERG (1984) noted that abundance of *Bythotrephes* increased when algal biomass increased from very low values (1–3 µg/l) in Norwegian lakes, but then declined owing to increasing fish predation pressure under more eutrophic conditions. BERGSTRAND (1990) invoked enhanced predation pressure by cyprinid fishes during cultural eutrophication of Lake Ringsjön, Sweden, as a possible explanation for changes in the zooplankton community that included the disappearance of *Bythotrephes*. *Bythotrephes* occurrence and abundance also are inversely related to planktivory pressure in Swedish and Dutch ecosystems (STENSON 1979, H. KETELAARS, unpubl. data). The clearest evidence supporting the hypothesis that Secchi depth is a proxy for planktivory intensity is provided by a study of thirty Danish lakes (JEPPESEN et al. 1996). In that study, mean zooplankton body size, Secchi depth and maximum depth declined with increasing planktivore density, while chlorophyll and total phosphorus concentrations increased. It appears, therefore, that fish predation may be a primary determinant of *Bythotrephes* occurrence, and that the influence of Secchi transparency and lake depth may not be as clear-cut as our study would at first indicate.

Invasion of nonindigenous species represents one of the greatest threats to integrity of aquatic ecosystems worldwide. Attempts to reduce the frequency of new invasions will require a thorough understanding of factors that cause or facilitate invasions. An examination of the role of humans as dispersal vectors is crucial to this objective. Human transfer of propagules from donor to recipient ecosystems is not only an essential aspect of invasion dynamics, it may represent the single greatest opportunity to predict geographic establishment patterns of nonindigenous species. For example, dispersal of zebra mussels to inland lakes in Wisconsin was closely associated with movement of trailered recreational boats in the state (BUCHAN & PADILLA 1999).

The Baltic Sea region likely served as host for transfer of *Bythotrephes* to the Great Lakes from Europe (D. BERG, unpubl. data). Once established in the Great Lakes, the species dispersed to inland waterbodies north and south of the lakes. The exact mechanism(s) responsible for these invasions has not been established, although human dispersal of propagules is an inviting possibility. In Ontario sport fishermen and recreational boaters move outdoor equipment (e.g. fishing equipment, boats) between Georgian Bay (Lake Huron) and inland lakes including Lake Temagami, the invaded lake most remote

from the Great Lakes in North America (YAN et al. 1992, Lake Temagami Cottagers Association, pers. comm.). These movements could be accompanied by accidental dispersal of *Bythotrephes* resting eggs with (dead) females snagged on fishing lines or on boat trailers, or of live females or resting eggs in 'live well' holding tanks in recreational boats. It is also possible that waterfowl could transfer *Bythotrephes* or its eggs from the Great Lakes to inland lakes. Attempts to distinguish human and waterfowl-assisted dispersal of *Bythotrephes* may be assisted by application of a geographic information system model involving consideration of human access to lakes via roads and watercourses, major waterfowl flyways, and proximity to possible donor sources.

Our model was unsuccessful in identifying lakes where *Bythotrephes* is not found in the Great Lakes basin. The model predicted that most (74 %) of the lakes presently considered to lack the species should in fact support it. This number could be inflated if *Bythotrephes* has already invaded some of these lakes. The species can be very difficult to detect in the plankton when its density is low (VEKHOV 1987, MILLS et al. 1992). Considering the relatively modest effort to collect zooplankton on some lakes in Ontario, it is clearly possible that the species may have been present but not detected in our samples.

The large percentage of noninvaded lakes in our study that appear vulnerable to invasion has troubling implications. If humans are the dominant dispersal vector, then public education efforts must be expanded in the regions where vulnerable lakes have been identified. Clearly lakes other than those utilized in our study are susceptible to invasion. Five inland lakes (Nipissing, Sugar, Ahmic, Bernard and Skeleton) in Ontario and three reservoirs (Knox, Pleasant Hill and Tappan) in Ohio were reported invaded during 1998, and five more lakes (Black Donald, Loon, Panache, Tyson, George) were invaded in Ontario during 1999 (OFAH 1998, FERRY & WRIGHT 2000, F. McDONALD, pers. comm.). Invasion of the reservoirs in Ohio is particularly troubling since they occur in the Ohio and Mississippi River drainage systems.

The ability to predict where species will invade is needed not only for *Bythotrephes*, but also for many other aquatic taxa. For example, another onychopod cladoceran *Cercopagis pengoi*, has invaded the Baltic Sea and the Great Lakes since 1992 (MACISAAC et al. 1999). We propose that aquatic ecologists focus management efforts on human mechanisms most likely to transport propagules of nonindigenous taxa to new biogeographic regions, and within newly invaded regions. Preventing further invasions of lakes by species like *Bythotrephes* will be an onerous task, however, considering the many dispersal vectors by which the species may be spread.

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Appendix 1. Sources of limnological, morphometric and *Bythotrephes* presence/absence data for European and North American lakes.

