NOTES

An Empirical Model to Predict in situ Grazing Rates of *Diaptomus minutus* Lilljeborg on Small Algal Particles

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Grazing rates of *Diaptomus minutus* were measured in situ in six lakes in south-central Ontario using the tracer species *Chlorella vulgaris* and *Scenedesmus ovalis*. An empirical model was constructed to predict grazing rate as a function of the relative proportion of small (<10 μm) to large (10–30 μm) algal particles in the nanoplankton. It accurately predicted diaptomid grazing rates for three lakes in an independent lake set; however, it produced overestimates for two other lakes. There was also a significant positive correlation between grazing rate and the biomass concentration of small algae in the lakes. Difference in ambient lake temperature did not contribute significantly towards explained variation in grazing rate; prosome length was also a poor predictor of grazing rate. In parallel experiments, diaptomid grazing rates were higher when *Pediastrum* was used than when *Scenedesmus* was used as the tracer; in a similar set of experiments, grazing rates were higher when *Chlamydomonas* was used than when *Scenedesmus* was used.

Les taux de broutage de *Diaptomus minutus* ont été mesurés in situ dans six lacs du centre-sud ontarien à l'aide de deux espèces traceurs : *Chlorella vulgaris* et *Scenedesmus ovalis*. Un modèle empirique a été mis au point pour prédire les taux de broutage en fonction de la proportion relative de petites (<10 μm) et de grosses (10–30 μm) particules d'algues dans le nanoplancton. Le modèle a permis de prédire avec précision les taux de broutage des diaptomides dans trois lacs d'un groupe indépendant de lacs, mais a surestimé les taux dans deux autres cas. Nous avons également observé une corrélation positive significative entre les taux de broutage et la concentration de la biomasse de petites algues dans les lacs. Les différences des températures ambiantes des lacs n'ont pas contribué de façon significative à expliquer les variations des taux de broutage; de même, la longueur des prosomas était une variable explicative peu utile pour les taux de broutage. Des expériences parallèles ont montré que les taux de broutage des diaptomides étaient plus élevés lorsque *Pediastrum* était utilisé comme traceur plutôt que *Scenedesmus*. Une série d'expériences semblables a révélé que les taux de broutage étaient supérieurs lorsque *Chlamydomonas* était utilisé plutôt que *Scenedesmus*.

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Diaptomus is commonly found in the plankton of the northern United States and southern Canada. In many lakes of south-central Ontario, their biomass constitutes up to 50% of the total herbivore biomass during the summer (P. Chow-Fraser, unpubl.). Because of their numerical abundance, accurate measurement of their grazing rate is a prerequisite to realistic assessment of energy transfer between plankton compartments in these lakes.

Published data for freshwater calanoids are rare compared with those of marine calanoids and freshwater cladocerans (see Peters and Downing 1984). Additionally, grazing rates measured in the field (Richman 1964; Haney 1973; Thompson et al. 1982) are more rarely documented than those measured under laboratory conditions (Richman 1966; McQueen 1970; Richman et al. 1980; Vanderploeg 1981; Vanderploeg et al. 1984). Therefore, field measurements of diaptomid grazing rates are desirable so that extrapolation from laboratory data or from studies of other herbivorous taxa will not be necessary.

In laboratory studies, investigators found that clearance rates of *Diaptomus* vary according to temperature (Comita 1964), algal concentration (Richman 1966), and algal size (McQueen 1970; Richman et al. 1980). Few studies have attempted to determine whether or not these laboratory findings are applicable under natural situations. In this paper, I measure grazing rates of *Diaptomus minutus* and *D. oregonensis* in six lakes in south-central Ontario to examine the effects of temperature and algal composition on the in situ grazing rates of *Diaptomus*. An

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TABLE 1. Description of study lakes. pH measurements are summer averages of epilimnetic samples. Nanoplankton biovolume concentrations are in $mg \cdot m^{-3}$.

