Reprinted from

Canadian Journal of Zoology

Réimpression du

Journal canadien de zoologie

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Received September 6, 1979

SEPHTON, T. W., C. G. PATERSON, and C. H. FERNANDO. 1980. Spatial interrelationships of bivalves and nonbivalve benthos in a small reservoir in New Brunswick, Canada. Can. J. Zool. **58**: 852–859.

Quantitative sampling of macrobenthos in Morice Lake, New Brunswick, showed that the numerical abundance of chironomid larvae and other nonbivalve detritivore species was significantly increased in the vicinity of bivalve molluscs. Experimentally, increased bivalve numbers in tanks led to an aggregated distribution of nonbivalve benthos. Numerical abundance near bivalves was increased, probably due to a behavioral response of the detritivores to an increased food source.

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Un échantillonnage quantitatif du macrobenthos dans le lac Morice, au Nouveau-Brunswick, a démontré que l'importance numérique des larves de chironomides et des autres organismes détritivores non bivalves augmente significativement dans le voisinage des mollusques bivalves. En laboratoire, l'augmentation du nombre de bivalves dans des aquariums entraîne une répartition par paquets des organismes benthiques non-bivalves. L'importance numérique devient plus grande au voisinage des bivalves, probablement à cause du comportement des détritivores en réaction à l'augmentation de la quantité de nourriture.

[Traduit par le journal]

Introduction

Variation in the abundance of lake benthos over contiguous areas is often considered to be a product of the heterogeneity of the environment. Some of the factors correlated with the spatial distribution and abundance of benthic macroinvertebrates are oxygen microstratification at the mud–water interface (Brundin 1951; Wilhm and McClintock 1978), substrate type and water depth (Lellak 1965; Slack 1967), substrate particle size (Cummins 1962) and water chemistry (Minshall and Minshall 1978), and differing concentrations of sedimented allochthonous and autochthonous detritus (Paterson and Fernando 1971). Detritus is an important food source for many benthic macroinvertebrates (Brinkhurst 1974; Merritt and Cummins 1978) which can affect the distribution and abundance of the benthos (Egglishaw 1964).

Chironomid larvae and oligochaetes are important detritivore components of the lake benthos; however, in certain bodies of water unionid bivalve molluscs form a large component of the benthic fauna, surpassing the combined biomass contribution of all other macroinvertebrate groups. Negus (1966) reported that the unionids comprised 90% of the bottom fauna biomass in the Thames River at Reading. Tudorancea and Florescu (1969) studied the Unionidae populations in Lake Crapira (the Danube delta) and found they contributed a total biomass of 278.6 kg ha^{-1} (dry tissue weight). Magnin and Stánczykowska (1971) reported that the Unionidae populations in Lac des Deux Montagnes, Québec, had a total biomass of 857.9 kg ha^{-1} (wet tissue weight).

Bivalve molluscs filter large quantities of water but use only a small amount of the seston filtered from the water column (Winter 1978). Most of the filtered seston is deposited in the form of faeces and pseudofaeces. Lewandowski and Stánczykowska (1975) reported that the unionid bivalves in Mikolajskie Lake filter approximately 2.5 t of dry seston per year, of which most is deposited on the

substrate. Bivalves can create a heterogeneous benthic environment by concentrating and depositing seston differentially on the sediments influencing the faunal community of lake ecosystems when they occur in substantial numbers.

Pseudofaeces consist of agglutinated seston, rich in organic matter mucus, that has not been ingested by the bivalve. This biodeposition forms a readily available food source that can be used by benthic detritivores. Izvekova and Lvova-Katchanova (1972) studied the effect of various natural food sources on the development of the chironomid larvae *Endochironomus albipennis* and *Chironomus arthracinus* and found that the faeces and pseudofaeces of *Dreissena polymorpha* were the most nutritive food sources used by the chironomids.

Among the numerous studies on the ecology of benthic communities, few deal with the interactions of the different species that comprise the community. The nonbivalve detritivore populations may react to the microenvironmental variations created by the bivalves in a negative, neutral, or positive fashion. These relationships could be elucidated if a quantitative benthic sampling program was conducted on a relatively simple community dominated by bivalves and poor in other benthic species. The present study was undertaken to provide such a quantitative assessment of the interactions of the other benthic fauna, particularly the Chironomidae, with the dominant unionid bivalves. Preliminary observations from controlled tank experiment studies are presented to further investigate the possible behavioral relationships between the bivalve community and the nonbivalve benthos.

