Population Characteristics of *Bythotrephes* in Lake Michigan

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ABSTRACT. *The population characteristics of* Bythotrephes *were evaluated at seven nearshore (45 m) and eight offshore (80 to 150 m) stations in Lake Michigan during July and September 2000.* Bythotrephes *was generally most abundant at offshore stations, but mean density was patchy (4 to 1,326/m²) among locations. During the year, there was a shift from reproduction by mainly instar III females to reproduction by instar II females. The shift generally reflected a change in the population structure of* Bythotrephes *at most sites during the same period.* Bythotrephes *populations in July were generally characterized by small body size at reproduction (instar II and III), large clutch size, and small neonates. Later in the season, body size at reproduction and neonates were larger and clutch size was smaller. Most growth (body length) of* Bythotrephes *occurred between instar I and II whereas little growth occurred between instar II and III. Spine length of* Bythotrephes *increased between July and September. The population characteristics and reproductive strategies of* Bythotrephes *appear to be adaptations to fish predation and food limitations.*

INDEX WORDS: Bythotrephes, *Lake Michigan, exotic species, zooplankton.*

INTRODUCTION

Bythotrephes cederstroemi, a predatory cladoceran native to the Palearctic region, became established in the Great Lakes in the 1980s (Rivier 1998). *Bythotrephes* has become an important part of the food web in the Lake Michigan since its introduction in 1986. Predation by *Bythotrephes* was linked to changes in size structure and community composition of herbivorous zooplankton populations in Lake Michigan (Lehman 1991, Lehman and Caceres 1993). The arrival of *Bythotrephes* also corresponded with decreases in a native predatory cladoceran, *Leptodora kindtii* (Lehman 1991,

Lehman and Caceres 1993). *Bythotrephes* is also a readily available food source for adult planktivorous fish in the Great Lakes (Mills *et al.* 1992) and predation may limit the abundance of *Bythotrephes* in some areas (Bilkovic and Lehman 1997, Pothoven *et al.* 2001).

Bythotrephes exhibits a high degree of phenotypic variation in life history characteristics (Bilkovic and Lehman 1997). Recent genetic work suggests that Palearctic and Nearctic populations of *B. cederstroemi* and Palearctic populations of *B. longimanus* might actually be one species with variable morphology (Berg and Garton 1994). Previous studies in southeastern Lake Michigan have reported seasonal and annual variation in abundance and size of *Bythotrephes* (Burkhardt 1994,

Pothoven *et al.* 2001). The variation was linked to temperature, food availability, and fish predation pressure (Burkhardt 1994, Pothoven *et al.* 2001). Life history traits also differ across the Great Lakes (Garton and Berg 1990, Bilkovic and Lehman 1997, Sullivan and Lehman 1998). However, most studies rely on data collected from one station or one small region within each lake. Differences in population structure, brood size, reproductive strategies, and abundance throughout the lake could affect estimates of *Bythotrephes* production, consumption, and overall effect on the pelagic food web.

Bythotrephes has become fully established in Lake Michigan since 1986 and the abundance, distribution, and life history of the species may have changed since its introduction into the system. The first objective of this study was to evaluate the abundance of *Bythotrephes* at several locations within Lake Michigan at nearshore and offshore stations during July and September 2000. The purpose was to determine whether there were any large-scale spatial patterns in abundance and whether there were differences in abundance of *Bythotrephes* between nearshore and offshore. The spatial distribution of a species such as *Bythotrephes* that is both a predator on herbivorous zooplankton as well as a prey item for planktivorous fish is needed to determine the role of invasive species and to more completely model the flow of energy in aquatic systems.

A second objective was to examine body and spine length, population structure, and reproductive characteristics of *Bythotrephes* throughout Lake Michigan. Life history characteristics can reflect the response of *Bythotrephes* to differing environmental conditions and could provide insight into how *Bythotrephes* has adapted to a non-native environment over time. The objective was to determine how single location sampling strategies might be affecting an understanding of this species in Lake Michigan.

METHODS

Bythotrephes were collected from seven nearshore and offshore stations in Lake Michigan (Fig. 1). Bottom depth was 45 m at nearshore stations and 100 to 110 m at offshore stations except off St. Joseph (80 m). Additionally, *Bythotrephes* were also collected at an offshore mid-lake station (150 m) located in the southern basin. Sampling took place during 10 to 20 July 2000 and 8 to 28 September 2000. Two replicate samples were col-
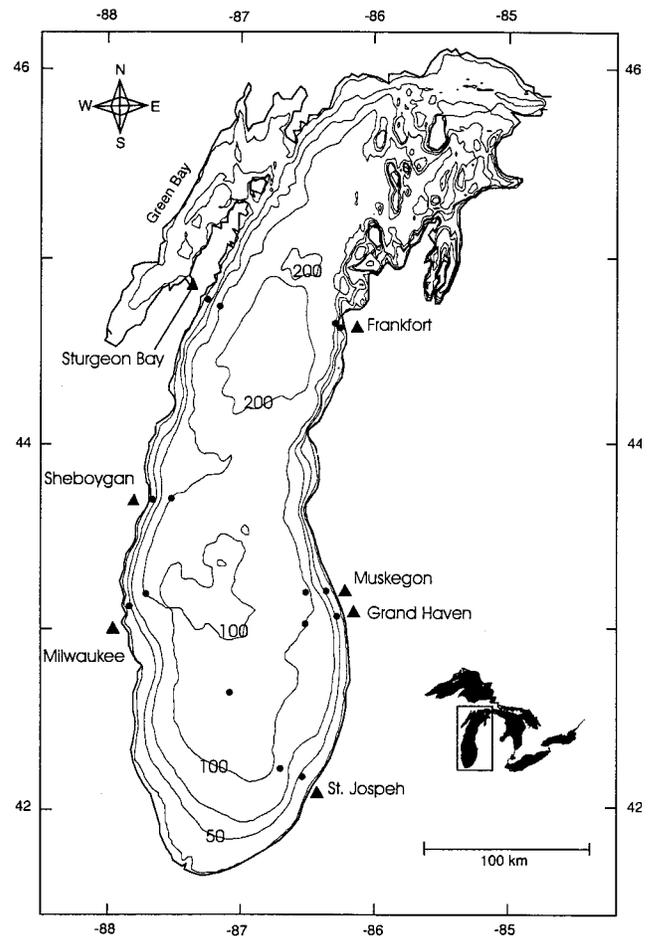
FIG. 1.   Map of stations in Lake Michigan that were sampled for Bythotrephes *in July and September, 2000. Depth contours expressed in meters.*

lected using a 1-m-diameter plankton net (363-μm mesh) towed vertically at approximately 0.5 m/s from just above the bottom to the surface. *Bythotrephes* were anesthetized with carbonated water and preserved in 10% sugar-buffered formalin.

