# Comparison of 5 benthic samplers to collect burrowing mayfly nymphs (*Hexagenia* spp.:Ephemeroptera:Ephemeridae) in sediments of the Laurentian Great Lakes

## DON W. SCHLOESSER<sup>1</sup>

Great Lakes Science Center, US Geological Survey, Ann Arbor, Michigan 48105 USA

## THOMAS F. NALEPA

Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, Michigan 48105 USA

Abstract. The recent return of burrowing mayfly nymphs (Hexagenia spp.) to western Lake Erie of the Laurentian Great Lakes has prompted a need to find a sampler to obtain the most accurate (i.e., highest mean density) and precise (i.e., lowest mean variance) abundance estimates of nymphs. The abundance of burrowing nymphs is important because it is being used as a measure of ecosystem health to determine management goals for fisheries and pollution abatement programs for waters in both North America and Europe. We compared efficiencies of 5 benthic grab samplers (Ponar, Ekman, petite Ponar, Petersen, and orange-peel) to collect nymphs from sediments of western Lake Erie and Lake St. Clair. Samplers were used at one site with soft substrates in both lakes in 1997 (Ponar, Ekman, petite Ponar, and Petersen) and 1998 (Ponar and Ekman), and at one site with soft and one site with hard substrates in Lake St. Clair in 1999 (Ponar and orange-peel). In addition, the Ponar, Ekman, and Petersen samplers were used at one site with soft substrates of western Lake Erie in 2000 to examine the causes of differences among samplers. The Ponar was more accurate than the other samplers; it collected the highest densities of nymphs for 31 of 32 date and site comparisons. In soft substrates, the order of decreasing overall densities was: Ponar>Petersen>petite Ponar>Ekman in western Lake Erie and Ponar>Petersen> Ekman>petite Ponar in Lake St. Clair in 1997, Ponar>Ekman in both lakes in 1998, and Ponar>orange-peel in Lake St. Clair in 1999. In hard substrates, the Ponar was more accurate than the orange-peel in Lake St. Clair in 1999. Precision of the Ponar was generally greater than the Ekman, petite Ponar, and Petersen but similar to the orangepeel. Higher densities of nymphs obtained with the Ponar than other grabs are attributed to its relatively heavy weight, which allows it to sample deeper in sediments than the Ekman and petite Ponar. Also, the Ponar has a screened top, which allows it to minimize hydraulic shock waves more than the Petersen, and uniform sides, which allow it to sample nymphs more uniformly through sediments than the orange-peel. We recommend that future estimates of burrowing mayfly densities be obtained with a standard Ponar sampler similar to the one used in our study because it will yield the most accurate and precise measurements of burrowing mayfly nymphs such as Hexagenia spp.

Key words: mayfly, sampler comparison, lentic sediments, Laurentian Great Lakes.

Various benthic samplers have been used to determine densities of ephemerid, burrowing mayfly nymphs (e.g., *Hexagenia* spp. and *Ephoron* spp.) in rivers of North America and Europe, including nearshore waters of the Laurentian Great Lakes (Wright 1955, Schneider et al. 1969, Mozley and LaDronka 1988, Reynoldson et al. 1989, bij de Vaate et al. 1992, Dermott 1994, reviewed in Schloesser et al. 2001). Many populations of nymphs in the Great Lakes disappeared from sediments during the 1950s because of pollution and resulting habitat degradation (Britt 1955, Beeton 1969, Cook and

Johnson 1974). Renewed interest in sampling mayfly nymphs occurred in the mid 1990s when studies noted that burrowing nymphs returned to several rivers in North America and Europe, and to lentic habitats in western Lake Erie (Fremling and Johnson 1990, bij de Vaate et al. 1992, Krieger et al. 1996, Schloesser et al. 2001). The recovery of burrowing mayflies, where they had been absent for decades, was of great interest to management agencies because nymphs are important in food webs supporting fishes and they are recognized as a sentinel species to measure progress of pollution-abatement programs (Fremling 1964, Reynoldson et al. 1989,

<sup>&</sup>lt;sup>1</sup> E-mail address: don\_schloesser@usgs.gov

TABLE 1. Sampling design used to compare 5 kinds of benthic grabs used at 2 sites with soft substrates (site 7M [lat 41°44.00′, long 83°17.83′] in western Lake Erie and site 1 [lat 42°25.00′, long 82°45.00′] in Lake St. Clair), and 1 site with hard substrates (site 2 [lat 42°22.91′, long 82°49.73′]in Lake St. Clair) in the Laurentian Great Lakes from 1997 to 2000.

Year	Samplers	Sites sampled	Frequency of sampling	Number of samples
1997	Ponar, Ekman, petite Ponar, Peterson	7M in Lake Erie 1 in Lake St. Clair	Monthly, May to Octo- ber (7M); June to October (1)	3/sampler/date (total site 7M = 72, site 1 = 60)
1998	Ponar, Ekman	7M in Lake Erie 1 in Lake St. Clair	Monthly, March to June	3/sampler/date (total site 7M = 12, site 1 = 12)
1999	Ponar, orange- peel	1 in Lake St. Clair 2 in Lake St. Clair	7 dates, June to September (1); 5 dates, June to August (2)	5/sampler/date (total site 1 = 70, site 2 = 50)
2000	Ponar, Ekman, Petersen	7M in Lake Erie	12 October	20/sampler (total = $60$ )

Krieger et al. 1996, Cochran 1992, Ohio Lake Erie Commission 1998).

Many benthic samplers have been used to obtain benthos containing burrowing mayfly nymphs (Brinkhurst 1974, Reynoldson et al. 1989, Clesceri et al. 1998). For example, Hexagenia spp. have been sampled in western Lake Erie with Ekman, Petersen, Franklin, Ponar, petite Ponar, and Shipek grabs, box corers, and 2 other unknown samplers (Reynoldson et al. 1989, Schloesser et al. 2001). Most of these samplers have been recommended as standard equipment to sample benthos in North America, but a review of density estimates of Hexagenia spp. nymphs obtained with different samplers in western Lake Erie led Schloesser et al. (2001) to conclude that density differences between studies were partly attributable to use of different samplers (Reynoldson et al. 1989, Clesceri et al. 1998). Historically, the choice of a sampler to obtain quantitative estimates of mayflies in Lake Erie was of little concern prior to the 1950s when few samplers were available, and between the 1950s and early 1990s when few or no nymphs were present in Lake Erie (Reynoldson et al. 1989, Schloesser et al. 2001). However, mayflies recolonized sediments of western Lake Erie in the mid 1990s and, as reported by Schloesser et al. (2001), 3 investigators used 3 different samplers (Ponar, Ekman, and petite Ponar) to determine densities of nymphs. Although the performance of some benthic samplers has been compared for some taxa (e.g., Sly 1969, Flannagan 1970, Nalepa and Robertson 1981), relative efficiencies of samplers for quantifying burrowing mayfly nymphs, such as *Hexagenia* spp., have not been determined.