The study area

This study was conducted in Morice Lake (45°56′ N, 64°21′ W), a small (1.5 km²) mesotrophic, polymictic reservoir located approximately 3 km north of Sackville, New Brunswick. The study was limited to the southwest arm of the Lake (Fig. 1). The total area of the arm is 1.1×10^5 m² and the area with a water depth less than 1.0 m is 2.0×10^4 m². It possesses a rather uniform depth and reflects the shallow nature of the rest of the reservoir. The sublittoral zone of the arm, defined as that area with a water depth greater than 1.0 m, is composed of three basic substrate types (Fig. 1), and their characteristic compositions are as follows: type A, a combination of wood chips, plant detritus, and silt; type B, plant detritus and silt; and type C, silt and gyttja.

Shaw (1973) monitored bottom water temperature over the year and found a range from 3°C during winter ice cover to approximately 20°C during July and August. There was no evidence of a thermocline. Dissolved oxygen content at 10 cm above the substrate was never less than 72% saturation over the year. The pH measurements varied little, with a mean of 6.5, while conductivity ranged from 35 to 55 μmhos cm⁻¹ (1 mho = 1S) at 20°C over the year (Shaw 1973). Comparable values have been obtained throughout our study.

Shaw (1973) sampled the bivalve populations quantitatively in the sublittoral zone of the arm and found approximately 19 individuals/m² with a total dry tissue weight of 90 kg ha⁻¹. The three dominant species, in order of decreasing abundance, are *Elliptio complanata* (Solander), *Anodonta cataracta* (Say), and *Lampsilis ochracea* (Say). Hyslop (1975) studied microdistributional patterns of *Elliptio complanata* and *Anodonta cataracta* and concluded that the sample data indicated an aggregated distribution for most of the summer that could be fitted to a negative binomial model. A standard cubical 9-in. (1 in. = 2.54 cm) Ekman grab covering 513.2 cm² of substrate was used in both of these studies.

Materials and methods

Benthic samples were obtained from the arm from May to August 1977 and again in May 1978. Random samples were collected from within a substrate area using a standard cubical 9-in. Ekman grab. The samples were placed individually into large buckets, examined for the presence or absence of bivalves, carefully washed into double thickness polyethylene bags, and returned immediately to the laboratory. Most often samples did not contain bivalves and in order to obtain a sufficient number of samples containing bivalves it was necessary to check the samples in the field. Samples were divided into one of three categories (0 bivalves, 1 bivalve, and 2+ (i.e., 2 or more) bivalves) and were collected from each of three substrate types.

The samples were sorted using the following combination of flotation and hand sorting techniques. The water overlaying the mud in a sample bag was strained through a 250-μm (square mesh) sieve and the material collected on the screen was preserved in 10% formalin. The remaining portion of the sample was equally divided into plastic quart containers to a depth of 3 to 4 cm. The containers were filled with a saturated solution of magnesium sulphate and stirred vigorously. The samples were allowed to settle for 15 min, the supernatant was decanted through the 250-μm sieve, and the material collected on the screen was added to the vial. This procedure was repeated three times after which the sample was gently washed through a 710-μm (square mesh) sieve. The contents of this sieve were placed in a white enamelled tray and hand sorted to obtain any organisms that did not float. The preserved macroinvertebrates were sorted from the organic detritus by examining small portions at a time in a counting tray under 40 × magnification, enumerated, and identified. The larval Chironomidae were mounted in ACS (Edward Gurr Ltd., London) and the gut contents were recorded as to composition.
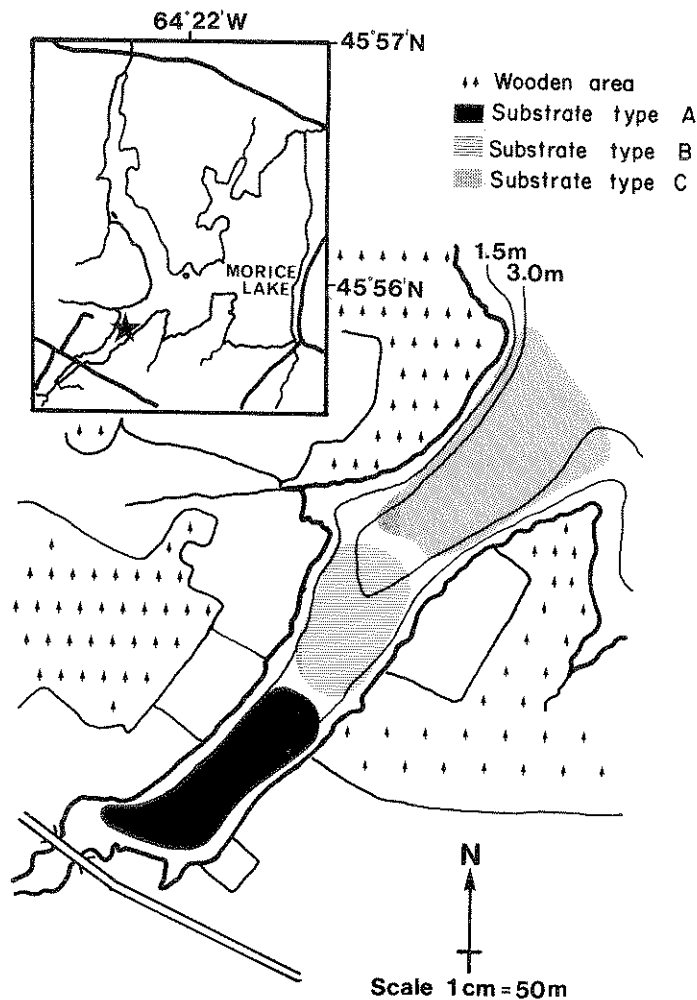
FIG. 1. The southwest arm of Morice Lake, near Sackville, New Brunswick, showing the 1.5- and 3.0-m depth contours.

