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NOTE

OCCURRENCE OF *BYTHOTREPHES CEDERSTROEMI* (SCHOEDLER 1877) IN LAKE SUPERIOR, WITH EVIDENCE OF DEMOGRAPHIC VARIATION WITHIN THE GREAT LAKES

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ABSTRACT. The predaceous cladoceran, Bythotrephes cederstroemi *(Schoedler 1877), was first noted in the Great Lakes in late 1984, and had spread to Lakes Huron, Erie, Ontario, and Michigan by late summer of 1986. Zooplankton samples collected from Batchawana Bay, Lake Superior on 15 September 1988 contained large numbers of* B. cederstroemi *(122.8 individuals/m^2). Geographic variation in Great Lakes* B. cederstroemi *was observed when this sample was compared to samples from Lake Erie. There was a greater percentage of males present in the Lake Superior sample as well as a greater number of females carrying sexual resting eggs.* B. cederstroemi *from Lake Superior weighed more than those from Lake Erie. These differences are probably the result of physiological responses to different environmental conditions, and not genetic differentiation of* B. cederstroemi *populations among the Great Lakes.*
INDEX WORDS: Zooplankton, Lake Superior, taxonomy.

INTRODUCTION

The European cladoceran, *Bythotrephes cederstroemi*, was first reported in the Great Lakes in Lake Huron, in December, 1984 (Bur *et al.* 1986). Subsequently, *B. cederstroemi* was discovered in Lakes Erie and Ontario in 1985 (Bur *et al.* 1986, Lange and Cap 1986). Lehman (1987) and Evans (1988) documented the appearance and spread of *B. cederstroemi* into Lake Michigan in the summer of 1986. *B. cederstroemi is* distinguished from its congener, *B. longimanus* (Leydig 1860), by the presence of a conspicuous S-bend in the long (up to 7-8 mm) caudal spine. Otherwise, these two European species are morphologically and ecologically similar, and the distinction between the two species is debatable (Bur et *al.* 1986, Evans 1988). Occurrence of *B. cederstroemi* in the stomach contents of salmon from Lake Superior was reported by Cullis and Johnson (1988). To date *B. cederstroemi* has not been reported from inland waters surrounding the Great Lakes region. The rapid spread of this predatory cladoceran has raised concern about its impact on zooplankton trophic dynamics in the Great Lakes.

For *Bythotrephes cederstroemi* to persist in habitats as diverse as the Great Lakes, it must be able to adapt to varying patterns of seasonality, predation pressure, and prey availability. The expected low initial genetic variability of a founding population allows comparison of variation in life history traits of *B. cederstroemi* under different environmental conditions, and ascribing of any observed variation to phenotypic plasticity rather than selection acting upon different genotypes. Here, we document an established population of *B. cederstroemi* in eastern Lake Superior, and describe differences in life history traits between samples collected from Lake Superior and Lake Erie.

METHODS AND MATERIALS

Batchawana Bay, located in eastern Lake Superior (Fig. 1), was sampled 1700-1830 hrs on 15 September 1988. Vertical hauls were made using 0.5 and 0.75 meter zooplankton nets (O. 112 and 0.505 mm mesh, respectively) equipped with General Ocean-