In the present study, we determined efficiencies of 5 grab samplers (Ponar, Ekman, petite Ponar, Petersen, and orange-peel) that have been used to obtain most quantitative estimates of mayfly nymphs in the Great Lakes and elsewhere (Mozley and LaDronka 1988, Clesceri et al. 1998, Schloesser et al. 2001, D. Klemm, USE-PA, Cincinnati, Ohio, personal communication). We believe this comparison will encourage future sampling of Hexagenia spp. using one sampler, thus allowing better comparability between studies and more accurate assessments of long-term trends. In addition, knowledge of sampler efficiencies may be used to adjust historical density estimates of nymphs by applying density conversion factors to data obtained with previously used samplers.

#### Methods

Study design

We evaluated the accuracy (i.e., highest mean densities) and precision (i.e., lowest mean variance) of 5 benthic grabs to collect burrowing mayfly nymphs in western Lake Erie and Lake St. Clair from 1997 to 1999 (Table 1). Four of the samplers (Ponar, Ekman, petite Ponar, and Petersen) account for  $\sim 95\%$  of the quantitative density estimates of burrowing mayfly nymphs in western Lake Erie, and the  $5^{\rm th}$  sampler (or-

TABLE 2. Statistical tests used to compare differences of densities (log<sub>10</sub> transformed) and lengths of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 5 kinds of benthic grab samplers in western Lake Erie and Lake St. Clair of the Laurentian Great Lakes from 1997 to 2000.

Year	Parameter	Factors tested	Statistical test
1997	Density of nymphs	Samplers per water body	2-way ANOVA
	Density of nymphs	Samplers per date per water body	2-way ANOVA and Tukey's multiple comparisons
	Density of nymphs	Samplers within date and water body	1-way ANOVA and Tukey's multiple comparisons
	Density of nymphs	Sampler × date interaction within water bodies	2-way ÂNOVA
1998–2000	Density of nymphs	Samplers per year and samplers per date	Student's t-tests
1997	Length of nymphs	Samplers per date	2-way ANOVA and Tukey's multiple comparisons
2000	Length of nymphs	Samplers	Student's t-tests
	Length of nymphs	mm-length categories	Student's t-tests

ange-peel) has been used to quantify nymphal densities in other waters of the Laurentian Great Lakes (Mozley and LaDronka 1988, Reynoldson et al. 1989, Schloesser et al. 2001). The October 2000 samples were collected to examine differences among grabs based on nymphal size and depth of grab penetration. There was a very low proportion of small nymphs in late summer 1997 and summer 1998 because of the absence of nymphal recruitment in 1997, and we believed the size of nymphs and resulting burrow depths of nymphs could affect density estimates obtained with different samplers.

Sediments at site 7M in western Lake Erie were soft, pudding-like mud typical of 90% of the substrates throughout the basin (Carr and Hiltunen 1965, Bolsenga and Herdendorf 1993). Sediments at site 1 in Lake St. Clair were similar to those at site 7M in western Lake Erie, but were a little firmer, whereas sediments at site 2 in Lake St. Clair were hard with clay, sand, stones, and rocks.

# Sampler design

A detailed description and operational evaluation of the 5 samplers used in the present study appear in Sly (1969) and Clesceri et al. (1998). Briefly, the Ponar and petite Ponar have ¼-cylinder jaw design, the Ekman has a box with ¼-cylinder design, the Petersen has a full-cylinder jaw design, and the orange-peel has a ½-sphere design (Hopkins 1964, Clesceri et al. 1998). The Ekman uses a spring tripping mech-

anism activated by a messenger dropped down from the surface, whereas the other 4 samplers are activated by weight-release triggers that allow the samplers to close when they contact sediments. The Ponar and petite Ponar have screens and the Ekman has movable plates on the top surfaces of the samplers to minimize water disturbance below the sampler as they are lowered to obtain samples. The Petersen and orange-peel have no mechanism to minimize water disturbance. Individual samplers weighed 19.7, 9.9, 6.4, 28.5, and 30.0 kg for the Ponar, Ekman, petite Ponar, Petersen, and orange-peel, respectively. In soft substrates of western Lake Erie, the Ponar and petite Ponar were usually full (90-100%, visually estimated) of sediment upon sample retrieval, the Ekman varied between ~30 to 50% full, and the Petersen varied between 80 and 100% full. The fullness of the orange-peel in both soft and hard substrates and the Ponar in hard substrates in Lake St. Clair varied dramatically (25-90%) as a result of sampler design and varying depth of penetration. Sample volumes were not used in the determination of densities because 1) depth of penetration varied, and 2) volumes appeared to vary each sampling period (0-10% difference per sampler) and between sampling periods (5-20% difference), probably in relation to local variations in substrate firmness and changing temperatures that resulted in firmer substrates during cold periods (5°C) than warm periods (25°C).

TABLE 3. Mean densities (numbers/ $m^2 \pm SE$ ) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 4 kinds of benthic grab samplers in western Lake Erie (site 7M) and Lake St. Clair (site 1) of the Laurentian Great Lakes from May 1997 to June 1998. The CV (%) and, in parentheses, number of samples needed to obtain a SE  $\pm$  10% of the mean appear on the 2nd line of each value. For each sampling period and lake, values followed by different superscript letters are significantly different at  $p \le 0.05$  and values followed by different superscript numbers are significantly different between p > 0.05 and  $p \le 0.10$ . Refer to Table 2 for statistical tests performed.

		We	stern Lake Erie			
	Sampler					
Date	Ponar	Ekman	Petite Ponar	Petersen	<i>p</i> -value	
1997						
28 May	$2100 \pm 65.7$ 5 (5)	1507 ± 502.3 58 (616)	$1560 \pm 337.9$ 38 (260)	$1423 \pm 161.9$ 20 (72)	0.53	
23 June	$1474 \pm 124.2^{1}$ $15 (39)$	$1462 \pm 90.2^{1}$ $11 (21)$	$1264 \pm 94.2$ $13 (31)$	$907 \pm 169.4^{2}$ $32 (194)$	0.05	
24 July	1116 ± 78.2 12 (27)	754 ± 201.7 46 (398)	861 ± 58.6 12 (26)	978 ± 53.0 9 (16)	0.28	
28 August	$937 \pm 24.8^{a}$ 5 (4)	374 ± 39.2 <sup>b</sup> 18 (61)	430 ± 35.6 <sup>b</sup> 14 (38)	$770 \pm 34.2^{a}$ 8 (11)	< 0.01	
22 September	$778 \pm 67.8^{a}$ 14 (42)	451 ± 56.2 <sup>b3</sup> 22 (86)	$484 \pm 61.6^{23}$ 22 (90)	$717 \pm 64.0$ <sup>124</sup> 15 (44)	0.01	
23 October	737 ± 65.7ª 15 (44)	322 ± 35.9 <sup>b</sup> 1 19 (69)	457 ± 35.6 <sup>b c 2</sup> 14 (34)	$584 \pm 19.0^{a c}$ 6 (6)	< 0.01	
Overall	$1190 \pm 212.5^{a1} \\ 11 (27)$	811 ± 221.5 <sup>b</sup> 29 (209)	$843 \pm 194.9^{2}$ $19 (80)$	896 ± 119.6 15 (57)	0.01	
1998						
24 March	682 ± 66.4 17 (52)	$380 \pm 45.1$ 21 (69)			0.02	
20 April	448 ± 34.4 13 (33)	412 ± 45.1 19 (78)			0.56	
22 May	$358 \pm 60.0$ 29 (156)	$335 \pm 35.9$ 19 (64)			0.84	
15 June	124 ± 20.7 28 (154)	64 ± 6.4 17 (55)			0.03	
Overall	403 ± 115.3 22 (99)	298 ± 79.4 19 (67)			0.29	

#### Field and laboratory procedures

Sediments of collected samples were washed in a sieve bucket lined with a US Standard No. 30 sieve (0.6-mm openings, Carr and Hiltunen 1965, Hiltunen 1983) using gentle, pressurized water, and the retained material was placed in containers on ice and returned to the laboratory. In the laboratory, retained material was placed in pans and individual nymphs were removed using unaided vision, enumerated, and measured within 24 to 48 h of collection. Nymphs were identified to genera because there is no way to separate the nymphal forms of the 2 species of *Hexagenia* spp. (i.e., *H. limbata* and *H. rig-*

*ida*) found in Lake Erie and Lake St. Clair (Schloesser et al. 2001, Schloesser and Nalepa 2001). Lengths of individual nymphs were measured from the frontal process of the head to the last abdominal segment, excluding tails (Schloesser and Hiltunen 1984).