These data were used to test the null hypothesis that the numbers of bivalves present in a sample (0, 1, or 2+ bivalves) have no effect on the numbers of other macroinvertebrates. Two additional sources of variation present in the data which could obscure the effects of increasing number of bivalves were time of sampling (season) and substrate type. These two variables were considered as covariates in the SPSS analysis of variance. The data were used in the calculation of the analysis of variance with covariates as outlined in the *Statistical package for social sciences* by Nie *et al.* (1975). The computational adjustments for the covariates (substrate type and time of sampling) were assessed before the main effect of increasing number of bivalves was calculated. The data were tested for the homogeneity of variances using Bartlett's test (Snedecor and Cochran 1967) and the appropriate transformation to remove the heterogeneity of variances was indicated by the application of Taylors' power law ($\log_{10} S^2 = \log_{10} a + b \log_{10} X$), where a and b are population parameters (Elliott 1977). The square root transformation was used for total benthos and the $\log_{10}(n + 1)$ transformation for individual taxa.

A series of controlled tank experiments was performed using the most abundant bivalve in Morice Lake, *Elliptio complanata*, to further investigate the possible relationships between bivalves and other benthic macroinvertebrates. Quantitative

9-in. Ekman grab samples were collected from the arm and poured into a large galvanized metal bucket with a 0.33-cm-square mesh bottom and the substrate was collected in a large pail. This coarse sieving removed any bivalves from the samples and throughly mixed the substrate into a uniform consistency. The substrate was then placed to a depth of approximately 7 cm in each of two polyethylene tanks measuring 55 cm × 115 cm in area and 43 cm in total depth and one fiber-glass tank measuring 50 cm × 105 cm in area and 35 cm in total depth. The tanks were filled with fresh reservoir water to a depth of 25 cm and allowed to acclimate for 24 h after which the water was siphoned off to within 2 cm of the substrate. Each tank was partitioned into eight quadrats, 25 cm square, by markers placed on the tank walls. Duplicate core samples were taken in each of the eight sample areas of the tanks, placed in double polyethylene bags, and returned to the laboratory where they were sorted using the techniques stated above. The core samples were taken using a modified soft-drink can that covered an area of 26.4 cm². One end of the can was removed and a hole (1 cm diameter) was punched into the other end. This sampler was easy to maneuver in small areas and no apparent pressure wave was generated. Placement of the thumb over the hole provided adequate suction to remove an intact core sample.