In the laboratory, all *Bythotrephes* were counted and mean areal density was calculated to allow comparisons between depths and with previous data collected from southeastern Lake Michigan (Lehman 1991, Lehman and Caceres 1993). Body and spine length of *Bythotrephes*, not corrected for shrinkage, were measured with a computerized digital image analysis system (Image Pro) (Burkhardt 1994) and the number of spine barbs counted for up to 100 individuals per sample. Body length was defined as the distance from the distal rim of the eye to the anus and spine length was defined as the dis-

tance from the anus to the tip of the spine (Burkhardt 1994). The number of barbs on the tail spine increases with instar (Yurista 1992). The size of sexual and asexual broods was determined for reproductive females in each sample or subsample. Resting eggs result from sexual reproduction and are distinguished from asexual eggs by their thick, hard, yellowish shells (Yurista 1992). Developmental stages of embryos produced asexually were not differentiated. Males were not distinguished from females without broods.

Micro-zooplantkon in each sample were diluted to a known volume and sub-sampled with a Hensen-Stemple pipette. Only *Daphnia* spp. (mostly *D. galeata mendotae*) were counted because they are likely the main prey for *Bythotrephes* in Lake Michigan (Lehman and Caceres 1993, Lehman and Branstrator 1995).

A Seabird CTD with an attached Sea Tech fluorometer was cast at most stations after dark. Water samples were taken from the epilimnion, deep chlorophyll layer, and hypolimnion (based on real-time CTD cast data). To determine chlorophyll levels, duplicate water samples from each depth were filtered onto Whatman GF/F filters, extracted with N,N-dimethylformamide, and analyzed fluorometrically. The chlorophyll data from the water samples was used to calibrate the fluorometer cast data using linear regression ($r^2 = 0.95$). Fluorometer data were determined for 1-m depth intervals. The mean epilimnion chlorophyll concentration and epilimnion temperature is reported.

The abundance of *Bythotrephes* was compared among sites using the Kruskal-Wallis test and between seasons and depths using the Mann-Whitney test. A non-parametric test was used because only two replicate tows were done at each station. Brood sizes, body lengths, and spine lengths were compared between nearshore and offshore stations during each month with separate ANOVA and Tukey's HSD tests. Comparisons were also made between months and depths using ANOVA. All statistics were done using SYSTAT (8.0). P-values $\leq$ to 0.05 were considered significant.

RESULTS

July

Bythotrephes were present at every station during each sampling effort in July (Table 1). The density of *Bythotrephes* was highly variable at some stations and did not differ among nearshore stations (p = 0.16). However, densities did differ significantly among offshore stations (p = 0.04), with the highest average densities off Muskegon ($1,326/m^2$) and the lowest off Frankfort ($9/m^2$). The density of *Bythotrephes* did not differ significantly between offshore and nearshore stations (p = 0.09), although the trend at each individual location was for densities to be higher offshore.

Epilimnion water temperature ranged from 13 to 20ºC in July. A strong upwelling was noticeable at the Grand Haven and Muskegon stations. The epilimnion chlorophyll concentration was generally similar among stations. *Daphnia* abundance was highly variable among stations. The density of *Bythotrephes* in July was not correlated with epilimnion temperature, epilimnion chlorophyll concentration, or *Daphnia* abundance (r < 0.42).

Instar III *Bythotrephes* generally dominated the population structure at nearshore stations in July, although in some cases instar I individuals made a sizable contribution (Fig. 2). At offshore stations, instar I dominated the population structure at most locations. Instar IV individuals were uncommon in July and never accounted for over 6% of the population structure.

In July the mean body length of neonates (instar I) and reproductive instar II and III females differed significantly among locations at nearshore (p < 0.02) and offshore (p < 0.01) stations (Table 2). Trends for body length of each instar differed among sites, but the body size of each instar was consistently high off Grand Haven nearshore and offshore stations relative to other locations. There was no difference in body length between nearshore and offshore for any instar (p > 0.10). Body length of instar II increased with *Daphnia* abundance (r = 0.77, p = 0.04), but instar I and III did not (r = 0.47 and 0.53, respectively). There was no relation between body length of any instar and epilimnion temperature or chlorophyll concentration (r < 0.40).

In July, the mean spine length of *Bythotrephes* differed among locations for each instar at nearshore (p < 0.01) and offshore (p < 0.01) stations except instar II nearshore (p = 0.28) (Table 3). There were no strong trends in spine length among locations except that spine length was relatively high at Grand Haven offshore (instar I and II) and low at the mid lake station. Mean spine length was higher at nearshore stations than offshore for each instar (p < 0.04).