Densities of nymphs were calculated based on the surface area of 4 of the samplers (Ponar =  $484 \text{ cm}^2$ , Ekman =  $518 \text{ cm}^2$ , petite Ponar =  $248 \text{ cm}^2$ , Petersen =  $930 \text{ cm}^2$ ) as it would make contact with sediments. Densities obtained with the orange-peel were calculated based on the surface area of holes created by the sampler in soft, wet, sandy sediments (mean =  $650 \text{ cm}^2$ , range 629-675, n = 3).

TABLE 3. Extended.

		Lake St. Clair		
	Sam	pler		_
Ponar	Ekman	Petite Ponar	Petersen	p-value
$1391 \pm 48.2^{14}$	$1243 \pm 46.4$	$982 \pm 140.4^{23}$	$1358 \pm 79.1^{4}$	0.05
5 (7)	6 (8)	25 (113)	32 (18)	
$765 \pm 31.6$	$674 \pm 51.1$	$619 \pm 107.6$	$724 \pm 52.8$	0.45
7 (9)	14 (37)	30 (168)	9 (29)	
$448 \pm 30.0^{1}$	$290 \pm 78.1$	$256 \pm 13.5^{2}$	$405 \pm 14.2$	0.04
12 (25)	47 (403)	9 (15)	8 (7)	
$413 \pm 11.9$	$283 \pm 23.2$	$377 \pm 81.8$	$437 \pm 17.9$	0.12
5 (7)	14 (37)	38 (262)	15 (9)	
$393 \pm 11.9$	$251 \pm 22.3$	$229 \pm 74.9$	$362 \pm 39.9$	0.20
5 (7)	15 (44)	57 (595)	6 (67)	
$682 \pm 189.8$	$541 \pm 189.1$	$492 \pm 140.5$	$657 \pm 186.4$	0.19
7 (10)	19 (106)	32 (231)	14 (26)	
289 ± 11.9	219 ± 23.2			0.11
7 (9)	18 (62)			
$255 \pm 27.5$	$71 \pm 34.1$			0.11
18 (64)	83 (1283)			
$255 \pm 24.8$	$71 \pm 17.0$			0.03
17 (53)	42 (321)			
$220 \pm 53.8$	$52 \pm 23.2$			0.05
42 (330)	78 (1127)			
$255 \pm 14.1$	$103 \pm 38.9$			< 0.01
21 (114)	55 (698)			

## Data analysis

Mean densities  $(\bar{x})$ , standard errors (SE), and coefficients of variation (CV) of the number of nymphs, and number of samples needed to obtain a SE  $\pm 10\%$  of the mean were determined for each kind of sampler on each sampling date (Elliott 1971, Elliott and Drake 1981). Statistical tests used to determine differences between densities and lengths of nymphs collected with the 5 samplers included: 1) 2-way ANOVAs to determine overall (e.g., per water body per year) differences and interactions between factors (e.g., sampler  $\times$  date); 2) Tukey's multiple comparisons to determine sources of significant dif-

ferences (e.g., per date) as determined by 2-way ANOVAs; 3) 1-way ANOVAs to determine differences within factors (e.g., samplers per date per water body); and 4) Student's t-tests to determine differences when only 1 factor was tested (e.g., 2 samplers on 1 date) (Table 2) (Sokal and Rohlf 1973). All densities were  $\log_{10}$  transformed. Results of statistical analysis to differentiate mean densities of nymphs for each sampling date and site, and each year and site are reported as actual probability levels (p), whereas differences between densities and lengths of nymphs per individual sampling date are reported as significant at the  $p \leq 0.05$  and between the p > 0.05 and  $p \leq 0.10$  levels.

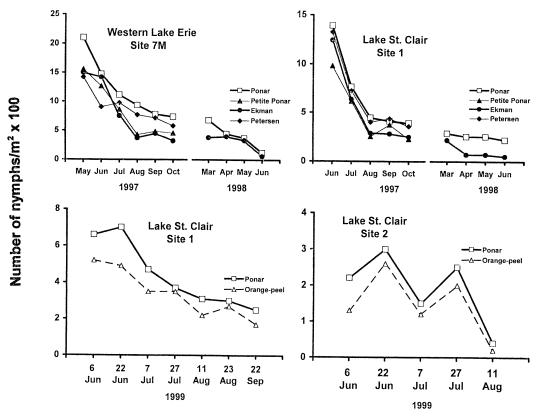


Fig. 1. Mean densites (numbers/m²) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 4 kinds of benthic grab sampers in 1997, 2 samplers in 1998, and 2 samplers in 1999 in western Lake Erie (site 7M) and Lake St. Clair (sites 1 and 2) of the Laurentian Great Lakes. Error bars not included for clarity (see Tables 3 and 4 for SE values).

#### Results

#### Accuracy

The standard Ponar grab almost always gave the highest density estimates of burrowing mayfly nymphs (31 of 32 date and site comparisons) in both western Lake Erie and Lake St. Clair (Fig. 1, Tables 3-5). Only the Petersen grab obtained a higher density than the Ponar in Lake St. Clair on 22 September 1997 (Table 3). The Ponar obtained higher densities than other samplers for 54 of 55 individual possible comparisons, including 20 of 20 possible comparisons with the Ekman, 11 of 11 with the petite Ponar, 11 of 12 with the Petersen, and 12 of 12 with the orange-peel (Tables 3-5). However, density differences between samplers were significant (p  $\leq$  0.05) for only 12 of 32 of the date and site comparisons, and densities using the Ponar were significantly greater ( $p \le 0.05$ ) than estimates from  $\geq 1$  of the other samplers for only 9 of 32 comparisons. At a decreased significance level of  $p \leq 0.10$ , the number of comparisons in which the Ponar yielded higher density estimates than  $\geq 1$  of the other samplers increased to 16 of 32 comparisons. Two-way ANOVAs indicated that a significant interaction between sampler type and date of sampling only occurred in western Lake Erie in 1997.