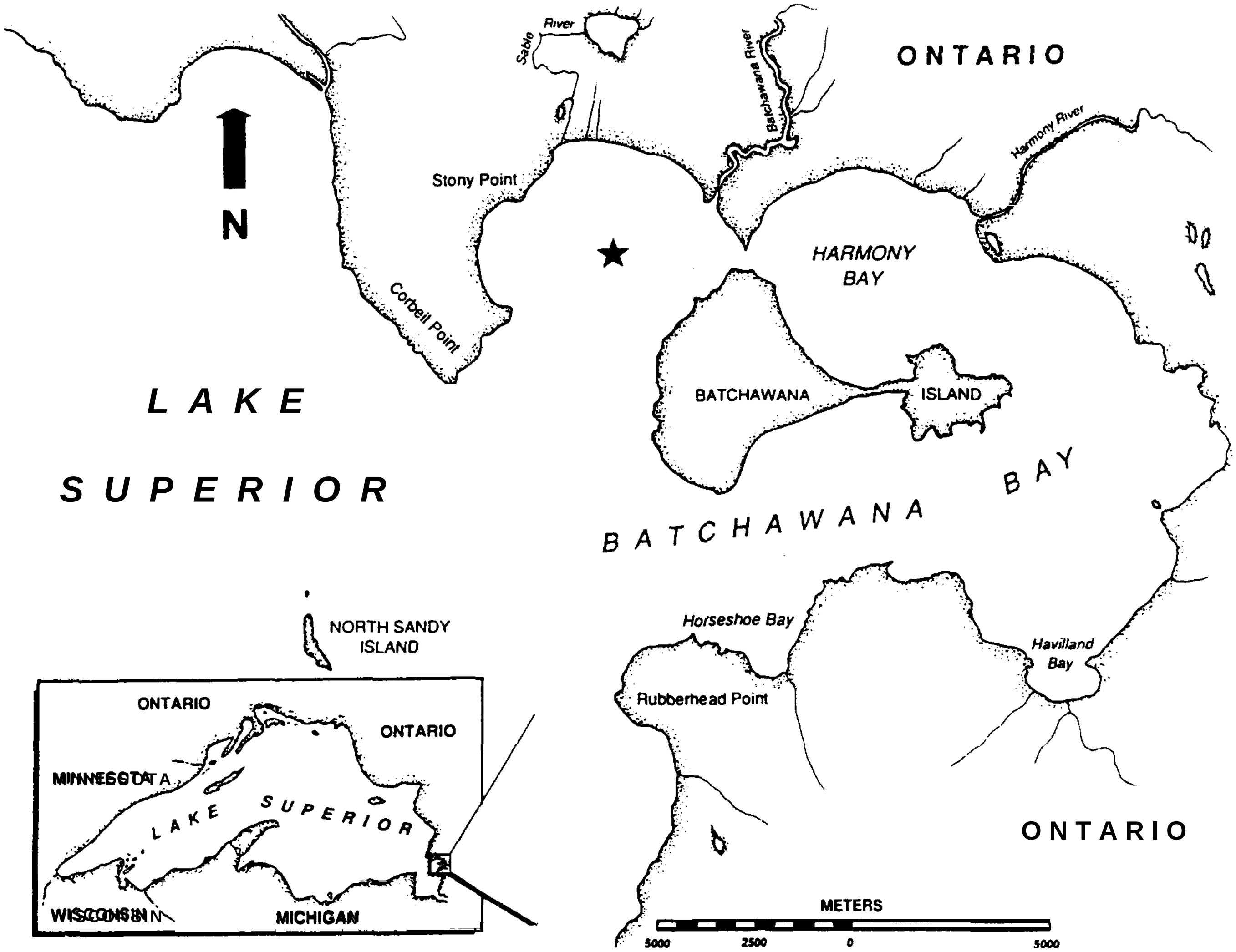

FIG. 1. The eastern shore of Lake Superior. The star in Batchawana Bay indicates the site where zooplankton samples were collected.

ics mechanical flowmeters. Water depth ranged from 10 to 30 meters. Samples were preserved in a sugar-formaldehyde solution (40 g sucrose/L of 4% v/v formalin). Enumeration, length, and weight measurements of individual *Bythotrephes cederstroemi* followed techniques described in Berg and Garton (1988). Phenotypic variation of life history traits in *B. cederstroemi* was examined by comparing demographic data for Lake Erie samples (Berg and Garton 1988) with the sample from Lake Superior. Life history traits compared were male: female ratio, frequency of asexual broods and sexual resting eggs, developmental stage distribution, mean and per capita reproductive efforts, body mass, and size (measured as caudal spine length). As water temperature is an important factor determining these traits (Culver 1980), Lake Erie samples (9 October-23 November 1987) were chosen in which water temperatures were similar to that in Lake Superior on the sampling date.