Nearly 100% of reproductive females had asexual broods in July (Fig. 3). Most reproductive females with asexual broods were instar III (70%) and instar II (27%). The overall proportion of re-

TABLE 1. *Mean density (no./m² (range from two replicate vertical net tows) of* **Bythotrephes,** *epilimnion temperature (°C), mean epilimnion chlorophyll concentration µg/l, and mean* **Daphnia** *abundance (replicate tows) at nearshore (45 m) and offshore (80 to 150 m) stations in Lake Michigan during July and September, 2000. NA = not available*

Depth zone	Date	Location	*Bythotrephes*	Temp.	CHL$_a$	*Daphnia*
Nearshore	10 July	St. Joseph, MI	12 (8–17)	19	NA	2,706
	20 July	Grand Haven, MI	653 (639–666)	15	1.0	133,690
	20 July	Muskegon, MI	120 (120–121)	13	0.9	14,006
	18 July	Frankfort, MI	116 (24–208)	14	1.2	1,496
	18 July	Sturgeon Bay, WI	19 (10–28)	18	0.8	15,183
	19 July	Sheboygan, WI	23 (6–39)	18	1.8	37,051
	20 July	Milwaukee, WI	14 (11–17)	18	0.9	16,106
		Mean (±1 SE)	137 (60)			
Offshore	10 July	mid-lake (South)	71 (70–71)	19	NA	137,510
	10 July	St. Joseph, MI	123 (93–153)	19	NA	4,584
	20 July	Grand Haven, MI	274 (201–346)	20	0.9	52,839
	20 July	Muskegon, MI	1,326 (1,320–1,332)	20	0.8	31,916
	18 July	Frankfort, MI	9 (6–11)	15	1.5	4,393
	18 July	Sturgeon Bay, WI	109 (108–109)	16	0.9	8,021
	19 July	Sheboygan, WI	269 (264–274)	19	0.6	21,199
	20 July	Milwaukee, WI	47 (43–51)	19	0.6	12,732
		Mean (±1 SE)	278 (105)			
Nearshore	8 Sept	St. Joseph, MI	21 (20–22)	18	NA	2,737
	28 Sept	Grand Haven, MI	63 (43–83)	13	NA	2,165
	9 Sept	Muskegon, MI	226 (205–247)	20	NA	12,053
	12 Sept	Frankfort, MI	1,023 (927–1,119)	19	1.5	955
	13 Sept	Sturgeon Bay, WI	173 (115–230)	18	1.5	25,592
	13 Sept	Sheboygan, WI	16 (5–27)	10	0.4	16,934
	14 Sept	Milwaukee, WI	4 (0–8)	15	1.1	4,711
		Mean (±1 SE)	218 (94)			
Offshore	9 Sept	mid-lake (South)	813 (726–900)	NA	NA	11,809
	8 Sept	St. Joseph, MI	118 (84–152)	18	NA	4,393
	28 Sept	Grand Haven, MI	544 (483–606)	NA	NA	68,755
	9 Sept	Muskegon, MI	822 (755–889)	20	NA	108,565
	12 Sept	Frankfort, MI	1,304 (1,235–1,374)	19	1.8	9,708
	13 Sept	Sturgeon Bay, WI	834 (736–932)	20	1.3	18,939
	13 Sept	Sheboygan, WI	85 (76–93)	16	1.1	39,916
	14 Sept	Milwaukee, WI	38 (34–41)	20	1.1	73,211
		Mean (±1 SE)	570 (111)			

productive females that were instar II or III differed somewhat among locations, particularly among some offshore stations where there was a higher percentage of reproductive instar II females. The difference largely reflects differences in overall population structure at these stations (Fig. 2). In July, 79% of all instar III *Bythotrephes* were females with broods, but only 21% of all instar II *Bythotrephes* were females with broods.

Brood size only differed among locations for instar III females from nearshore (p < 0.01) and offshore (p < 0.01) in July (Table 4). Too few instar II females were caught from nearshore stations for analysis in July. Broods were relatively large off Milwaukee (nearshore) and at the mid lake station in July. Overall the mean asexual brood size of instar III females (5.22 ± 0.16 eggs/embryos) was not significantly different from instar II females (4.70 ± 0.17 eggs/embryos) (p = 0.07). Broods of instar III females from offshore were larger than broods from females collected nearshore (p < 0.01), but there was no difference between depths for brood size of instar II females (p = 0.16). Brood sizes in July were not correlated with epilimnion temperature,
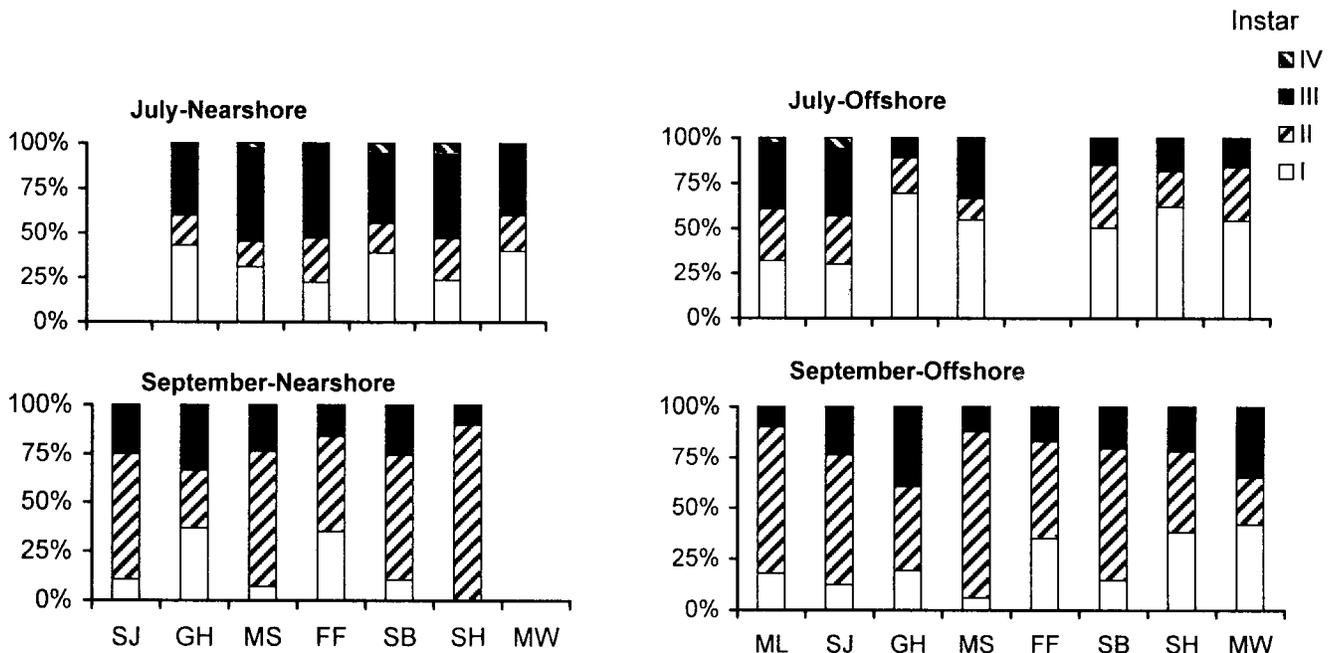
FIG. 2.   *Population structure (percent by instar) of* **Bythotrephes** *at eight sampling locations in Lake Michigan during July and September, 2000. ML = mid lake(south); SJ = St. Joseph, MI; GH = Grand Haven, MI; MS = Muskegon, MI; FF = Frankfort, MI; SB = Sturgeon Bay, WI; SH = Sheboygan, WI; MW = Milwaukee, WI.*