Overall densities provided by each sampler in 1997 were Ponar>Petersen>petite Ponar>Ekman in western Lake Erie and Ponar>Petersen>Ekman>petite Ponar in Lake St. Clair (Fig. 1, Table 3). In general, heavier samplers such as the Petersen (heaviest) and Ponar (2nd heaviest) collected higher densities of nymphs than the lighter petite Ponar (3rd heaviest) and Ekman (4th heaviest) samplers. The number of times a sampler collected a significantly ( $p \le 0.05$  and  $p \le 0.10$ ) greater num-

TABLE 4. Mean densities (numbers/ $m^2 \pm SE$ ) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with Ponar and orange-peel grab samplers from soft (site 1) and hard (site 2) substrates in Lake St. Clair of the Laurentian Great Lakes from June to September 1999. The CV (%) and, in parentheses, number of samples needed to obtain a SE  $\pm 10$  of the mean appear on the 2nd line of each value. Refer to Table 2 for statistical tests performed.

	Ş	Soft substrates			Hard substrates			
•	Sampler			Sampler				
Date	Ponar .	Orange-peel	<i>p</i> -value	Ponar	Orange-peel	<i>p</i> -value		
6 June	657 ± 48.6 17 (21)	523 ± 37.4 16 (20)	0.06	223 ± 81.4 82 (522)	132 ± 34.3 58 (263)	0.88		
22 June	$702 \pm 53.9$ 17 (23)	492 ± 21.2 10 (7)	<0.01	302 ± 87.6 65 (330)	255 ± 82.8 72 (412)	0.57		
7 July	$467 \pm 36.7$ $18 (24)$	$354 \pm 36.4$ 23 (41)	0.08	$153 \pm 47.4$ $69 (377)$	$123 \pm 36.7$ 67 (349)	0.79		
27 July	$372 \pm 34.6$ 21 (34)	$351 \pm 17.8$ $11 (10)$	0.68	248 ± 31.3 28 (63)	203 ± 23.5 26 (53)	0.31		
11 August	$310 \pm 48.9$ 35 (98)	$218 \pm 19.7$ $20 (32)$	0.12	37 ± 15.2 91 (653)	22 ± 9.2 96 (720)	0.52		
23 August	298 ± 14.0 11 (9)	$246 \pm 20.6$ $19 (28)$	0.08	)	yo (. <b>1</b> 0)			
22 September	252 ± 17.8 16 (19)	$175 \pm 32.1$ $41 (132)$	0.09					
Overall	$437 \pm 67.9$ $41 (33)$	$337 \pm 50.6$ $40 (39)$	0.01	193 ± 60.4 53 (389)	$147 \pm 49.6$ $60 (359)$	0.57		

ber of nymphs than  $\geq 1$  of the other samplers for individual date and site comparisons were 6 for the Ponar, 4 for the Petersen, and 1 each for the Ekman and petite Ponar. Significant ( $p \leq 0.05$ ) differences occurred for only 8 of 66 possible comparisons (6 comparisons/date/location), and all differences occurred in August through October in Lake Erie. The number of significant differences at the decreased significance level of  $p \leq 0.10$  increased to 18 of 66 comparisons.

The Ponar sampled significantly greater ( $p \le$ 0.05) numbers of nymphs than the Ekman and orange-peel samplers for individual sampling dates and locations for 4 of 8 individual comparisons in 1998 and 1 of 12 comparisons in 1999 (Tables 3, 4). No additional differences in densities between the Ponar and Ekman were found in 1998 at the decreased significance level of  $p \le 0.10$ , but 4 additional differences were found between the Ponar and orange-peel when used in soft substrates in 1999. In October 2000, densities obtained with the Ponar (1144  $\pm$  88.8) and Ekman (1027  $\pm$  60.7) were not significantly different (p > 0.05) from each other, but both were significantly greater than that collected with the Petersen (Table 5).

Precision

The Ponar was more precise than other samplers for 18 of 32 date and site comparisons from 1997 to 2000 (Tables 3-5). Individual comparisons indicated the Ponar was more precise than the Ekman, petite Ponar, and Petersen samplers and similar to the orange-peel sampler. Of the 55 possible individual comparisons between the Ponar and other samplers, the Ponar obtained the lowest CV and lowest number of samples needed to obtain ±10% of the mean for 16 of 20 Ekman comparisons, 7 of 11 petite Ponar comparisons, 8 of 12 Petersen comparisons, but only 5 of 12 orange-peel comparisons. The Ponar had the highest precision for 13 of 19 comparisons in 1997 and 1998 (Table 3). In 1999, overall precision with which the Ponar and orange-peel sampled were about the same at comparable sites (Table 4). However, of the 12 comparisons in 1999, the Ponar was more precise 5 times and the orange-peel was more precise 7 times. In 2000, the Ponar was the least precise of the 3 samplers (Table 5).

TABLE 5. Mean densities (numbers/ $m^2 \pm SE$ ) and lengths (mm  $\pm SE$ ) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 3 kinds of benthic grab samplers from soft sediments in western Lake Erie (site 7M) of the Laurentian Great Lakes 12 October 2000. For each column and factor (density and length), values followed by different superscript letters are significantly different at  $p \le 0.05$ . Numbers of nymphs examined are in parentheses. The CV (%) of density for all nymphs appears on the 2nd line of each value. Refer to Table 2 for statistical tests performed.

		Length of nymphs (mm)	
	All nymphs	2–13 mm	>13 mm
Density			
Ponar (1107)	$1144 \pm 88.8^{a}$ $34$	$803\pm75.8^{\mathrm{a}}$	$341 \pm 22.3^{a}$
Ekman (1068)	$1027 \pm 60.7^{a}$ $26$	$834 \pm 50.7^{a}$	$197 \pm 17.0^{b}$
Petersen (1480)	$796 \pm 35.1^{\text{b}}$ 20	$475 \pm 31.8^{b}$	$320 \pm 15.2^{a}$
Length			
Ponar Ekman Petersen	$9.7 \pm 0.22^{a}$ $8.0 \pm 0.20^{b}$ $11.7 \pm 0.21^{c}$	$5.1 \pm 0.05^{a}$ $5.0 \pm 0.05^{a}$ $5.3 \pm 0.05^{b}$	$\begin{array}{l} 20.6  \pm  0.14^{\rm a} \\ 20.6  \pm  0.18^{\rm a} \\ 21.1  \pm  0.11^{\rm b} \end{array}$

### Lengths

The size of collected nymphs was related to sampler weight. Heavier samplers tended to collect nymphs of larger mean and maximum lengths than lighter samplers (Tables 5, 6). In 1997, the Petersen collected significantly ( $p \le$ 

0.05) larger nymphs than ≥1 of the other samplers for 6 of 11 date and site comparisons, the Ponar for 2 of 11 comparisons, the petite Ponar for 2 of 11, and the Ekman sampler for 0 of 11 comparisons (Table 6). Maximum nymphal lengths (including samplers with equal maximum lengths) also occurred more often in

TABLE 6. Mean lengths (mm  $\pm$  SE) and maximum lengths (mm, 2nd line of value) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 4 kinds of benthic grab samplers from soft substrates in western Lake Erie (site 7M) and Lake St. Clair (site 1) of the Laurentian Great Lakes from May to October 1997. For each sampling period, values followed by different superscript letters are significantly different at  $p \le 0.05$  and values followed by different superscript numbers are significantly different between p > 0.05 and  $p \le 0.10$ . Refer to Table 2 for statistical tests performed.

