

Short communication

Palearctic predator invades North American Great Lakes

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Summary. Bythotrephes cederstroemii Schoedler, a predatory freshwater zooplankter (Crustacea: Cladocera), was first found in the Laurentian Great Lakes in December 1984. The first individuals were from Lake Huron, followed in 1985 with records from Lakes Erie and Ontario. By late August, 1986 the species had spread to southern Lake Michigan (43° N). Bythotrephes has not previously been reported from North America, but has been restricted to a northern and central Palearctic distribution. Its dramatic and widespread rise in abundance in Lake Michigan was greatest in offshore regions. Bythotrephes appears to be invading aggressively, but avoiding habitats presently occupied by glacio-marine relict species that became established in deep oligotrophic North American lakes after the Wisconsin glaciation. Because it is a voracious predator its invasion may lead to alterations in the native zooplankton fauna of the Great Lakes. It offers the chance to study how invading plankton species join an existing community. Judging from its persistence and success in deep European lakes, Bythotrephes may now become a permanent member of zooplankton communities in the Nearctic.

Key words: Bythotrephes – Lake Michigan – invasion

The sudden spread of a new genus of freshwater zooplankton from Eurasia into North America is still at an early colonizing stage (Lange and Cap 1986; Bur et al. 1986). Previous accounts of Bythotrephes record the presence of the genus in Scandinavia, the British Isles, Europe as far south as northern Italy, and across the USSR to northern China (Lilljeborg 1901; Benisch 1930; Chiang 1964; Scourfield and Harding 1966; Giussani 1974). B. longimanus Leydig is the more common species, overlapping with B. cederstroemii Schoedler in the northern part of its range. The genus possesses a long and characteristic tail spine which typically exceeds individual body lengths by three-fold or more (Ischreyt 1934). Total length can exceed 1 cm, thus making Bythotrephes one of the largest crustacean zooplankton presently in the Laurentian Great Lakes. Zozulya and Mordukhai-Boltovskoi (1977) have argued that B. longimanus and B. cederstroemii are polymorphisms of a single species. Morphological distinction between the forms is based primarily on a kink in the tail spine of B. cederstroemii, and its associated setation, but Ischreyt reports other

quantitative character distinctions. To date only *B. ceder-stroemii* has been found in Lake Michigan.

Plankton studies underway in southern Lake Michigan recorded the arrival of Bythotrephes cederstroemii in August, 1986. Plankton collections from a research cruise on 6 August 1986 contained no specimens, but on 25 August the species was present. Plankton were collected with Puget Sound closing nets (Eastside Net Shop, Bothell, WN) with 1-m diameter and 130 µm nylon mesh aperture. Four vertical series on 6 August 1987 at 43°N 86°40'W (102 m water depth) sampled the water column from 90 m to the surface. No individuals of Bythotrephes were present in the samples, representing almost 300 m³ water volume. Samples from an earlier synoptic survey in August 1985 with closing nets and 1 m² Tucker Trawl (Eastside Net Shop) showed the species to be absent throughout Lake Michigan as far north as 45° N, based on ca. 1000 m³ of water sampled at each of six stations from 43° N to 45° N. Distributional data from 25-29 August 1986 (Fig. 1) are consistent with invasion from the north, through the straits of Mackinaw. An inshore to offshore transect completed 12-14 September 1986 revealed that Bythotrephes was becoming established as a predominantly offshore species (Fig. 1, inset).

Bythotrephes exhibited diel vertical migration during its early invasion of Lake Michigan (Fig. 2). Individuals avoided the illuminated epilimnion during the day and concentrated within the metalimnion at depths where light was attenuated to 0.1 percent of surface intensity. At night the population distributed throughout the epilimnion. This behavior is consistent with genetically-entrained avoidance of planktivorous fish that hunt by sight. Bythotrephes has been identified as a preferred item in the natural diets of whitefish (Coregonus), trout (Salmo), and arctic char (Salvilinus) (Giussani 1974; Fitzmaurice 1979; Langeland 1978), and is eaten by perch (Perca) although small juvenile fish avoid the prey (Guma'a 1978), possibly because of its long tail spine.