Lake	Mean depth (m)	Max. depth (m)	Volume (Mm^3)	pH	Nanoplankton biovolume <10 μm	Nanoplankton biovolume 10–30 μm	Blue-green filament biovolume
Model							
Head[a]	3.5	8.3	32.13	7.5	76.3	120.7	15.7
Moore[a]	7.5	21.6	13.80	6.0	42.3	104.6	0.4
Gull[a]	16.5	49.1	164.34	7.5	23.2	133.3	1.2
Blue Chalk[b]	9.3	21.9	4.70	6.0	47.5	319.0	0
Plastic[b]	8.1	16.7	2.64	5.6	13.3	124.9	0
Picard[b]	10.1	35.0	7.69	7.4	15.7	252.3	13.2
Test							
Hall's[a]	27.9	79.2	150.66	6.0	14.9	96.6	4.7
Mountain[b]	13.4	31.3	44.12	6.5	6.8	92.8	4.7
Brady[b]	4.5	11.5	4.08	5.8	32.5	146.1	1.4
Three-Mile[b]	3.4	10.9	32.33	6.6	56.5	25.7	211.9
Young[b]	4.3	10.4	4.00	8.1	559.0	820.0	287.0

[a]From Ontario Ministry of Natural Resources, Minden, Ont., unpubl. data.
[b]From Zimmerman et al. (1983) and Paloheimo and Zimmerman (1983).

empirical model was constructed to predict grazing rate of *D. minutus* from the relative abundance of small algal particles in the nanoplankton. I then test the applicability of this model by comparing predicted with measured rates obtained in an independently sampled lake set.

Methods and Materials

Six study lakes were sampled between late June and August in 1981 to provide data for the empirical model. Five additional lakes were sampled in 1982 to provide data for testing the applicability of the models. These lakes were all located in south-central Ontario and vary considerably in mean depth, volume, and pH values as well as algal standing stock (Table 1).

In situ grazing experiments were conducted with a 2-L Haney (1971) chamber at several depths in the water column of one station (usually at the deepest part of the lake). Experiments were usually performed between 10:00 and 16:00. The same procedures for grazing experiments, algal labelling, and determination of grazing rates were used in Chow-Fraser and Knoechel (1985). Ambient temperature was taken at the depth of the Haney chamber.

The labelled tracers used to measure grazing rates included *Chlorella vulgaris* (Carolina Biological; longest linear dimension 6–8 μm), *Scenedesmus ovalis* (Indiana Culture Collection; unicellular form, 4–6 μm), *Chlamydomonas* sp. (10–12 μm), *Pediastrum* sp. (coenobium, 30–40 μm; provided by P. Stokes, Botany Department, University of Toronto), and *Anabaena* sp. (vegetative cells approximately 4 μm in diameter, 6–8 μm in length, 25 cells·filament^{-1}; provided by S. Keal, Biology Department, Erindale College; toxic nature uncertain). The final concentration of *Scenedesmus, Chlamydomonas*, and *Chlorella* in the grazing chamber was calculated to be 1000 cells·mL^{-1}, 100 filaments·mL^{-1} for *Anabaena*, and 350 coenobia·mL^{-1} for *Pediastrum*. These represented an addition of less than 10% to the total phytoplankton biomass concentration in any experiment.

Parallel grazing experiments were conducted in Three-Mile and Mountain lakes with labelled *Chlorella* and *Scenedesmus* to determine the effect of using the two different tracers on grazing rates. No statistically significant differences were found between means (t-test, $P < 0.01$), and data from experiments with both tracer species were combined for construction of the model.

Zooplankton were stored on dry ice (Chow-Fraser and Knoechel 1985) and sorted without addition of preservative. I measured the prosome length of *Diaptomus* with the aid of a dissecting microscope. Grazing rates represent the average rates of groups of three to five animals of the same species of approximately the same size from a specific experiment. The developmental stage of the copepod was broadly noted as mature or immature but no attempt was made to determine the sex or the developmental stage of the immature instars.

Integrated phytoplankton samples from each lake were collected from the epilimnion (at the same place where grazing experiments were conducted). These were preserved and enumerated as in Chow-Fraser and Knoechel (1985). Besides total phytoplankton, the biomasses of algae with maximum linear dimension less than 10 μm (small nanoplankton; SNANO) and between 10 and 30 μm (large nanoplankton; LNANO) and blue-green filaments were also recorded (Table 1).