		W	estern Lake Erie				
·	Sampler						
Date	Ponar	Ekman	Petite Ponar	Petersen	<i>p</i> -value		
28 May	$10.3 \pm 0.27$ $27$	10.2 ± 0.28 26	11.0 ± 0.51 29	10.4 ± 0.26 29	0.61		
23 June	$11.2 \pm 0.29^{a}$	$12.1 \pm 0.27^{a}$ $28$	$11.2 \pm 0.41^{a}$	$13.1 \pm 0.29^{\text{b}}$	< 0.01		
24 July	$15.1 \pm 0.21$ 22	$14.8 \pm 0.32$	$14.3 \pm 0.30$ 19	$14.8 \pm 0.18$ $23$	0.33		
28 August	$16.4 \pm 0.25^{a}$ $25$	$15.2 \pm 0.32^{b}$ $21$	$18.0 \pm 0.42^{\circ}$ $28$	$16.4 \pm 0.18^{a}$ 25	< 0.01		
22 September	$18.1 \pm 0.27^{a}$ $25$	$16.5 \pm 0.28^{b}$	$17.1 \pm 0.41$	$17.6 \pm 0.25^{ac}$	< 0.01		
23 October	$   \begin{array}{r}     25 \\     19.1 \pm 0.27 \\     26   \end{array} $	$17.7 \pm 0.28^{b}$ 22	$17.6 \pm 0.48^{b}$ 22	$19.5 \pm 0.23^{ac}$ $25$	<0.01		

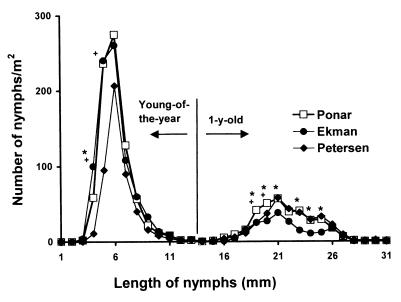


FIG. 2. Mean densities (numbers/ $m^2$ ) of burrowing mayfly nymphs (*Hexagenia*) spp. in whole-mm-length categories obtained with 3 kinds of samplers in western Lake Erie (site 7M) on 12 October 2000. \*= significantly different ( $p \le 0.05$ , Student's t-tests) numbers of nymphs in individual-mm categories obtained with the Ponar and Ekman, + = with the Ponar and Petersen.

heavier than lighter samplers: 8 in the Petersen, 4 in the Ponar, 2 in the petite Ponar, and 1 in the Ekman. In October 2000, the Petersen collected nymphs of significantly greater mean

lengths in 2 length categories (young-of-the-year nymphs = 2-13 mm and 1-y-old nymphs = >13 mm) than the Ponar and Ekman samplers (Table 5). The Ponar obtained significantly greater den-

TABLE 6. Extended.

	Lake St. Clair						
	Sampler						
<i>p</i> -value	Ponar Ekman Petite Ponar Petersen						
0.43	$11.2 \pm 0.16$	$11.5 \pm 0.30$	$11.5 \pm 0.22$	$11.1 \pm 0.24$			
	27	17	18	21			
< 0.01	$17.6 \pm 0.20^{b}$	$16.2 \pm 0.44^{a}$	$16.1 \pm 0.33^{a}$	$16.2 \pm 0.31^{a}$			
	26	22	22	22			
0.01	$20.0 \pm 0.25^{b}$	$18.8 \pm 0.50$	$19.0 \pm 0.35$	$18.8 \pm 0.34^{a}$			
	26	23	23	24			
0.07	$19.3 \pm 0.25^{1}$	$20.5 \pm 0.60^{2}$	$19.5 \pm 0.40$	$19.2 \pm 0.30^{1}$			
	25	27	28	24			
0.28	$18.6 \pm 0.25$	$18.3 \pm 0.51$	$17.9 \pm 0.38$	$18.9 \pm 0.31$			
	24	21	21	24			

sities of 1-y-old nymphs than the Ekman and greater densities of young-of-the-year nymphs than the Petersen. Although total densities and mean lengths obtained with the Ponar and Ekman were similar, the heavier Ponar collected significantly greater ( $p \le 0.05$ ) numbers of 1-yolds in the 18 to 20- and 22 to 24-mm length categories (Fig. 2). Total density obtained with the Petersen was significantly lower than that obtained with the Ponar primarily because of lower collection efficiency of small, young-ofthe-year nymphs in individual length categories between 3 and 7 mm, although differences were significant for only the 3- and 4-mm length categories. In addition, the Ponar collected greater numbers of 17- and 18-mm nymphs than the Petersen.

#### Discussion

## Accuracy and precision

The Ponar was more accurate (i.e., higher densities) and precise (i.e., lower variances) than the Ekman, petite Ponar, Petersen, and orange-peel samplers in collecting *Hexagenia* spp. Few studies have investigated sampler differences for specific taxa (Powers and Robertson 1967, Sly 1969, Word 1976, Elliot and Drake 1981), and only Hudson (1970) compared samplers in relation to burrowing mayfly nymphs. Hudson (1970) compared the Ponar and orange-peel grabs, and also showed the Ponar collected more burrowing mayfly nymphs than the orange-peel.

Difficulty in determining the accuracy and precision of benthic samplers is attributed to high natural variability in the distribution and abundance of benthic taxa. Natural distributions of benthos in most habitats is usually a result of organism selection of environmental factors, which yields uneven distributions of organisms and high variability of density estimates (Elliott 1971). The measured variability can be reduced by increasing the number of sample replicates (Elliott 1971, Brinkhurst 1974). Our study showed that the number of samples needed to obtain a SE  $\pm 10\%$  of the mean of any one sampler and date varied between 5 and 1283. Natural variability and the low number of samples could account for the significant interaction between sampler type and sampling date observed in western Lake Erie in 1997. However,

this interaction was attributed to the Petersen sampler, which collected lower densities than other samplers in May and June and higher densities than the Ekman and petite Ponar thereafter. Most nymphs were of small to medium size in May and June 1997, whereas from July to October most nymphs were relatively large because of growth of 1-y-old nymphs and the lack of recruitment of small young-of-the-year nymphs in summer 1997 (Schloesser and Nalepa 2001). The Petersen collected larger nymphs more efficiently than smaller nymphs (Fig. 2) so densities collected with the Petersen in fall would be expected to contain a disproportionately greater number of large nymphs than small nymphs compared to other samplers. An increase in efficiency of nymphs collected in the Petersen relative to other samplers in fall, when compared to spring, would result, thus causing the sampler and date interaction discovered in 1997.

Several studies have concluded that the Ponar was the best overall sampler for macroinvertebrates, primarily because it yielded higher mean densities with lower variability, and obtained an intact sample more often than other samplers from a wider variety of habitats (Powers and Robertson 1967, Flannagan 1970, Howmiller 1971, Lewis et al. 1982). However, samplers other than the Ponar continue to be used for a variety of reasons. For example, 2 studies of mayflies in western Lake Erie, conducted during the same time period as this study, used the petite Ponar and Ekman because of equipment availability, limited laboratory capabilities, and the belief that the Ekman is a better sampler than the Ponar in soft substrates (Krieger et al. 1996, Schloesser et al. 2001). In addition, larger and heavier samplers such as the Ponar, Petersen, and orange-peel require heavier and larger equipment to deploy and retrieve than smaller and lighter samplers, such as the petite Ponar and Ekman samplers. In general, samples collected with larger samplers require more laboratory time to analyze than samples collected with smaller samplers.