epilimnion chlorophyll concentration, or *Daphnia* abundance ($r < 0.66$).

September

Bythotrephes were present at every station during each sampling effort in September (Table 1). Similar to July, the density of *Bythotrephes* was highly variable at some stations and did not differ among nearshore sites ($p = 0.06$). However, densities did differ significantly among offshore stations ($p = 0.05$), with the highest average densities off Frankfort ($1,304/m^2$) and the lowest off Milwaukee ($38/m^2$). The mean density of *Bythotrephes* was higher offshore than nearshore ($p = 0.02$). The overall density of *Bythotrephes* did not differ between July and September for nearshore ($p = 0.33$) or offshore stations ($p = 0.09$).

Epilimnion water temperature ranged from 10 to 20°C in the summer. A strong upwelling was evident at the Sheboygan and Milwaukee stations. The epilimnion chlorophyll concentration was not available for most southernmost stations and was generally similar among stations at the northern sites. *Daphnia* abundance was highly variable but was generally higher offshore. There was a weak but

significant trend for the abundance of *Bythotrephes* to increase with epilimnion temperature ($r = 0.58$, $p = 0.04$) and epilimnion chlorophyll concentration ($r = 0.73$, $p = 0.04$). Abundance was not correlated with *Daphnia* abundance ($r = 0.17$).

In contrast to July, the population structure of *Bythotrephes* in September was dominated by instar II at both nearshore and offshore stations, except at the Milwaukee offshore station (Fig. 2). No instar IV individuals were caught in September.

In September, the mean body length of neonates (instar I) and reproductive instar II and III females differed among locations at both nearshore ($p < 0.01$) and offshore ($p < 0.01$) stations (Table 2). Trends for body length of each instar differed among sites, but the body length of each instar was generally highest at the mid-lake station, Muskegon, and St. Joseph. Body length of instar I was higher offshore than nearshore ($p = 0.01$). Body size of reproductive instar II and III did not differ between nearshore or offshore ($p > 0.82$). Body length of each instar was higher in September than July at both nearshore ($p < 0.01$) and offshore ($p < 0.01$) stations. The body length of instar II was correlated with epilimnion temperature ($r = 0.58$, $p = 0.04$), but instar I and III body lengths were not

TABLE 2.   Mean body length (mm) ± 1 SE of instar I (neonates) and reproductive instar II and III **Bythotrephes** *from nearshore (45 m) and offshore (80 to 150 m) stations in Lake Michigan during July and September, 2000. Stations within each grouping that were not significantly different (Tukey's HSD) share a common letter (see text for further explanation).*

Depth zone	Date	Location	I	II	III
Nearshore	10 July	St. Joseph, MI	1.40 (0.08) ab		
	20 July	Grand Haven, MI	1.99 (0.04) c	2.43 (0.10)	2.79 (0.07) b
	20 July	Muskegon, MI	1.79 (0.04) b		2.40 (0.04) a
	18 July	Frankfort, MI	1.82 (0.11) bc		2.32 (0.09) a
	18 July	Sturgeon Bay, WI	1.41 (0.05) a		2.07 (0.16) a
	19 July	Sheboygan, WI	1.90 (0.16) bc		2.38 (0.05) a
	20 July	Milwaukee, WI	1.30 (0.10) a		2.08 (0.18) a
		Mean	1.80 (0.03)		2.47 (0.04)
Offshore	10 July	mid-lake (South)	1.62 (0.04) ab	2.33 (0.14) a	2.39 (0.06) a
	10 July	St. Joseph, MI	1.51 (0.05) a	2.20 (0.10) ab	2.35 (0.05) a
	20 July	Grand Haven, MI	2.07 (0.04) d	2.36 (0.14) ab	2.79 (0.17) b
	20 July	Muskegon, MI	1.86 (0.04) c		2.70 (0.05) b
	18 July	Frankfort, MI	1.43 (0.08) ab		
	18 July	Sturgeon Bay, WI	1.43 (0.03) a	1.92 (0.04) b	2.20 (0.06) a
	19 July	Sheboygan, WI	1.78 (0.04) bc	2.20 (0.08) ab	2.47 (0.07) ab
	20 July	Milwaukee, WI	1.54 (0.06) a	2.04 (0.09) ab	2.33 (0.12) ab
		Mean	1.74 (0.02)	2.13 (0.18)	2.46 (0.03)
Nearshore	8 Sept	St. Joseph, MI	2.92 (0.11) c	3.96 (0.18) d	3.81 (0.15)a
	28 Sept	Grand Haven, MI	1.52 (0.08) a	2.75 (0.17) ab	2.83 (0.10) b
	9 Sept	Muskegon, MI	2.64 (0.10) c	3.45 (0.06) c	3.51 (0.12) a
	12 Sept	Frankfort, MI	2.22 (0.04) b	3.14 (0.07) b	3.22 (0.13) ab
	13 Sept	Sturgeon Bay, WI	1.85 (0.07) c	3.47 (0.06) c	3.06 (0.15) ab
	13 Sept	Sheboygan, WI		2.58 (0.21) a	
	14 Sept	Milwaukee, WI	1.91 (0.32) ab		
		Mean	2.00 (0.06)	3.36 (0.04)	3.20 (0.07)
Offshore	9 Sept	mid-lake (South)	2.82 (0.06) d	3.56 (0.08) cd	3.83 (0.16) b
	8 Sept	St. Joseph, MI	2.47 (0.15) e	3.28 (0.11) bc	3.63 (0.12) b
	28 Sept	Grand Haven, MI	2.11 (0.08) a	2.94 (0.11) ab	2.86 (0.06) a
	9 Sept	Muskegon, MI	2.60 (0.10) de	3.70 (0.05) d	3.82 (0.09) b
	12 Sept	Frankfort, MI	2.05 (0.04) ac	2.83 (0.12) a	3.02 (0.09) a
	13 Sept	Sturgeon Bay, WI	1.99 (0.06) ac	3.17 (0.11) abc	2.98 (0.09) a
	13 Sept	Sheboygan, WI	2.04 (0.05) ac	2.98 (0.09) ab	3.14 (0.07) a
	14 Sept	Milwaukee, WI	1.80 (0.06) c	2.91 (0.13) ab	2.99 (0.11) a
		Mean	2.16 (0.03)	3.35 (0.04)	3.21 (0.04)