To test the effect of temperature on clearance rates (equivalent to grazing rates), experiments were conducted at 5, 10, 17, and 20°C in Picard Lake by lowering the grazing chamber to depths corresponding to these temperatures. Three experiments were conducted at each temperature. Only adult *D. minutus* were included in this analysis to avoid the confounding effects of developmental stage and species. I used a two-level hierarchical analysis of variance model to test for significant differences in grazing rates due to temperature effects and the nested effect of different grazing chambers within the four temperatures.

To test the effect of prosome length (equivalent to cephalothorax length) on clearance rate, I regressed data for both species of *Diaptomus* (conducted with labelled *Scenedesmus* and *Chlorella* only) against prosome length in a general linear regression analysis (Sokal and Rohlf 1981). Subsequently, I sorted the data and performed a separate regression analysis on *D. minutus* data only.

TABLE 2. Two-level nested analysis of variance to test the effect of temperature on clearance rate of *D. minutus* in Picard Lake.

Source	df	SS	MS	*F*	*P*
Among temperatures (5, 10, 17, 20°C)	3	0.1255	0.0418	0.07	0.98
Among grazing chambers within temperatures	8	9.7223	1.2153	1.89	0.11
Error	24	15.4051	0.6419		
% variance components					
Temperature	0				
Grazing chamber	23				
Unexplained variance	77				

I tested the effect of phytoplankton concentration on adult grazing rates of *D. minutus* in a correlation analysis. Clearance rates (measured with *Chlorella* and *Scenedesmus*) were correlated with total phytoplankton (TOTAL), nanoplankton biomass concentration (longest linear dimension <30 μm; NANO), SNANO (algae <10 μm), and LNANO (algae 10–30 μm) as well as the ratio of SNANO to LNANO (PROP).

The effect of tracer species on clearance rates of adult *Diaptomus* was tested by performing an analysis of variance on data obtained from grazing experiments in which labelled *Scenedesmus*, *Chlorella*, *Chlamydomonas*, and *Pediastrum* were fed to native zooplankton in Gull and Three-Mile lakes.

Results and Discussion

Temperature — The two-level nested analysis of variance indicated that temperature did not contribute significantly to the variation in grazing rate ($P = 0.98$; Table 2). Although differences among chambers were not statistically significant ($P = 0.11$), it accounted for 23% of the variation in the grazing rate of *D. minutus*. The overwhelming proportion of variation (77%) was unexplained by the model.

This analysis indicates that grazing rates measured at 5, 10, 17, and 20°C were statistically homogeneous. I suggest that any real effect of temperature was probably masked by individual variation among copepods as well as by microclimatic differences among chambers. Chow-Fraser and Knoechel (1985) also observed the lack of a significant temperature effect on the in situ grazing rates of cladocerans in lakes within this geographic region. Thus, the effect of temperature on diaptomid grazing rate is less predictable in nature than is demonstrated under controlled laboratory conditions (i.e. Comita 1964).

Prosome length — I regressed diaptomid clearance rates against prosome length ($n = 118$) and obtained the following:

$$(1)\quad \log CR = 2.07(\pm 0.90) \log L + 0.50(\pm 0.20)$$

where $r^2 = 0.04$, $P = 0.0001$, numbers in parentheses = SE, CR = clearance rate (millilitres per day), and L = prosome length (millimetres) (Fig. 1). Although the slope is significantly different from zero, prosome length only explained 4% of the variability in grazing rate.

Vanderploeg et al. (1984) also found that body size was a minor contributor to residual variation in the functional feeding curve of *D. sicilis*, mostly because of relatively invariant body size. L. B. Holtby (Pacific Biological Station, Nanaimo, B.C., unpubl. data) also conducted similar Haney grazing experiments with labelled yeast (maximum linear dimension approximately 3 μm), and when I regressed his data against measured prosome length, I found no statistically significant slope ($P = 0.57$). Body length generally appears to have weak predictive power for diaptomid grazing rate, and this contrasts sharply with the strong predictive power of length in describing cladoceran filtering rate (see Chow-Fraser and Knoechel 1985).