It has been suggested that the Ekman is more efficient than the Ponar because it may create less hydraulic disturbance (i.e., shock wave) as it descends and contacts sediments (Howmiller 1971, Lewis et al. 1982). Although never measured, hydraulic disturbance would push small organisms near the sediment surface away from

the sampled area. Flannagan (1970) found the Ekman collected total benthos with more accuracy and higher precision than the Ponar when used in soft substrates. This difference was attributed to small worms and midges that were in the top few mm of sediments where shock waves would be most pronounced (Flannagan 1970, Howmiller 1971). However, the Ponar and Ekman sampled young-of-the-year mayfly nymphs with equal efficiency in our study, indicating that even small nymphs burrow deep enough to avoid possible effects of hydraulic disturbance created by the Ponar (Hunt 1953, Charbonneau and Hare 1998). Hydraulic shock waves created by benthic samplers is undoubtedly related to sampler design and the speed of sampler descent (Howmiller 1971, Sly 1969). Sly (1969) recommended that descent of samplers be of 'moderate' speed. The descent of our samplers was determined by operation of a manual winch (Ponar and Petersen) and manual handover-hand (Ekman and petite Ponar) operation at a moderate speed (mean  $\pm$  SE, 0.17  $\pm$  0.002 m/s and  $0.14 \pm 0.006$  m/s, number of timed descents = 22 and 12, respectively).

## Reason for sampler differences

The reason for higher densities and larger nymphs in heavier samplers (i.e., Ponar and Petersen) than in lighter samplers (Ekman and petite Ponar) was probably depth of penetration of samplers into sediments. Burrowing benthos such as mayfly nymphs often burrow deep in sediments (e.g., 10-12 cm) (Berg 1938, Hunt 1953, Dugdale 1955, Eriksen 1968, Charbonneau and Hare 1998). Depth of penetration of samplers in western Lake Erie (based on measurements and fullness of samplers) in order of heaviest to lightest grab was Petersen (20.5 cm), Ponar (16.0 cm), petite Ponar (10.0 cm), and Ekman (12.0 cm). Lower densities obtained with the Petersen than the Ponar, even though the Petersen had greater penetration depth than the Ponar, is partially attributed to the Petersen not always retrieving a full sample (visual estimates as low as 80%). The Petersen may not collect a full sample in soft substrates because the center portion of the sample (running along the length) can be lost as the jaws close (Gallardo 1965, Brinkhurst 1974). However, this sample loss from the Petersen was probably less important than the effect of hydraulic disturbance caused

by this sampler because density differences between smaller nymphs (1-13 mm) collected with each sampler were much larger than differences between large nymphs collected with each sampler. Although the orange-peel was the heaviest sampler used, it was less efficient than the Ponar. This result is not attributed to the lack of penetration by the orange-peel (estimated to be ≤40 cm in soft substrates), but rather to the nonuniform shape of sediment collected (a sphere with minimum surface area of sediment collected at maximum depth of penetration). In hard substrates, orange-peel penetration ( $\sim$ 5–10 cm) was more than the Ponar ( $\sim$ 2– 5 cm), but sediment obtained by the orange-peel was shaped like an inverted cone with its point at the deepest penetration. Overall, densities obtained with the 2 lightest, shallowest-penetrating samplers, the Ekman and petite Ponar, were lower than densities obtained with heavier samplers.

Further evidence that density differences of mayflies between samplers were a function of depth of penetration can be observed from changes of seasonal patterns. Density estimates were similar among samplers in May and June 1997, but not in July through October. By fall, when size and burrowing depths of nymphs increased, the 2 heavier and deeper-penetrating samplers (Ponar and Petersen) obtained substantially higher densities than the lighter and shallower-penetrating samplers (Ekman and petite Ponar). However, this seasonal pattern could also be attributable to observations that mayfly nymphs burrow shallower in spring than in summer and fall (Charbonneau and Hare 1998).

### Density conversion factors

Conversion factors to change densities of nymphs obtained with other samplers to Ponar equivalents varied greatly in the present study and, in general, appeared related to substrate type and mayfly size distribution (Table 7). Ranges of conversion factors for individual samplers to convert to Ponar equivalents were: 1.01 to 4.23 for the Ekman, 1.10 to 2.18 for the petite Ponar, 0.95 to 1.63 for the Petersen, and 1.06 to 1.69 for the orange-peel. In general, conversion factors were higher in summer and fall than spring 1997 and in early summer than spring 1998, which may be attributed to the lack of small nymphs in summer and fall 1997 and

TABLE 7. Conversion factors to change density (numbers/m²) of burrowing mayfly nymphs (*Hexagenia* spp.) obtained with 4 kinds of benthic grab samplers (Ekman, petite Ponar, Petersen and orange-peel) to Ponar equivalents in western Lake Erie and Lake St. Clair of the Laurentian Great Lakes from 1997 to 2000.

Soft substra  Petite an Ponar  1.35		Ekman	Petite	Soft substrat	es	Hard substrates
an Ponar	Petersen	Ekman				
) 1.35			Ponar	Petersen	Orange- peel	Orange- peel
1.35						
1.17 3 1.30 1 2.18 3 1.61 9 1.61 4 1.54 0.147	1.48 1.63 1.14 1.22 1.09 1.26 1.30 0.085	1.12 1.14 1.54 1.46 1.56 1.36 0.097	1.42 1.23 1.75 1.10 1.72 1.44 0.129	1.02 1.06 1.11 0.95 1.08 1.04 0.277		
) 7 1 7		1.32 3.59 3.59 4.23 3.18 0.639				
					1.26 1.43 1.32 1.06 1.42 1.21 1.44 1.31 0.057	1.69 1.18 1.24 1.22 1.68
1 44						
	9 1.61 4 1.54	9 1.61 1.26 4 1.54 1.30 82 0.147 0.085	1.61 1.26 1.56 1.54 1.30 1.36 32 0.147 0.085 0.097  1.32 3.59 3.59 4.23 3.18 29 0.639	9 1.61 1.26 1.56 1.72 1 1.54 1.30 1.36 1.44 32 0.147 0.085 0.097 0.129 1.32 3.59 4.23 7. 3.18 9. 0.639	1.61 1.26 1.56 1.72 1.08 1.54 1.30 1.36 1.44 1.04 32 0.147 0.085 0.097 0.129 0.277  1.32 3.59 3.59 4.23 3.18 29 0.639	1.61

spring 1998 (Schloesser and Nalepa 2001). In general, average conversion factors were similar for comparable samplers used at different sites except for the Ekman sampler in 1998, when very low densities of relatively large nymphs occurred in soft substrates of Lake St. Clair. Available literature contains data to allow calculation of conversion factors for total benthos and a few abundant taxa (e.g., chironomids) (Powers and Robertson 1967, Hudson 1970, Howmiller 1971, Lewis et al. 1982, Manny and Schloesser 1999), but only one study (Hudson 1970) examined the efficiency of collecting burrowing mayfly

nymphs with different samplers. Hudson (1970) compared the Ponar to the orange-peel and found a conversion factor of 1.43 for burrowing mayflies, which is similar to the mean conversion factors determined in our study (i.e., 1.31 and 1.40 in soft and hard substrates, respectively). Other available conversion factors include total benthos and typically are <1 because of inclusion of small epibenthic oligochaetes and chironomids that are usually 1 to 3 orders of magnitude greater in density than burrowing mayflies.