Elliptio complanata 5.0–7.0 cm in maximum length were ob-

tained from the arm using a qualitative sampling method. Twenty-five centimetre square partitions, with a height of 15 cm, were constructed of galvanized square wire mesh (0.33 cm). These "corrals" inhibited the movement of bivalves but would have little effect on the movement of the nonbivalve benthos. Corrals were placed in an alternating pattern in four of the eight sample areas in each tank. Two *E. complanata* of approximately the same size were placed into each of the corrals so that they were adjacent to one another. The tanks were refilled with fresh reservoir water, taking care not to disturb the surface of the sediment. Water temperatures were monitored in the tanks and did not vary by more than 3°C from the reservoir water temperature. The tanks were maintained for 10 days, a period of time that was considered sufficient to allow for populations to stabilize (Paterson and Fernando 1971) and also to allow the bivalves to deposit substantial amounts of faeces and pseudofaeces. The water in the tanks was siphoned off to within 2.5 cm of the substrate and replaced with fresh reservoir water every 24 h. Care was taken not to disturb the clams or the substrate surface during the emptying or refilling period.

At the termination of the 10-day period, the water was siphoned off to within 2.0 cm of the substrate. Duplicate core samples were taken in each of eight quadrats, placed into double polyethylene bags, and returned to the laboratory. Final core samples were sorted and counted in the same manner as the initial samples. The null hypothesis was that there should be equal numbers of the nonbivalve species found in areas with and without bivalves at the termination of the experimental period. The alternate hypothesis was that the bivalves would cause an increase in numerical abundance of nonbivalve benthos in areas where bivalves were located as compared with areas without bivalves. The t-test for two means was used, and the t-test statistic was compared with the critical t for a one-sided test with degrees of freedom equal to 14 (i.e., $n_1 + n_2 - 2$), for both initial and final core samples.

Results

Sublittoral zone fauna and substrate effects

The nonbivalve benthos consisted of approximately 20 taxa of common macroinvertebrates with eight other taxa appearing rarely over the sampling periods of 1977 and 1978 (Table 1). Chironomid larvae were the most abundant benthic macroinvertebrates and their percentage contribution to the total non-bivalve benthic fauna never fell below 58% in any samples. The three most numerically abundant chironomid larvae were *Procladius*, comprising 35% of the total chironomids, *Harnischia* (25%), and *Tanytarsus* (25%). The remainder of the Chironomidae genera (individual abundances were grouped and designated "other Chironomidae") were encountered consistently but in low numbers. Examination of the gut contents of the chironomid larvae indicated that most were detritivores–herbivores. The only exception was *Procladius* which was considered an omnivore as its gut contents sometimes included head capsules from second- and third-instar *Harnischia* and *Tanytarsus* larvae.

The average total numerical standing stock per square metre for each of the three substrates is shown in Table 2. Substrate type A had a greater numerical abundance than B ($t = 2.98, p < 0.006$)

TABLE 1. Composition of the benthic fauna of Morice Lake, N.B.

Common fauna	Rare fauna
Chironomidae larvae	*Hyalella azteca*
Chironominae	*Bidessonotus* sp.
Chironomini	*Helobdella* sp.
Chironomus (Meigen)	Hydracarina (Unionicolidae)
Dicrotendipes (Kieffer)	*Pisidium* sp.
Einfeldia (Kieffer)	*Caenis* sp.
Harnischia (Kieffer)	Nematoda
Parachironomus (Lenz)	Odonata nymphs (Aeshnidae)
Phaenopsectra (Kieffer)	
Polypedilum (Kieffer)	
Pseudochironomus	
(Johannsen)	
Tanytarsini	
Tanytarsus (v.d. Wulp)	
Micropsectra (Kieffer)	
Orthocladiinae (two species)	
Tanypodinae	
Procladius (Skuse)	
Enchytraeus sp. (Henle)	
"Other oligochaetes" (Lumbriculidae)	
Hexagenia sp.	
Phylocentropus sp.	
Sialis sp.	
Bezzia sp.	
Chaoborus sp.	

TABLE 2. Average total numerical standing stock of nonbivalve benthos on the three substrate types in the arm of Morice Lake. Data for each substrate are divided into samples with and without bivalves

	Substrate type	Without bivalves	With bivalves
A	$\bar{X}$ (No./m²)	5875.84	8600.02
	N	18	14
	SEM	863.87	750.07
	95% CI	±1822.77	±1620.16
B	$\bar{X}$ (No./m²)	2771.99	4441.56
	N	16	35
	SEM	525.30	406.13
	95% CI	±1119.41	±825.26
C	$\bar{X}$ (No./m²)	1813.12	3514.02
	N	17	24
	SEM	334.87	412.62
	95% CI	±709.92	±853.71

and C ($t = 4.29, p < 0.129$). There was an increased average numerical abundance of macroinvertebrates in samples containing bivalves compared with those without bivalves within any substrate type. The standing stock was low in early spring 1977 (2000 individuals/m²) and gradually increased in all three substrates to a summer maximum (5000/m²).