(r = 0.53 and 0.39 respectively). There was no significant relation between body length of any instar and *Daphnia* abundance or epilimnion chlorophyll concentration (r < 0.58).

Mean spine length differed among nearshore stations for instar II (p = 0.02) and among offshore stations for instar I and II (p < 0.01) (Table 3). There were no consistent trends in spine length among locations in September. Spine length did not differ between nearshore and offshore in the autumn for any instar (p > 0.14). Spine length was longer in September than July for each instar at both nearshore (p < 0.01) and offshore (p < 0.01) stations.

About 96% of reproductive females had asexual broods in September (Fig. 3). In contrast to July, most reproductive females with asexual broods were instar II (62%) and the remainder instar III (37%). The overall proportion of reproductive females that were instar II or III differed somewhat among locations, mainly because of a relatively high percentage of reproductive instar III females at

TABLE 3.   Mean spine length (mm) ± 1 SE of instar I (neonates), instar II and III **Bythotrephes** *from nearshore (45 m) and offshore (80 to 150 m) stations in Lake Michigan during July and September, 2000. Stations within each grouping that were not significantly different (Tukey's HSD) share a common letter (see text for further explanation).*

Depth zone	Date	Location	I	II	III
Nearshore	10 July	St. Joseph, MI	4.77 (0.22) ab		
	20 July	Grand Haven, MI	6.13 (0.35) c	6.82 (0.56)	7.80 (0.69) a
	20 July	Muskegon, MI	5.53 (0.75) ab	6.63 (0.82)	7.08 (1.32) b
	18 July	Frankfort, MI	5.83 (0.46) ac	6.83 (0.61)	7.82 (0.76) ab
	18 July	Sturgeon Bay, WI	5.22 (0.43) ab	6.34 (0.41)	8.30 (0.98) a
	19 July	Sheboygan, WI	5.55 (0.87) abc	7.07 (0.71)	8.14 (0.67) ab
	20 July	Milwaukee, WI	4.98 (0.62) b	6.12 (0.17)	7.58 (0.91) ab
		Mean	5.72 (0.07)	6.65 (0.10)	7.55 (0.09)
Offshore	10 July	mid-lake (South)	4.50 (0.90) a	5.66 (1.35) a	5.79 (1.12) b
	10 July	St. Joseph, MI	4.69 (0.68) ab	5.70 (0.66) a	7.07 (0.88) a
	20 July	Grand Haven, MI	6.23 (0.41) c	7.22 (0.84) b	7.89 (1.02) a
	20 July	Muskegon, MI	5.75 (0.59) d	6.84 (0.33) bc	7.42 (1.11) a
	18 July	Frankfort, MI	5.57 (0.28) cde		
	18 July	Sturgeon Bay, WI	5.12 (0.44) e	6.59 (0.41) bc	8.02 (0.71) a
	19 July	Sheboygan, WI	5.37 (0.58) e	6.31 (0.72) ac	7.54 (0.74) a
	20 July	Milwaukee, WI	5.07 (0.62) be	6.75 (0.61) bc	7.75 (1.36) a
		Mean	5.42 (0.04)	6.35 (0.08)	7.10 (0.10)
Nearshore	8 Sept	St. Joseph, MI	6.45 (0.19)	7.21 (0.43) a	8.67 (0.77)
	28 Sept	Grand Haven, MI	5.95 (0.56)	7.18 (1.00) a	8.51 (1.03)
	9 Sept	Muskegon, MI	6.39 (0.54)	7.07 (0.50) a	7.97 (0.56)
	12 Sept	Frankfort, MI	6.09 (0.55)	7.12 (0.39) a	8.50 (0.65)
	13 Sept	Sturgeon Bay, WI	5.83 (0.42)	7.12 (0.59) a	8.03 (0.79)
	13 Sept	Sheboygan, WI		6.43 (0.68) b	
	4 Sept	Milwaukee, WI	6.02 (0.65)		
		Mean	6.15 (0.06)	7.10 (0.04)	8.25 (0.08)
Offshore	9 Sept	mid-lake (South)	6.28 (0.27) ab	6.97 (0.45) bc	7.61 (0.33)
	8 Sept	St. Joseph, MI	6.50 (0.47) b	7.20 (0.46) ab	8.09 (0.58)
	28 Sept	Grand Haven, MI	6.46 (0.65) ab	7.16 (0.43) ac	8.38 (0.83)
	9 Sept	Muskegon, MI	6.10 (0.30) ab	6.89 (0.48) c	7.87 (0.46)
	12 Sept	Frankfort, MI	6.09 (0.58) ab	7.11 (0.39) ac	8.35 (0.82)
	13 Sept	Sturgeon Bay, WI	5.85 (0.25) a	6.91 (0.39) c	8.14 (0.52)
	3 Sept	Sheboygan, WI	6.06 (0.58) ab	7.07 (0.56) ac	8.03 (0.87)
	4 Sept	Milwaukee, WI	5.97 (0.70) ab	7.52 (1.10) a	8.24 (0.87)
		Mean	6.14 (0.04)	7.04 (0.02)	8.16 (0.06)

Grand Haven. In September, 74% of all instar III *Bythotrephes* were females with broods and 49% of all instar II *Bythotrephes* were females with broods.