RESULTS AND DISCUSSION

Bythotrephes cederstroemi was present in daytime vertical tows from Batchawana Bay, Lake Superior, at an abundance of 122.8 individuals/m^2, as compared to 111.2 individuals/m^3 on 9 October

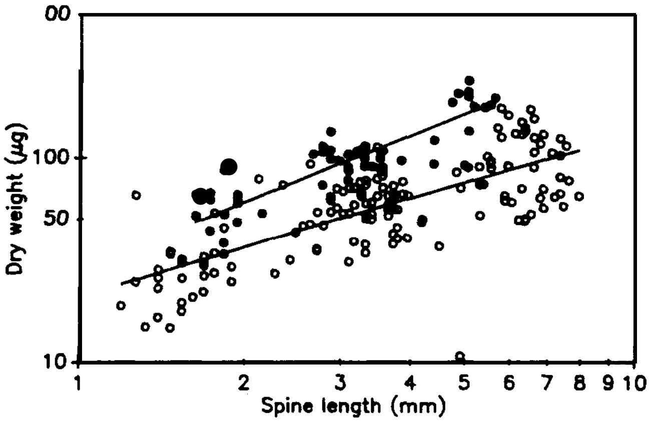

FIG. 2. Bythotrephes cederstroemi. Regression of dry weight (µg) on spine length (mm); data log transformed. Lake Superior (closed circles) regression equation: log(dry weight, µg) = 1.428(log spine length, mm) + 1.670, $r^2 = 0.88$, N = 53. Lake Erie (pooled samples from 9 October-23 November 1987) (open circles) regression equation: log(dry weight, µg) = 1.044(log spine length, mm) + 1.478, $r^2 = 0.73$, N = 150. Both regressions are significant at $p < 0.0001$ level. Adjusted B. cederstroemi mean weight for Lake Superior: 168.7 µg; Lake Erie: 78.2 µg.

1987, in the western basin of Lake Erie. The Lake Erie samples were collected by a different method, nocturnal horizontal surface tows, therefore abundance estimates between the two lakes are not directly comparable. However, *B. cederstroemi* has established a permanent population in Lake Superior, as indicated by high abundance and the occurrence of mature males and females, some with sexual resting eggs.

Water temperature in Batchawana Bay was 15.4°C in the epilimnion and 12.6°C in the hypolimnion on 15 September 1988. Water temperatures at the times of collection for the Lake Erie samples ranged between 6-11.6°C.

Life history traits of the Lake Superior sample differed considerably from the Lake Erie samples (Table 1). The Lake Superior sample contained 42% males; the maximum frequency of males observed in Lake Erie samples over a full season was 4070 (Berg and Garton 1988). This difference in relative frequency of males was also reflected in the occurrence of sexual eggs in the Lake Superior sample. In the Lake Superior sample, 15070 of the females carried sexual eggs, while 24% had asexual broods. In contrast, 56-80% of females had asexual broods in the Lake Erie sample, and sexual eggs were completely absent. Mean asexual brood size was similar in both samples, but the per capita asexual brood size was greater in the Lake Erie sample. Sexual eggs in Lake Superior females contributed to reproductive effort, however, total per capital reproductive effort was lower (O. 86) than in Lake Erie females (0.94-3.70) (Table 1).

Bythotrephes cederstroemi from Lake Superior weighed more at a given spine length than those from Lake Erie (Fig. 2). This difference might be explained by temperature, with Lake Superior having lower summer water temperatures than Lake Erie. *B. cederstroemi* in Lake Erie, standardized for spine length, weighed less during warm summer months than during cooler fall months (Berg and Garton 1988). Fecundity was also higher in the fall than in the summer (Berg and Garton 1988). Although the Lake Superior sample was collected at a similar temperature as the Lake Erie samples, its thermal history was unknown. Furthermore, short generation times of Cladocerans (1-3 weeks) allow rapid phenotypic responses of growth, maturity, and fecundity to changing water temperature (Culver 1980). Therefore, attributing *B. cederstroemi* body mass differences between the two lakes to either thermal history or other environmental parameters requires additional data.