There is no statistical basis on which to de-

termine the validity of applying conversion factors between grab samplers using available data. Therefore, we recommend that correction factors be obtained from samples collected simultaneously with the standard Ponar and other grabs in future studies. However, if simultaneous sample collections are not possible then the use of conversion factors like those determined in the present study is recommended. Changes of conversion factors attributed to sediment type and nymphal size distributions in our study indicate that conversion factors could improve the accuracy and, thus, the comparability between density estimates obtained with ≥2 grab samplers.

#### Sampler recommendation

Our study indicated that the Ponar was the best sampler to estimate density of burrowing mayfly nymphs in soft substrates typical of lentic habitats, such as western Lake Erie and Lake St. Clair of the Great Lakes. However, there are 6 types of quantitative samplers (Ponar, Petersen, Van Veen, Smith-McIntyre, Shipek, Ekman, and corer) recommended for collecting benthos in nonwadable waters (Clesceri et al. 1998). In addition, many other types of samplers (e.g., Friedinger, box corer, box corer with subcores, Birge-Ekman, Allen) have been used to sample benthos in nonwadable waters. Many of these samplers are modifications of the first grab-type sampler described by Petersen and Jensen (1911) (Gallardo 1965, Powers and Robertson 1967, Sly 1969, Elliott and Drake 1981). Several studies have examined efficiencies of various benthic samplers and, in general, the Ponar appears to be the overall sampler of choice for benthos in lentic habitats (Powers and Robertson 1967, Sly 1969, Flannagan 1970, Word 1976, Elliott and Drake 1981, Lewis et al. 1982, Clesceri et al. 1998). The Ponar grab was first used in the Great Lakes in the mid 1960s and has become widely used to sample total benthos throughout the Great Lakes and elsewhere in North America (Powers and Robertson 1967, Schloesser and Hiltunen 1984, Schloesser et al. 1991, Clesceri et al. 1998). The Ponar most completely includes the 4 major beneficial characteristics of a benthic sampler (Brinkhurst 1974): 1) repeatability of sample size, 2) sufficient penetration, 3) minimal shock wave, and 4) a closure mechanism that prevents sample loss. Design characteristics that

make the Ponar a preferred sampler for benthos include: a screened top to reduce shockwaves in front of the sampler as it is lowered, end plates that prevent escape of sediments when its jaws close, relatively heavy weight and location of weights on the sampler that increase depth of penetration in firm substrates, rubber flaps on top of the screen to provide a suction seal during retrieval, and relatively simple mechanical operation that maximizes intact samples (Powers and Robertson 1967, Sly 1969, Elliott and Drake 1981). Therefore, we believe that, when possible, burrowing mayfly nymphs and possibly other burrowing benthic organisms should be collected with a standard Ponar, and that it be used at a similar descent rate as used in our study.

Use of the Ponar will lead to more accurate density estimates of burrowing mayfly nymphs and possibly other benthos that are important to food webs, fish energetics, and monitoring of habitat quality (Fremling 1964, Harris et al. 1987, Haywood and Margraf 1987, Ritchie and Colby 1988, Reynoldson et al. 1989, Kolar et al. 1997, Madenjian et al. 1998, Ohio Lake Erie Commission 1998). As pollution-abatement programs continue, burrowing mayfly nymphs will undoubtedly return to sediments in other areas of the Great Lakes where they were once abundant but have been absent for decades. This recolonization will undoubtedly increase the need for accurate and precise measurements of organisms such as Hexagenia spp. that are used as indicator/sentinel species of environmental health in both North America and Europe (Fremling and Johnson 1990, bij de Vaate et al. 1992, Krieger et al. 1996, Schloesser et al. 2001).

## Acknowledgements

Contribution number 1167 of the Great Lakes Science Center and number 1223 of the Great Lakes Environmental Research Laboratory. We thank personnel of the Sandusky Biological Station, USGS, Sandusky, Ohio, for assistance in sample collections and Linda Gode, University of Michigan, Ann Arbor, for use of the orange-peel sampler.

#### Literature Cited

BEETON, A. M. 1969. Changes in the environment and biota of the Great Lakes. Pages 150–187 *in* Eutro-

- phication: causes, consequences, correctives. Proceedings of a Symposium. National Academy of Sciences, Washington, DC.
- BERG, K. 1938. Studies on the bottom animals of Esrom Lake. Det Kongelige Danske Videnskabernes Selskab. Skrifter, Naturvidenskabelig og Mathematisk Afdeling 9 Raekke VIII.
- BIJ DE VAATE, A., A. KLINK, AND F. OOSTERBROEK. 1992. The mayfly, *Ephoron virgo* (Olivier), back in the Dutch parts of the rivers Rhine and Meuse. Hydrobiological Bulletin 25:237–240.
- BOLSENGA, S. J., AND C. H. HERDENDORF. 1993. Lake Erie and Lake St. Clair handbook. Wayne State University Press, Detroit, Michigan.
- Brinkhurst, R. 1974. The benthos of lakes. St. Martin's Press, New York.
- Britt, N. W. 1955. *Hexagenia* (Ephemeroptera) population recovery in western Lake Erie following the 1953 catastrophe. Ecology 36:520–522.
- CARR, J. F., AND J. K. HILTUNEN. 1965. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnology and Oceanography 10:551–569.
- CHARBONNEAU, P., AND L. HARE. 1998. Burrowing behavior and biogenic structures of mud-dwelling insects. Journal of the North American Benthological Society 17:239–249.
- CLESCERI, L. S., A. E. GREENBERG, AND A. D. EATON (EDITORS). 1998. Standard methods for the examination of water and wastewater. 20th edition. American Public Health Association, Washington, DC.
- COCHRAN, P. A. 1992. The return of *Hexagenia* (Ephemeroptera: Ephemeridae) to the lower Fox River, Wisconsin. Great Lakes Entomologist 25:79–81.
- COOK, D. G., AND M. G. JOHNSON. 1974. Benthic invertebrates of the St. Lawrence Great Lakes. Journal of the Fisheries Research Board of Canada 31: 763–782.
- DERMOTT, R. 1994. Benthic invertebrate fauna of Lake Erie 1979: distribution, abundance and biomass. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2018. Fisheries and Oceans Canada, Canada Center for Inland Waters, Burlington, Ontario.
- DUGDALE, R. C. 1955. Studies in the ecology of the benthic Diptera of Lake Mendota. PhD Thesis, University of Wisconsin, Madison, Wisconsin.
- ELLIOTT, J. M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Scientific Report Number 25. Freshwater Biological Association, Ambleside, Westmorland (Cumbria), UK.
- ELLIOTT, J. M., AND C. M. DRAKE. 1981. A comparative study of seven grabs used for sampling benthic macroinvertebrates in rivers. Freshwater Biology 11:99–120.
- ERIKSEN, C. H. 1968. Ecological significance of respi-