Lake, Country	Europe		North America				
	<i>Bythotrephes</i> Present?	Limnological Data Source	<i>Bythotrephes</i> Data Source	Lake, Country	<i>Bythotrephes</i> Present?	Limnological Data Source	<i>Bythotrephes</i> Data Source
Gräfenhain, Germany	N	1, 2	1, 3	Boulder, USA	N	105, 106	107
Dagow, Germany	N	4, 5, 6	4	Fish, USA	N	105, 106	107
Bautzen, Germany	N	1, 2	3	Blue Chalk, Canada	N	108	109
Große Fuchskuhle, Germany	N	7	4	Chub, Canada	N	108	109
Haussee, Germany	N	5, 8, 9	4, 10, 11	Crosson, Canada	N	108	109
Pääjärvi, Finland	N	12, 13	14, 15, 16	Dickie, Canada	N	108	109
Paasivesi, Finland	N	17	14	Plastic, Canada	N	108	109
Gribsø, Denmark	N	18	18	Red Chalk, Canada	N	108	109
Ringsjön, Sweden	N	19	20	Big Rideau, Canada	N	108	109
Neusiedler See, Austria	N	21, 22	21	Wolfe, Canada	N	108	109
Loosdrecht, Netherlands	N	23, 24	23, 24	Balsam, Canada	N	108	109
Ijsselmeer, Netherlands	N	25	25	Cameron, Canada	N	108	109
Breukelerveen, Netherlands	N	23, 24, 26	23, 24, 26	Upper Rideau, Canada	N	108	109
Tjeukemeer, Netherlands	N	25, 27	25, 27	Scugog, Canada	N	108	109
Vechten, Netherlands	N	28, 29	24, 25, 28, 29	Big Clear, Canada	N	108	109
Zwemlust, Netherlands	N	30, 31	24, 30, 31	Birch, Canada	N	108	109
Wolderwijd, Netherlands	N	32	24	Bob's, Canada	N	108	109
Vuntus, Netherlands	N	23, 24	24	Buck, Canada	N	108	109
Candia, Italy	N	33	33, 34	Crow, Canada	N	108	109
Estwaite Water, Britain	N	35, 36, 37	37, 38	Desert, Canada	N	108	109
Lowes, Scotland	N	35, 37, 39, 40	37, 40	Eagle, Canada	N	108	109
Forfar, Scotland	N	39, 40	40	Devil, Canada	N	108	109
Balgavies, Scotland	N	39, 40	40	Knowlton, Canada	N	108	109
Balaton, Hungary	N	41	42, 43	Three Mile, Canada	N	108	109
Constance, Germany-Switzerland	Y	44	44, 45, 46, 47	Loughborough, Canada	N	108	109

Appendix 1. Continued.

Europe				North America			
Lake, Country	<i>Bythotrephes</i> Present?	Limnological Data Source	<i>Bythotrephes</i> Data Source	Lake, Country	<i>Bythotrephes</i> Present?	Limnological Data Source	<i>Bythotrephes</i> Data Source
Schöhsee, Germany	Y	48	49	Upper Mazinaw, Canada	N	108	109
Stechlin, Germany	Y	5, 6	4, 11	Silver, Canada	N	108	109
Pyhäselkä, Finland	Y	50	14	Island, USA	Y	105	106, 107
Puruvesi, Finland	Y	51	15, 52	Joseph, Canada	Y	108	110
Estrom Sø, Denmark	Y	53	18, 53, 54	Muskoka, Canada	Y	108	110
Furesø, Denmark	Y	55	11, 18, 45	Rosseau, Canada	Y	108	110
Vänern, Sweden	Y	56, 57, 58	56, 59	Lake of Bays, Canada	Y	108	111
Mälaren, Sweden	Y	56, 57, 60	59, 61	Kashagawigamog, Canada	Y	108	108
Hjälmarén, Sweden	Y	56, 57	61	Harp, Canada	Y	108	112
Vättern, Sweden	Y	57, 58, 60	61, 62	Fairy, Canada	Y	108	110
Gårdsjön, Sweden	Y	63, 64	63, 65	Mary, Canada	Y	108	110
Mondsee, Austria	Y	66	67, 68, 69	Peninsula, Canada	Y	108	110
Petrusplaat, Netherlands	Y	70	71	Vernon, Canada	Y	108	110
Volkerak-Zoom, Netherlands	Y	70	24, 71	Simcoe, Canada	Y	108	113
De Gijster, Netherlands	Y	70	70	Canning, Canada	Y	108	108
Honder en Dertig, Netherlands	Y	70	70	Go Home, Canada	Y	108	110
Broechem, Belgium	Y	70	72	Pigeon, Canada	Y	108	118
Garda, Italy	Y	73, 74	74	Skeleton, Canada	Y	108	109
Lugano, Italy	Y	73, 74	74	Soyers, Canada	Y	108	112
Mergozzo, Italy	Y	73, 74	75	Ontario, USA-Canada	Y	114	115
Maggiore, Italy	Y	73, 74	76, 77, 78	Erie, USA-Canada	Y	114	116
Windermere, Britain	Y	35, 37	79, 80	Huron, USA-Canada	Y	114	116
Lomond, Scotland	Y	81	81, 82, 83	Michigan, USA	Y	114	117
Ladoga, Russia	Y	84, 85, 86, 87	88, 89	Superior, USA-Canada	Y	114	118
Onega, Russia	Y	90, 91	88, 89				

## Appendix 1. Continued.

Europe				North America			
Lake, Country	<i>Bythotrepes</i> Present?	Limnological Data Source	<i>Bythotrepes</i> Data Source	Lake, Country	<i>Bythotrepes</i> Present?	Limnological Source	<i>Bythotrepes</i> Data Source
Rybinsk, Russia	Y	89	89, 91				
Tyrifjorden, Norway	Y	92, 93	92, 94				
Mjøsa, Norway	Y	93, 95	96, 97				
Biel, Switzerland	Y	98, 99	100				
Geneva, Switzerland—France	Y	99, 101, 102	11, 103, 104				

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## Appendix 1. Continued.

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