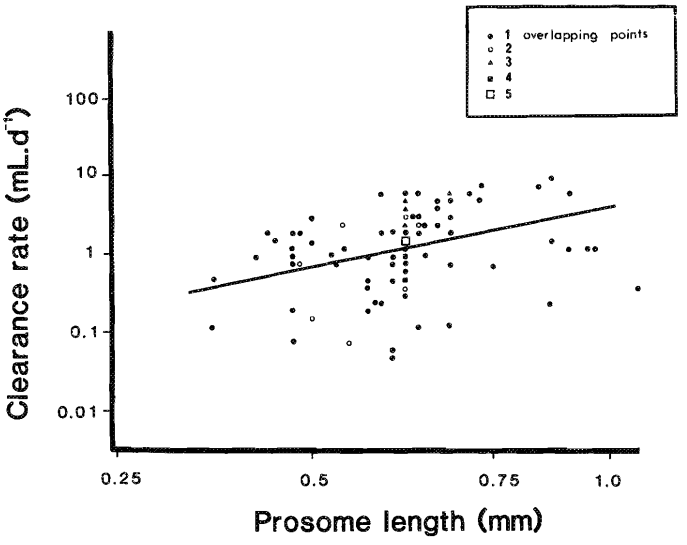

FIG. 1. Clearance rate of *Diaptomus* sp. versus prosome length. Solid line is the least-squares regression line through data; Eq. 1 in the text.

Regression of clearance rate against prosome length data for *D. minutus* ($n = 67$) increased the r^2 value relative to that for the combined mixed-species regression equation (Eq. 1) and resulted in the following:

$$(2)\quad \log CR = 3.00(\pm 1.26) \log L + 0.72(\pm 0.25)$$

where $r^2 = 0.09$ and $P = 0.02$. Since the r^2 value was significantly improved by 5% in the reduced dataset, a contributing factor to the large residual variation in Fig. 1 was probably inclusion of the two different species in the combined dataset. A probable reason is that sizes of developmental stages overlap considerably among species. Thus, the size of an early instar of *D. oregonensis* overlaps with that of a late *D. minutus* instar and yet may have comparatively different grazing rates. No attempt was made in this study to determine the relationship between grazing rate and developmental stages in *Diaptomus*.

Phytoplankton biomass concentrations — I next correlated grazing rate of *D. minutus* adults with various fractions of phytoplankton biomass concentration because food concentration in laboratory experiments was known to have an effect on clearance rates of *D. oregonensis* (Richman 1966). The best correlate of grazing rate was PROP ($r = 0.99$; Table 3), the next best being SNANO ($r = 0.80$). Regression of mean clearance rates for the six model lakes against PROP resulted in the following predictive regression (Fig. 2):

$$(3)\quad CR = 12.92\text{PROP} - 0.09.$$

I found supporting evidence for the positive correlation between grazing rate and relative proportion of small cells reported in other studies. Marshall and Orr (1955) found that *Calanus* supplied with a microflagellate (<10 μm) had greatest