The arrival of *Bythotrephes* in North America raises the possibility of species changes in existing communities. The Laurentian Great Lakes contain several plankton species derived from marine ancestors which invaded these freshwater environments during and subsequent to the last continental glaciation (Hutchinson 1967). Invasion by *Bythotrephes*, a planktivorous predator with its evolutionary history in fresh water, could potentially pose a challenge to the success of the glacio-marine species. The effect of *Bythotrephes* on these species, however, promises to be min-

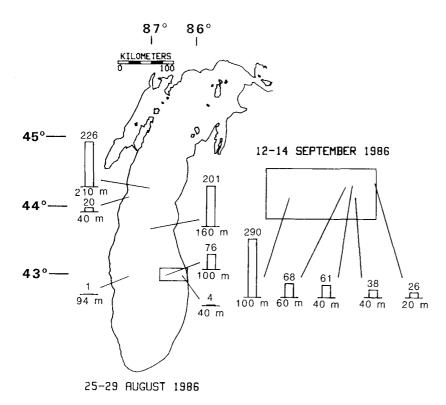


Fig. 1. Abundances of Bythotrephes cederstroemii (individuals m⁻²) at stations in central and southern Lake Michigan during two cruises in August and September 1986. Depths of water column at sampling stations are indicated. Inset: Abundances from nearshore to offshore at 43° N near Grand Haven, Michigan

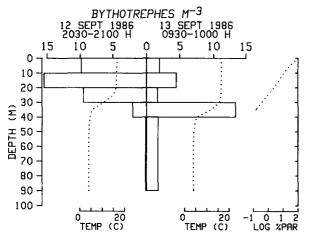


Fig. 2. Vertical distributions of *B. cederstroemii* at 43°N 86°40′W, in relation to temperature and light. Night samples were collected from 2030 to 2100 H and Day collections were 0930 to 1000 H. Temperature was measured by mechanical bathythermograph, and photosynthetically active rediation (PAR: 400–700 nm) was measured with a Li-Cor (LI–192S) spherical quantum sensor. PAR is expressed as the logarithm of percent of surface intensity. The 5 m difference in epilimnion depth from night to day results from an internal seiche, or whole-basin standing wave oscillation

imal because the vertical distribution of the invader overlaps little with the glacial relict species (Mysis relicta, Limnocalanus macrurus, and Senecella calanoides). These relict taxa are cold stenotherms (Balcer et al. 1984) which avoid the epilimnion during thermal stratification. Interactions during the winter when cold stenotherms are distributed throughout the water column are unlikely because cold water temperatures generally lead to gametogenic resting egg formation by Bythotrephes and to mid-winter population declines.

Bythotrephes co-occurs instead with zooplankton that have broad regional or cosmopolitan distributions, and it is among these species that the impact of the predator will be greatest. Because the prey of Bythotrephes include juvenile Cladocera and copepods (Monakov 1972), most of which are herbivores, the initial deleterious effects on these taxa may be large, and the effects may extend to other trophic levels. The introduction of the planktivorous crustacean Mysis relicta to Lake Tahoe, for instance, caused severe mortality on Cladocera and removed Daphnia from all but shallows bays of the lake (Threlkeld et al. 1980). Such perturbations are the consequence of much shorter generation times by planktivorous zooplankton than by planktivorous fish. Bythotrephes reproduces primarily by parthenogenesis, and its generation time is only 11 to 14 days at temperatures from 13 to 16.5° C (Mordukhai-Boltovskaya 1957). Initial population growth by Bythotrephes, therefore, can be far faster than that of any fish populations which may eat the invader, and thus its success is expected to continue for at least several years.

The future course of the *Bythotrephes* invasion in North America may reveal much about the role of invertebrate predators in plankton communities. *Bythotrephes* will likely remain a permanent resident of the Great Lakes, and will penetrate into may smaller lakes as well. In Europe, *Bythotrephes* is not obligately restricted to deep water bodies, but high rates of predation by fish can exclude the animal from small lakes (Stenson 1978; 1979). Persistence of *Bythotrephes* in North America may parallel the success of another Palearctic cladoceran, *Eubosmina coregoni*, resulting from a supposed similar invasion in which the Laurentian Great Lakes were among the first habitats colonized (Deevey and Deevey 1971). The invader will probably become a permanent link in the existing food web of Lake Michigan. The dominant offshore planktivorous fish in Lake Mi-

chigan are the bloater chub (*Coregonus hoyi*) and the alewife (*Alosa pseudoharengus*). *Coregonus* species, especially, are noted for preferential feeding on *Bythotrephes* (Giussani 1974). Interactions within the food web will be doubtlessly complex, because *Bythotrephes* feeds on *Daphnia* species which constitute the major prey of juvenile *C. hoyi. Bythotrephes* may thus be able to reduce recruitment in populations of its potential predator.

Previous absence of this taxon from the Nearctic is assured not only by absence of the conspicuous and large specimens from all reported plankton collections, but by the absence of its fossil remains in lake sediments. The distinctive tail spine is a unique and characteristic component only of recent sediments in the Laurentian Great Lakes (J. Bowers, personal communication). Although waterfowl have been invoked as agents of dispersal for *Bythotrephes* among small lakes in Europe (Steinwender 1935), the absence of the taxon from North America before this decade probably rules out that vector in this case. More likely, freshwater or mud with resting eggs from northern Europe or the British Isles was transported to North America by humans.

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