Brood size differed among locations for instar II and III females from nearshore (p < 0.01) and offshore (p < 0.01) in September (Table 4). In general, brood size was relatively high at the nearshore station off Grand Haven and the offshore station at Milwaukee. Overall the mean asexual brood size of instar III females (3.26 ± 0.09 eggs/embryos) was larger than that of instar II females (2.65 ± 0.06 eggs/embryos) (p < 0.01), but there were exceptions

at some locations. Brood sizes of instar II and III females were similar between nearshore and offshore in September (p > 0.61). Brood size in September was smaller than in July for instar II and III at both nearshore (p < 0.01) and offshore (p < 0.01) stations. Brood sizes in September were not significantly correlated with epilimnion temperature, epilimnion chlorophyll, or *Daphnia* abundance (r < 0.73).

Nearly all females with sexual broods were collected in September at offshore sites (77%). The highest percentage of sexual reproduction was at
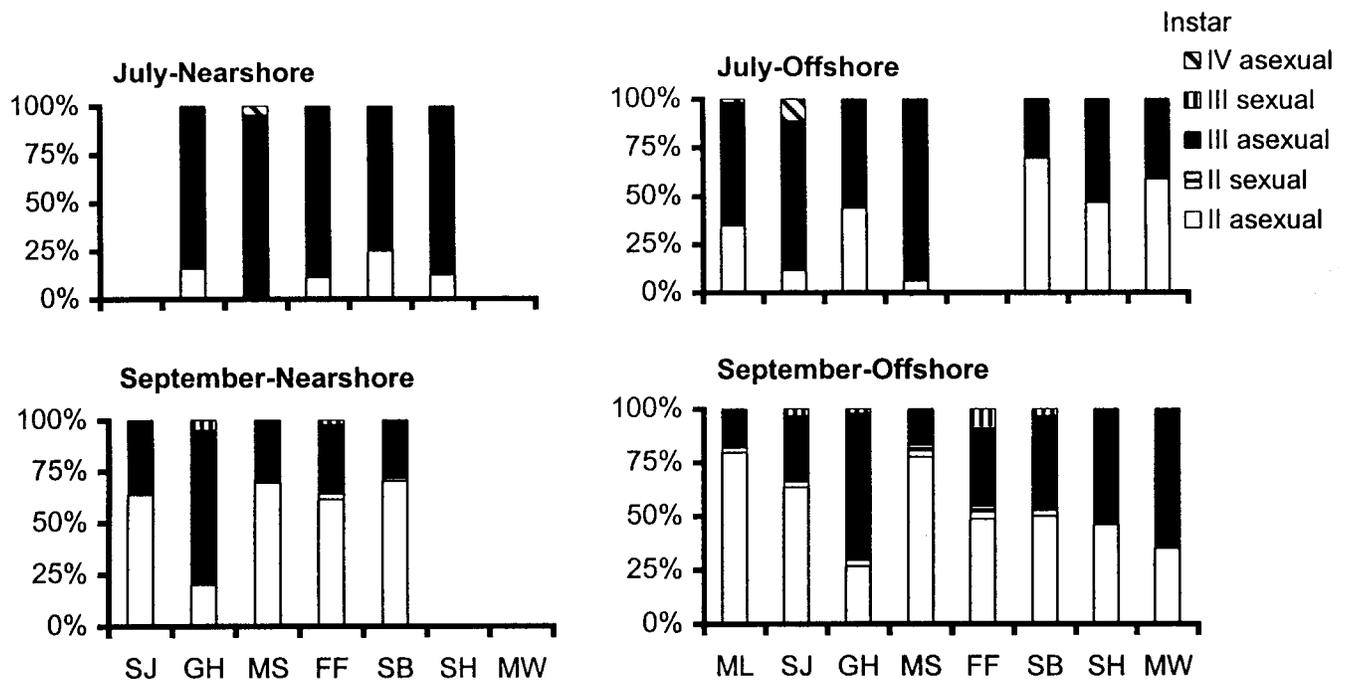
FIG. 3. *Percentage of instar II–IV females that reproduced sexually and asexually at eight locations in Lake Michigan during July and September, 2000. See Figure 2 legend for site abbreviations.*

the offshore station at Frankfort (15%), whereas no females with resting eggs were collected off Sturgeon Bay or Milwaukee (Fig. 3). Females with sexual broods were mainly instar II (62%) and the remainder were instar III. The mean sexual brood size was 5.04 ± 0.26 resting eggs.

DISCUSSION

Bythotrephes abundance was variable throughout Lake Michigan and in general did not appear to be dependent upon the physical or biological factors that were examined. To some extent, *Bythotrephes* was generally more abundant offshore than nearshore. This distribution is similar to observations from the late 1980s after the initial establishment of the species in the lake (Lehman 1987, 1991). Fish predation likely limits the abundance of *Bythotrephes* in nearshore areas during most of the year and could contribute to the patchy distribution of the species (Bilkovic and Lehman 1997, Pothoven *et al.* 2001). Geographic location did not appear to be as consistent of a factor that determined the abundance of *Bythotrephes*. In the late 1980s, there were no consistent trends in geographic distribution of *Bythotrephes* in Lake Michigan, especially for stations of the same bottom

depth (Lehman 1987, 1991; Jin and Sprules 1990). The densities of *Bythotrephes* in 2000 were generally within the range of densities from southeastern Lake Michigan during 1987 to 1998. However, the high variability observed in net tows suggests that intense sampling could be required to accurately document spatial and temporal trends in abundance of *Bythotrephes*.