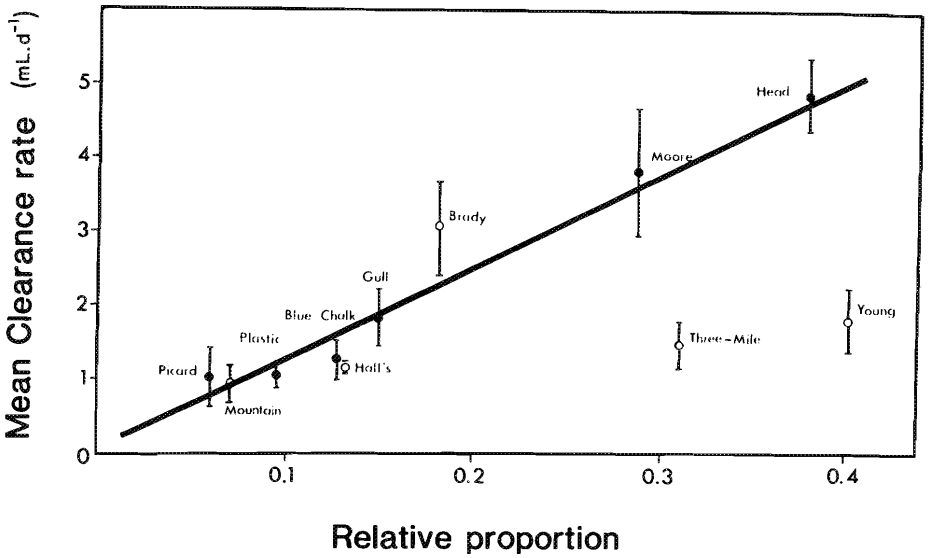

FIG. 2. Clearance rate of *D. minutus* versus the relative proportion of small cells (<10 μm) in the nanoplankton. Solid line is the least squares-regression line through solid circles only; Eq. 3 in the text. Open circles are values for the test lakes. Bars are 1 SE of the means. Labelled tracer species were *Chlorella* and *Scenedesmus*.

TABLE 3. Correlation between clearance rate of *D. minutus* and biovolume concentration of nanoplankton (<30 μm, NANO), small Nanoplankton (10 μm, SNANO), large nanoplankton (10−30 μm, LNANO), total phytoplankton (TOTAL), and the ratio of SNANO:NANO (PROP). *P* less than 0.05 indicates that the correlation coefficient, *r*, is significantly different from zero ($n = 6$).

Variable	*r*	*P*
NANO	−0.38	0.4598
SNANO	0.81	0.0529
LNANO	−0.60	0.2049
TOTAL	0.22	0.6766
PROP	0.99	0.0002

grazing rates when food was supplied at the highest concentration. In a time-series study, Richman et al. (1980) found that *D. oregonensis* increased its grazing rate on particles between 6 and 10 μm as the experiment progressed from 2 to 6 h. They noted that this increase in grazing rate of small cells was accompanied by a depletion of their supply of large cells (12−18 μm). Since the relative proportion of small cells increased as large cells became depleted, grazing rate on small cells in fact increased with the increase in relative proportion of small cells. Thus, both these studies provided evidence consistent with this study.

The positive correlation between grazing rate and SNANO biomass concentration (Table 3) is inconsistent with the conventional view that grazing rate is maximal and constant at phytoplankton concentrations below the incipient limiting concentration (ILC) and thereafter varies inversely with phytoplankton concentrations (Rigler 1961; McMahon and Rigler 1963; Richman 1966). It is, however, consistent with observations that grazing rates of certain marine calanoid copepods increase with phytoplankton concentration at extremely low algal concentrations (Parsons et al. 1967; Frost 1975; Reeve and Walter 1977; Gamble 1978). Since the phytoplankton concentrations in these lakes are as low or lower than those reported in these marine studies, it is probable that the increase in grazing rate with algal concentration noted here reflects a similar behavioral response in dilute environments as discussed by Frost (1975) for marine calanoids.

Test of the model — I plotted mean clearance rates from five test lakes (open circles) in Fig. 2 to test the applicability of the predictive model for other lakes in the region. Data for three, Hall's, Brady, and Mountain lakes, were close to the least-squares regression line (solid line) whereas those for Three-Mile and Young lakes were relatively distant. Therefore, the model appears to be applicable for three of the five test lakes.

Clearance rates for Three-Mile and Young lakes were much lower than predicted by the model. Both lakes had a high biomass concentration of small cells (Table 1) and a high relative proportion of SNANO compared with the other study lakes. Yet, the grazing rates were uniformly as low as those in lakes with much lower relative proportions of small cells. Both lakes were also unique in that blue-green filaments (such as *Anabaena, Oscillatoria*, and *Aphanizomenon*) were abundant.

I suspected that blue-green algal filaments in Three-Mile and Young lakes were responsible for reducing in situ grazing rate of *D. minutus* in a fashion similar to that observed by Richman and Dodson (1983). Tentative support for the negative effect of *Anabaena* on clearance rate is demonstrated by the statistically lower grazing rate when labelled *Anabaena* was used (mean 0.33 $mL \cdot d^{-1}$) in Three-Mile grazing experiments than when labelled *Scenedesmus* was used (mean 1.47 $mL \cdot d^{-1}$; *t*-test, $P = 0.03$). This represents a 4.5 times reduction in grazing rate between labelled tracers and indicates at the very least that labelled *Anabaena* was not ingested readily by *D. minutus* in Three-Mile Lake.