Statistical analysis of quantitative data

Table 3 presents the results of the analysis of covariance to determine if there were any significant effects of increasing number of bivalves

TABLE 3. Summary of the results of the analysis of covariance to determine if there were any significant effects of increasing number of bivalves on the numerical abundance of total nonbivalve benthos and of individual taxa. The summary results for the effect of substrate type and time of sampling on the numerical abundance of nonbivalve benthos are shown. Transformed data calculations are indicated

Dependent variable	df	Increasing bivalve effect		Substrate type		Time of sampling	
		F	Sign of F	F	Sign of F	F	Sign of F
Total nonbivalve benthos							
transformation*	2, 119	7.107	$p < 0.001$	54.447	$p < 0.001$	15.432	$p < 0.001$
		9.191	$p < 0.001$	49.868	$p < 0.001$		
"Other oligochaetes"							
transformation	2, 119	8.519	$p < 0.001$	0.253	NS	0.587	NS
		11.158	$p < 0.001$		NS	1.344	NS
Enchytraeus sp.							
transformation	2, 119	7.854	$p < 0.001$	22.001	$p < 0.001$	0.813	NS
		5.469	$p = 0.005$	29.974	$p < 0.001$	1.093	NS
Procladius							
transformation	2, 119	6.716	$p = 0.002$	35.020	$p < 0.001$	8.491	$p = 0.004$
		9.410	$p < 0.001$	31.930	$p < 0.001$	1.129	NS
Harnischia							
transformation	2, 119	3.076	$p = 0.050$	13.732	$p < 0.001$	1.304	NS
		7.002	$p = 0.001$	18.520	$p < 0.001$	5.404	NS
Tanytarsus							
transformation	2, 119	0.233	NS	28.531	$p < 0.001$	2.539	NS
		5.978	$p = 0.003$	37.341	$p < 0.001$	5.080	NS
"Other Chironomidae"							
transformation	2, 119	6.401	$p = 0.002$	23.696	$p < 0.001$	41.653	$p < 0.001$
		12.332	$p < 0.001$	34.413	$p < 0.001$	77.421	$p < 0.001$
Dicrotendipes transformation	2, 89	7.212	$p = 0.001$	12.298	$p < 0.001$	20.624	$p < 0.001$
Micropsectra transformation	2, 89	3.422	$p = 0.037$	1.196	NS	55.766	$p < 0.001$
Polypedilum transformation	2, 89	6.553	$p = 0.002$	2.899	NS	6.747	$p = 0.011$
Orthocladiinae transformation	2, 89	30.386	$p < 0.001$	6.627	$p = 0.012$	3.546	NS
Bezzia sp. transformation	2, 119	1.709	NS	0.517	NS	5.060	NS
Hexagenia sp. transformation	2, 119	0.998	NS	0.006	NS	0.213	NS
Phylocentropus sp. transformation	2, 119	2.103	NS	41.885	$p < 0.001$	1.749	NS
Sialis sp. transformation	2, 119	1.125	NS	1.197	NS	1.811	NS
Chaoborus sp. transformation	2, 119	1.864	NS	16.751	$p < 0.001$	22.012	$p < 0.001$

*For the total nonbivalve benthos the square root transformation was used, for all others a $\log_{10}(x + 1)$ transformation was used.

on the numerical abundance of total benthos and of individual taxa. Results of analysis with raw and transformed data are presented. The main effect of bivalves was positively significant ($\alpha = 0.05$) for the total nonbivalve benthos, "other oligochaetes," *Enchytraeus* sp., *Procladius*, *Harnischia*, *Tanytarsus*, "other Chironomidae," *Dicrotendipes*, *Micropsectra*, *Polypedilum*, and Orthocladiinae. The bivalve effect was not significant on the remainder of the benthos. A greatly increased number of quantitative samples would probably enable a more accurate interpretation of the analysis and reduce some of the sampling error that is inherent in attempting to sample rare taxa. Insignificant numbers of relatively rare taxa (e.g., those included in the "other Chironomidae" designation) rendered difficult valid interpretations of the results of the analysis. Substrate type had a

significant effect on abundances of all taxa except "other oligochaetes," *Bezzia* sp., *Hexagenia* sp., and *Sialis* sp. *Chaoborus* sp. was the only taxon to show a preference for substrate type C.