Population structure and life history characteristics provide additional insight into the adaptation of *Bythotrephes* to changing environmental factors (Yan and Pawson 1998, Straile and Halbich 2000). One life history strategy that appears to be adaptive to life in the Great Lakes was the seasonal changes in the developmental stage of reproductive females. During the year, there was a shift from reproduction by instar III females to reproduction by instar II females. The shift generally reflected a change in the population structure of *Bythotrephes* at most sites during the same period. When *Bythotrephes* were first found in Lake Michigan, there was little or no reproduction by instar II females (Yurista 1992, Lehman and Branstrator 1995). By the mid 1990s, instar II females were reproducing in southeastern Lake Michigan (Pothoven *et al.* 2001). Some have suggested that reproduction by instar II females reflects good conditions for *Bythotrephes* (Ketelaars

TABLE 4. *Mean asexual brood size ± 1 SE of instar II and III* **Bythotrephes** *from nearshore (45 m) and offshore (80 to 150 m) stations in Lake Michigan during July and September, 2000. Stations within each grouping that were not significantly different (Tukey's HSD) share a common letter (see text for further explanation).*

Depth zone	Date	Location	II	III
Nearshore	10 July	St. Joseph, MI		
	20 July	Grand Haven, MI	2.80 (0.20)	3.30 (0.20) a
	20 July	Muskegon, MI		3.85 (0.15) ac
	18 July	Frankfort, MI		3.38 (0.42) a
	18 July	Sturgeon Bay, WI		5.67 (0.67) b
	19 July	Sheboygan, WI		5.43 (0.75) bc
	20 July	Milwaukee, WI		6.75 (1.97) b
		Mean		3.99 (0.17)
Offshore	10 July	mid-lake (South)	5.11 (0.50)	7.84 (0.46) b
	10 July	St. Joseph, MI	5.80 (0.37)	7.00 (0.35) bc
	20 July	Grand Haven, MI	3.57 (0.61)	4.11 (0.59) ad
	20 July	Muskegon, MI		3.45 (0.18) a
	18 July	Frankfort, MI		
	18 July	Sturgeon Bay, WI	5.08 (0.22)	7.00 (0.43) bc
	19 July	Sheboygan, WI	4.00 (0.39)	5.38 (0.43) c
	20 July	Milwaukee, WI	5.30 (0.33)	6.14 (0.60) bcd
		Mean	4.79 (0.11)	6.01 (0.21)
Nearshore	8 Sept	St. Joseph, MI	2.71 (0.47) a	4.25 (0.85) ab
	28 Sept	Grand Haven, MI	5.25 (0.25) b	4.87 (0.42) b
	9 Sept	Muskegon, MI	2.44 (0.14) a	2.89 (0.25) a
	12 Sept	Frankfort, MI	2.85 (0.19) a	3.07 (0.20) a
	13 Sept	Sturgeon Bay, WI	2.60 (0.13) a	2.44 (0.22) a
	13 Sept	Sheboygan, WI	2.40 (0.24) a	
	14 Sept	Milwaukee, WI		
		Mean	2.62 (0.09)	3.21 (0.18)
Offshore	9 Sept	mid-lake (South)	2.20 (0.15) a	2.50 (0.19) a
	8 Sept	St. Joseph, MI	2.60 (0.15) ad	2.94 (0.25) ab
	28 Sept	Grand Haven, MI	3.33 (0.25) bd	3.43 (0.25) ab
	9 Sept	Muskegon, MI	2.38 (0.12) ac	2.50 (0.20) a
	12 Sept	Frankfort, MI	2.94 (0.27) ab	3.75 (0.25) ab
	13 Sept	Sturgeon Bay, WI	2.53 (0.27) ab	2.85 (0.22) ab
	13 Sept	Sheboygan, WI	3.18 (0.23) bc	3.40 (0.24) ab
	14 Sept	Milwaukee, WI	3.86 (0.34) b	4.00 (0.32) b
		Mean	2.46 (0.08)	3.07 (0.12)

et al. 1995), but this does not appear to be necessarily true (Yan and Pawson 1998). In the European Lake Constance where *Bythotrephes* are native, few instar III individuals are present after the early summer and instar II females account for most reproduction (Straile and Halbich 2000). Another study in Lake Constance suggested that size selective fish predation by coregonids limits the abundance of instar III *Bythotrephes* (Palmer *et al.* 2001). As adult fish in Lake Michigan adapted to *Bythotrephes* as a readily available prey, *Bythotrephes* may have had to switch to earlier reproduction in order to persist.

Changes in the zooplankton community could also favor earlier reproduction by *Bythotrephes*. When *Bythotrephes* was first found in Lake Michigan, the zooplankton community was dominated by *Daphnia pulicaria*, *D. retrocurva*, and *D. galeata* (Barbiero *et al.* 2001). After the arrival of *Bytho-*

trephes, calanoid copepods and *D. galeata* became the dominate zooplankton, *Daphnia* spp. abundance declined by midsummer each year, and the large bodied *D. pulicaria* became rare (Lehman and Caceres 1993, Barbiero *et al.* 2001). Additionally, the vertical migration patterns of *D. galeata* changed after the arrival of *Bythotrephes* (Lehman and Caceres 1993). Instar III *Bythotrephes* are more dependent on large-bodied *Daphnia* than earlier instars that consume calanoid copepods and small cladocerans (Yurista and Schulz 1995, Schulz and Yurista 1999). Therefore, the current zooplankton community may favor earlier maturity for *Bythotrephes*. Food types or availability is a plausible explanation for at least some of the observed changes in *Bythotrephes* population structure because the seasonal changes in community structure were observed at the mid lake station, where it is assumed that the risk of predation by pelagic fish is low (Brandt *et al.* 1991).