Males in the Lake Superior sample were mostly Stage II (developmental stages I, II, and III are identified by the number of pairs of lateral spines on the large caudal spine, after Ishreyt (1930)), whereas females were mostly Stage III (Table 1). In a demographic study, Ishreyt (1930) reported finding only Stage I and II males for populations of *Bythotrephes longimanus* from Lake Konstanz and northern Scandinavian lakes (Lappland), but did not elaborate on sexual differences in development. The observed developmental stage distribution of males could result from sexually related differences in growth and molting, or from males being younger than females, having been produced recently in response to environmental cues (decreasing temperature, photoperiod, or prey). In addition to developmental differences, males weighed slightly more than females of the same length (analysis of covariance, $p < 0.023$).

Life history differences of *Bythotrephes cederstroemi* in these two lakes are indicative of adaptive physiological plasticity. Any invading species must adapt to novel environmental conditions, either by selection acting upon specific genetic variants or by phenotypic variation of fixed genotypes. Ishreyt (1930) recognized different "kolo-

TABLE 1. Life history data for Bythotrephes cederstroemi from Lakes Superior and Erie. Lake Superior data collected 15 September 1988; Lake Erie data collected 9 October, 2 and 23 November 1987. For Lake Erie, values represent the range for the three sample dates, with the exception of the number of males, females, and development stage, which are the total for all three samples. Data for Lake Erie from Berg and Carton (1988).

	Lake Superior	*Lake Erie*
Abundance	122.8 (#/m^2)	17.2-111.2 (#/m^3)
Females		
Stage I	27	33
II	27	67
III	143	53
Total	197	153
Males		
Stage I	18	1
II	118	6
III	7	0
Total	143	7
% Females with Asexual Eggs	24	56-80
Mean Asexual Brood Size	4.0	4.4-7.1
Per Capita Asexual Brood Size	0.56	0.94-3.70
% Females with Sexual Eggs	15	0
Mean Sexual Brood Size	3.4	0
Per Capita Sexual Brood Size	0.30	0
Combined Asexual and Sexual Reproductive Effort	0.86	0.94-3.70

nies" of *B. longimanus* in Europe which occupied different habitats (eurythermal and littoral versus stenothermal and limnetic). Preliminary electrophoretic investigation of 12 enzyme loci in *B. cederstroemi* from Lakes Erie, Huron, and Superior has revealed only minimal levels of genetic variability and no evidence of genetic differentiation of *B. cederstroemi* populations in the three lakes (Berg and Garton, unpublished data). Therefore, observed variation in life history traits, associated with environmental differences between lakes, most likely is a result of phenotypic plasticity in *B. cederstroemi*.

The ability to adapt rapidly to different environmental conditions has contributed to the spread of *Bythotrephes cederstroemi* throughout the Great Lakes. With a probable first introduction into Lake Huron (Bur *et al.* 1986), *B. cederstroemi* was able to spread by passive downstream transport into Lakes Erie and Ontario (Evans 1988). Mixing of water masses through the Straits of Mackinac was responsible for introduction into Lake Michigan, and probably occurred during the summer of 1986 (Lehman 1987, Evans 1988). Great Lakes ship traffic (already implicated in the transport of *B. cederstroemi* from Europe) may have contributed to the upstream movement from Lake Huron into Lake Superior. *B. cederstroemi* has successfully established itself in all five Great Lakes in the short period between December, 1984, and September, 1988. The question remains, *when* (rather than if) *B. cederstroemi* will spread to other inland lakes in the Great Lakes region, and what will be its ultimate impact on zooplankton communities?

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