Controlled tank experiments

The controlled tank experiments were replicated five times using three tanks. The organisms sampled consistently during the experimental period were *Procladius*, *Harnischia*, and "other oligochaetes." Occasionally *Sialis* sp. and *Hexagenia* sp. would occur in a sample.

The statistical analyses of the preliminary samples, using the *t*-test, all showed no significant differences ($\alpha = 0.05$). There was insufficient evidence to reject the null hypothesis; thus, it can be assumed that there were no significant differences among any of the areas of the tanks at the beginning

TABLE 4. Summary of the results of the *t*-test for the null hypothesis of equality of numerical abundance of macroinvertebrates between those areas with and without bivalves in experimental tanks

Expt. start date	Expt. No.	Tank No.	df	*t* statistic	Significance of *t*	Average tank temp.
21 June 78	1	1	14	0.19	NS	19.0°C
		2	14	0.45	NS	
		3	14	1.26	NS	
3 July 78	2	1	14	0.86	NS	19.0°C
		2	14	1.63	NS ($p < 0.10$)	
		3	14	1.91	$p < 0.05$	
14 July 78	3	1	14	2.74	$p < 0.001$	21.0°C
		2	14	0.76	NS	
		3	14	0.26	NS	
25 July 78	4	1	14	2.21	$p < 0.025$	22.0°C
		2	14	1.70	NS ($p < 0.10$)	
		3	14	1.89	$p < 0.05$	
3 August 78	5	1	14	1.41	NS ($p < 0.10$)	21.0°C
		2	14	0.314	NS	
		3	14	2.063	$p < 0.05$	

of the time period. Table 4 shows the results of the *t*-test analysis of the final core samples comparing areas with and without bivalves. Significant results were recorded for five of the experiments, with an additional three others being relatively close ($0.10 > p < 0.05$). If the results were pooled for all experiments, comparing all areas with bivalves with all those without bivalves, areas with bivalves were significantly different from areas without bivalves ($t = 2.62$, df $= 230$, $p < 0.01$) for a one-sided *t*-test. The bivalves were undisturbed during the experiments and small mounds of faeces–pseudofaeces were noted. An estimation of the total amount of faeces and pseudofaeces produced by a single *Elliptio complanata* in a tank over 10 days would be 190 mg (dry weight) (Sephton 1979).

Discussion

The nonbivalve fauna of Morice Lake is a simple community composed of a relatively small number of different taxa that can accurately be separated at the generic level. Comparisons of the estimates of benthic standing stocks of this mesotrophic reservoir to values in the literature (Armitage 1977; Brinkhurst 1974; Hamilton 1971; Wetzel 1975) indicate it has a standing stock that is lower than most estimates for this type of lake system. The fauna is also not as diverse as other mesotrophic reservoirs (cf., Kajak and Dugose 1975, 1976; Mason 1977).

Substrate composition and water depth are two factors that can affect the distribution and abundance of benthos. It is recognized that the substrate categories defined in this study are overly simplified as there are undoubtedly variations in the organic content within a substrate type. Total numerical abundance of benthos (Table 2) showed that the woodchips – plant detritus – silt substrate (A) supported a higher abundance than the plant detritus – silt substrate (B). The silt–gyttja substrate supported the lowest numerical standing stock. Substrate type A is in the shallowest part of the arm and substrate type C is in the deeper part (Fig. 1), approaching the main part of the reservoir. A relationship exists between increasing depth and decreasing numerical standing stock of benthos in many lakes and reservoirs, perhaps as a product of decreasing amounts of detritus (Brinkhurst 1974; Fillion 1967; Kajak and Dugose 1975, 1976). Silt–gyttja substrates usually support lower numbers of benthic macroinvertebrates than plant detritus substrates (Kajak and Dugose 1975; Swanson 1967).