- ration and substrate for burrowing Ephemeroptera. Canadian Journal of Zoology 26:93–103.
- FLANNAGAN, J. F. 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. Journal of the Fisheries Research Board of Canada 27: 1691–1700.
- Fremling, C. R. 1964. Mayfly distribution indicates water quality in the upper Mississippi River. Science 146:1164–1166.
- Fremling, C. R., and D. K. Johnson. 1990. Recurrence of *Hexagenia* mayflies demonstrates improved water quality in Pool 2 and Lake Pepin, Upper Mississippi River. Pages 243–248 in I. C. Campbell (editor). Mayflies and stoneflies; life histories and biology. Proceedings of the 5th International Ephemeroptera Conference and the 9th International Plecoptera Conference. Kluwer Academic Publishers, Dordrecht, The Netherlands
- Gallardo, V. A. 1965. Observations on the biting profiles of three  $0.1\ m^2$  bottom-samplers. Ophelia 2: 319-322.
- Harris, H. J., P. E. Sager, S. Richman, V. A. Harris, and C. J. Yarbrough. 1987. Coupling ecosystem science with management: a Great Lakes perspective from Green Bay, Lake Michigan, USA. Environmental Management 11:625–629.
- HAYWARD, R. S., AND F. J. MARGRAF. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. Transactions of the American Fisheries Society 116:210–223.
- HILTUNEN, J. K. 1983. Versatile bucket for sieving benthos samples. Progressive Fish-Culturist 45:229– 231.
- HOPKINS, T. L. 1964. A survey of marine bottom samplers. Pages 213–256 *in* M. Sears (editor). Progress in Oceanography, Volume 2. Pergamon Press, New York.
- HOWMILLER, R. P. 1971. A comparison of the effectiveness of Ekman and Ponar grabs. Transactions of the American Fisheries Society 100:560–564.
- HUDSON, P. L. 1970. Quantitative sampling with three benthic dredges. Transactions of the American Fisheries Society 3:603–607.
- HUNT, B. P. 1953. The life history and economic importance of the burrowing mayfly, *Hexagenia limbata* in southern Michigan lakes. Michigan Conservation Department Bulletin Number 4. Institute for Fisheries Research, University of Michigan, Ann Arbor, Michigan.
- KOLAR, C. S., P. L. HUDSON, AND J. F. SAVINO. 1997. Conditions for the return and simulation of the recovery of burrowing mayflies in western Lake Erie. Ecological Applications 7:665–676.
- KRIEGER, K. A., D. W. SCHLOESSER, B. A. MANNY, C. E. TRISLER, S. E. HEADY, J. J. H. CIBROWSKI, AND K. M. MUTH. 1996. Recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: Hexagenia) in

- western Lake Erie. Journal of Great Lakes Research 22:254–263.
- LEWIS, P. L., W. T. MASON, AND C. I. WEBER. 1982. Evaluation of three bottom grab samplers for collecting river benthos. Ohio Journal of Science 82: 107–113.
- MADENJIAN, C. P., D. W. SCHLOESSER, AND K. A. KRIE-GER. 1998. Population models of burrowing mayfly recolonization in western Lake Erie. Ecological Applications 8:1206–1212.
- MANNY, B. A., AND D. W. SCHLOESSER. 1999. Changes in the bottom fauna of western Lake Erie. Pages 197–217 in M. Munawar, T. Edsall, and I. F. Munawar (EDITORS). State of Lake Erie—past, present, and future. Ecovision World Monograph Series. Backhuys Publishers, Leiden, The Netherlands.
- MOZLEY, S. C., AND R. M. LADRONKA. 1988. *Ephemera* and *Hexagenia* (Ephemeridae, Ephemeroptera) in the Straights of Mackinac, 1955–56. Journal of Great Lakes Research 14:171–177.
- NALEPA, T. F., AND A. ROBERTSON. 1981. Vertical distribution of the zoobenthos in southeastern Lake Michigan with evidence of seasonal variation. Freshwater Biology 11:87–96.
- Ohio Lake Erie Commission. 1998. State of Ohio 1998: state of the lake report. Ohio Lake Erie Commission, Toledo, Ohio. (Available from: Ohio Lake Erie Commission, One Maritime Plaza, 4th Floor, Toledo, Ohio 43604–1866, USA.)
- Petersen, C. G., and P. B. Jensen. 1911. Valuation of the sea; animal life of the sea-bottom, its food and quantity. Report of the Danish Biological Station, Copenhagen 20:1–76.
- Powers, C. F., and A. Robertson. 1967. Design and evaluation of an all-purpose benthos sampler. Pages 126–131 *in* J. C. Ayers and D. C. Chandler (editors). Studies on the environment and eutrophication of Lake Michigan. Special Report No. 30. Great Lakes Research Division, University of Michigan, Ann Arbor, Michigan.
- REYNOLDSON, T. B., D. W. SCHLOESSER, AND B. A. MANNY. 1989. Development of a benthic invertebrate objective for mesotrophic Great Lakes waters. Journal of Great Lakes Research 15:669–686.
- RITCHIE, B. J., AND P. J. COLBY. 1988. Even-odd year differences in walleye year-class strength related to mayfly production. North American Journal of Fisheries Management 8:210–215.
- SCHLOESSER, D. W., T. A. EDSALL, B. A. MANNY, AND

- S. J. NICHOLS. 1991. Distribution of *Hexagenia* nymphs and visible oil in sediments of the upper Great Lakes connecting channels. Hydrobiologia 219:345–352.
- SCHLOESSER, D. W., AND J. K. HILTUNEN. 1984. Life cycle of a mayfly *Hexagenia limbata* in the St. Marys River between Lakes Superior and Huron. Journal of Great Lakes Research 10:435–439.
- SCHLOESSER, D. W., K. A. KRIEGER, J. J. H. CIBOROWSKI, AND L. CORKUM. 2001. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. Journal of Aquatic Ecosystem Stress and Recovery 8:125–141.
- SCHLOESSER, D. W., AND T. F. NALEPA. 2001. Abundance and life-history characteristics of *Hexagenia* mayfly nymphs in western Lake Erie of the Laurentian Great Lakes: impediments to assessment of lake recovery? International Review of Hydrobiology 86:87–103.
- Schneider, J. C., F. F. Hooper, and A. M. Beeton. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Pages 80–90 *in* Proceedings of the 12th Conference on Great Lakes Research, 5–7 May 1969, University of Michigan, Ann Arbor, Michigan. International Association for Great Lakes Research, Ann Arbor, Michigan.
- SLY, P. G. 1969. Bottom sediment sampling. Pages 883–898 in Proceedings of the 12th Conference on Great Lakes Research, 5–7 May 1969, University of Michigan, Ann Arbor, Michigan. International Association for Great Lakes Research, Ann Arbor, Michigan.
- SOKAL, R. R., AND F. J. ROHLF. 1973. Introduction to biostatistics. W. H. Freeman and Company, San Francisco, California.
- WORD, J. Q. 1976. Biological comparison of grab sampling devices. Pages 189–194 in Report of the Southern California Coastal Water Research Project. Southern California Coastal Water Research Project, Westminster, California. (Available from: Southern California Coastal Water Research Project, 7171 Fenwick Lane, Westminster, California 92683 USA.)
- WRIGHT, S. 1955. Limnological survey of western Lake Erie. Special Scientific Report, Fisheries No. 139. US Fish and Wildlife Service, Washington, DC.

Received: 20 June 2001 Accepted: 3 May 2002