The changes in population structure of *Bythotrephes* could affect the Lake Michigan food web. A shift toward shorter development time and earlier maturity could shift the predation pressure to smaller prey (Yurista and Schulz 1995, Schulz and Yurista 1999). The change could reduce the overall consumptive demands of individual *Bythotrephes*, even though early instars do not use energy resources as efficiently as instar III (Yurista and Schulz 1995). The change in prey types could also affect competitive interactions between *Bythotrephes* and other predaceous invertebrates or zooplanktivorous fish.

Another temporal change in population structure was the near convergence in body size of instar II and III at most locations. Most growth (body) of *Bythotrephes* occurred between instar I and II, whereas little growth occurred between instar II and III. The lack of growth between instar II and III, along with decreased body size and the appearance of resting eggs in late summer have been attributed to both food limitation and size selective fish predation in inland lakes and southeastern Lake Michigan (Yan and Pawson 1998, Pothoven *et al.* 2001). After their introduction into Lake Michigan, *Bythotrephes* demonstrated considerable growth between instar II and III at an offshore site near Grand Haven in September 1989 (Burkhardt 1994). The average increase in body length between instar II and III was 0.54 mm in 1989 compared to 0.22 mm at the same station in 2000. Changes in abundance, behavior, and species composition of *Daphnia* spp. in Lake Michigan could be affecting the growth of

instar III *Bythotrephes* in Lake Michigan. On the other hand, as fish have adapted to the presence of the large bodied *Bythotrephes* as a prey item, size selective predation could be limiting the abundance of larger *Bythotrephes* (Bilkovic and Lehman 1997, Sullivan and Lehman 1998).

Some other life history traits demonstrated the plasticity of *Bythotrephes* although they did not appear to be responses to new environmental conditions. *Bythotrephes* populations in the summer were generally characterized by small body size at reproduction (instar II and III), large clutch size, and small neonates. Later in the season, body size at reproduction was larger, clutch size was smaller, and neonates were larger. Similar results were observed for *Bythotrephes* in Europe (Ketelaars *et al.* 1995, Straile and Halbich 2000) and southeastern Lake Michigan (Burkhardt 1994, Pothoven *et al.* 2001). One explanation behind the seasonal variation in life history strategy is gape-limited fish predation (Straile and Halbich 2000). Although gape-limited juvenile fish can be numerous in Lake Michigan in early fall, larger size at reproduction and larger neonates would make both reproductive females and neonates more vulnerable to non-gape-limited adult alewife (Mills *et al.* 1992, Straile and Halbich 2000).

The decrease in brood size and increase in neonate size may also be attributable to food scarcity because larger neonates may be more resistant to starvation (Ketelaars *et al.* 1995). Most energetic analyses suggest that the consumption demands of *Bythotrephes* can exceed the daily production levels of their preferred prey in Lake Michigan (Lehman and Caceres 1993, Burkhardt and Lehman 1994). The appearance of resting eggs in the fall at most locations also indicates that food may have been limited in Lake Michigan (Burkhardt and Lehman 1994, Yan and Pawson 1998). However, body and brood sizes were generally not correlated with *Daphnia* abundance in this study. Another factor that has been attributed to seasonal differences in body size is water temperature (Ketelaars *et al.* 1995, Burkhardt 1994), but there was little correlation between body size and water temperature in this study. Water temperature was probably not a factor because it was generally similar between July and September, and most differences in temperature appeared to be related to short-term upwelling events that might not be reflected in the overall growth of *Bythotrephes*. Most likely, a complex interaction of fish predation, food

availability, and water temperature controls the seasonal changes in brood and body sizes.

Another life history trait that varied seasonally was spine length. *Bythotrephes* may allocate more energy to spine growth in the presence of gape-limited predators, and therefore spine length can be an indicator of fish predation pressure (Barnhisel 1991, Ketelaars *et al.* 1995, Straile and Halbich 2000, Sullivan and Lehman 1998). Spine length generally increased between July and September. Increased spine length in the autumn has been attributed to higher fish predation as juvenile fish become large enough to feed on *Bythotrephes* (Straile and Halbich 2000). In a Dutch reservoir with few fish, spine length did not differ substantially during the year (Ketelaars *et al.* 1995). If the seasonal increase in spine length is a response to increased fish predation, it is surprising to observe the change at the mid lake station, where few fish are likely present (Brandt *et al.* 1991). The effects observed at the mid lake station could reflect water exchange between nearshore and offshore stations.

Most general trends in life history strategies were generally similar among geographic locations. However, there were differences in the population characteristics among locations within the lake. For example, abundance, body and spine length, population structure, and brood size all differed among locations. These differences need to be accounted for in any large-scale population model of *Bythotrephes* production or consumption estimates. Other studies have found that the some population characteristics differ among the Great Lakes (Bilkovic and Lehman 1997, Sullivan and Lehman 1998) as well as seasonally and annually at a single location within one lake (Pothoven *et al.* 2001). Because population characteristics differ within large lakes, analysis and monitoring of *Bythotrephes* populations could be quite complex and labor intensive. The abundance of zooplankton (Barbiero *et al.* 2001) and fish (Fabrizio *et al.* 2000) can all differ spatially within Lake Michigan and could combine to account for local population differences of *Bythotrephes*.

The results of this study indicate that population characteristics of *Bythotrephes* are changing as this species adapts to Lake Michigan. In order to assess the role of *Bythotrephes* in the Lake Michigan food web, up-to-date data with good spatial coverage of the lake are needed. As new potential competitors such as *Cercopagis* arrive, *Bythotrephes* may continue to adapt different life history strategies as its role in the food-web continues to change. Additionally, because *Bythotrephes* and *Cercopagis* are similar species, researchers should account for the potential for spatial and temporal variability in *Cercopagis* sampling protocols.

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