The trophic conditions and interactions of the benthos are decisive for the numerical abundance and fauna distribution. The benthos is a dynamic community (Brinkhurst 1974) and reacts quickly to environmental fluctuations, especially to changing food quality conditions (Kajak 1977). Driscoll (1975) studied the marine sediment – animal–water interactions in Buzzard's Bay, Massachusetts, and found that the biodeposits from deposit feeders were colonized by microorganisms. This made the biodeposit a readily available nutrient source which in turn caused an increase in the deposit feeder abundance. A similar situation occurs in freshwater with the detritus food chain (Brinkhurst 1974; Wetzel 1975).

The basic concept for the present study was that the unionid bivalve community produced substantial amounts of faeces and pseudofaeces in a form

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readily available as a food source to the benthic detritivore organisms (Izvekova and Lvova-Katchanova 1972). This concentration and deposition of seston would aggregate the nonbivalve benthos in close vicinity to the bivalves. The effect of natural differences in numbers of bivalves (0, 1, and 2+ bivalves) on the numerical abundance of organisms was significant, as determined by the analysis of covariance (Table 3), for the total benthos and some individual taxa. The gut contents of the dominant chironomids, for which the analysis of covariance was significant, indicated that they were detritivores, with one genus, *Procladius*, being an omnivore. The positive association of *Procladius* to the bivalves could be an indirect one as a predator in responding to higher prey densities in the vicinity of the bivalves. The analyses suggest that there is an association between some of the nonbivalve benthos and the bivalves that could be a response by the nonbivalve benthos to an increased food source.

Large variability occurs among samples collected on the same date and among samples from the same substrate type (Sephton 1979). The sampling procedure was subject to error as it was not known where the sampler was obtaining benthic samples. It is conceivable that samples collected from the edge of a clump of bivalves would contain a substantial number of benthic organisms showing the influence of the deposition of seston by the bivalves, even though none were present in that particular sample. This was an innate source of error that could not be controlled.

Controlled experiments using the dominant bivalve, *Elliptio complanata*, and natural reservoir substrate containing nonbivalve benthos were conducted to further analyze the effects of bivalve abundance on benthos distribution. It was assumed that there was a uniform environment at the beginning of the experiment as there was no difference in the average abundance of benthos. Five of the 15 experiments were statistically significant with an increase in numerical abundance of the benthos in areas where bivalves were located (Table 4). The pooled experimental data were also significant. The majority of the macroinvertebrates detected during the experimental studies were those found to have statistically significant associations with bivalves in the reservoir data analyses. The experimental data support the idea of aggregation by a behavioral response to an increasd food supply contributed by the bivalves.

The results of the tank experiments are equivocal as the experimental design criteria were not critical enough in controlling all the factors. Ten of the experiments did not show any significant associations between the nonbivalve benthos and the bivalves; however, this could be a product of the time element. It is thought that the movement of macroinvertebrates in search of food is an active, random process. Once a food source is located, movement would slow and the organism would tend to stay in the area of the food source. Therefore, it is thought that a pyramid effect would occur as the rate of incoming benthos movement would be higher than the rate of outgoing movement from the food source area. Thus the time required for this pyramid effect to be observed is an uncontrollable factor. Substrate collected from the reservoir was probably rich in organic detritus from the bivalves in the reservoir. The higher the organic detrital content of the substrate, the more food there is available to the detritivores, and consequently their active random movement of food searching is slowed.

Woodin (1978) noted that the refuges created by marine polychaete worms, who themselves or through their burrows and tubes, inhibited predation, stabilized the substrate, or buffered the impact of physiological stress, caused an increased numerical abundance and species richness of the other members of the fauna in close proximity. A major effect of the bivalves in Morice Lake, other than the role in enhancing a food source, could be the increased circulation of water due to filtering. The filtering effect could reduce oxygen microstratification at the mud–water interface and distribute soluble waste material.

The interrelationships of factors that determine the distribution and abundance of benthic organisms in a particular substrate are largely unknown (Paterson and Fernando 1971). To state that a single factor controls the distribution of any species would be näive, but to suggest an interaction of physical factors (Rinne 1978) and behavioral mechanisms (McLachlan 1977; Paterson and Fernando 1971; Segerstråle 1978) would be more realistic. In summary, the analysis of the benthic samples and experimental tank data indicates that the bivalve community in Morice Lake causes an increase in the numerical abundance of the nonbivalve fauna in close proximity to the bivalves. The effect of the biodeposition of the bivalves is an additional factor which influences the distribution of benthos.

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