Although the empirical model should be modified to reflect other species of *Diaptomus* in many other geographical regions (something I am doing presently), the relatively close agreement of predicted to measured rates in at least some of the test lakes indicates that the model holds promise for predicting diaptomid grazing rates in lakes with a relatively low concentration of small planktonic algae.

Limitations of the model — The empirical relationship between clearance rate and relative proportion of small cells

TABLE 4. Mean clearance rates ($mL \cdot d^{-1} \pm 1$ SE) of *Diaptomus*.

Lake	Tracer species	Animal species	*n*	Clearance rate
Gull	*Scenedesmus*	*D. minutus*	10	1.76±0.38
	Pediastrum		10	4.81±0.78
	Scenedesmus	*D. oregonensis*	12	2.86±0.44
	Pediastrum		11	4.41±0.44
Three-Mile	*Scenedesmus*	*D. minutus*	9	1.47±0.31
	Chlorella		5	1.32±0.26
	Chlamydomonas		6	2.89±1.02

(Eq. 3) is only useful for predicting rates of *D. minutus* grazing on algae similar in size to *Scenedesmus* and *Chlorella*. When I measured grazing rates of *Diaptomus* using labelled *Pediastrum* and *Chlamydomonas*, both of which were larger than *Scenedesmus* and *Chlorella*, I obtained rates that were statistically different (*t*-tests and analysis of variance) than those measured in parallel experiments with labelled *Scenedesmus* or *Chlorella* (Table 4). Thus, differences in grazing rate due to size of algal tracer may limit the generality of the grazing model for predicting diaptomid feeding rates.

Discussion

Recently, Vanderploeg et al. (1984) used laboratory data to show that *D. sicilis* has an invariant selection for small algal particles. One probable explanation for this is that it feeds passively on small cells (4 μm) and that this feeding mode is constantly in operation (Vanderploeg and Paffenhöfer 1985). Invariant selection does not appear to apply to *D. minutus* in these lakes in view of Fig. 2. My results appear to be more consistent with findings of Richman et al. (1980) and Poulet (1973, 1974) that calanoid copepods feed opportunistically on the most abundant particles. However, since I did not conduct parallel experiments with large algal particles in all lakes, I do not know that *D. minutus* in fact changs its selection for small cells as a function of the relative abundance of small cells in the environment.

The apparent pattern of selection for small cells may be affected by the technique used to measure grazing rates. Vanderploeg et al. (1984) used an incubation period of longer than 18 h, whereas I used an incubation period of only 15 min in this study. Since selection for certain sizes of phytoplankton can change as the food size spectrum becomes altered when the preferred items are systematically depleted (Richman et al. 1977, 1980; Paffenhöfer 1984), selectivity observed at the end of an 18-h period may not necessarily reflect selectivity in the initial hours. Thus, grazing rates measured with the radiotracer method may more accurately reflect instantaneous selection, whereas those from coulter counter or direct microscope counting methods reflect the overall selection that has taken place during the long grazing period. Since the animal can respond to changes in the environment in minutes rather than hours (Cowles and Strickler 1983; Price et al. 1983; Vanderploeg and Paffenhöfer 1985; C. K. Wong, University of Toronto, unpubl. data), data that reflect instantaneous selection are probably more appropriate for interpreting the pattern of selection for animals grazing in a dynamic environment such as that in a lake.

High-speed filming similar to that used by Vanderploeg and Paffenhöfer (1985) should be conducted to determine whether or not *D. minutus* feeds on *Scenedesmus* and *Chlorella* actively and/or passively. Parallel experiments should also be performed to elucidate the relationship between relative abundance of seston fractions and the grazing rate of *D. minutus* on these size fractions to determine if "switching" or "peak tracking" occurs similar to that noted for other calanoids (Poulet 1973, 1974; Richman et al. 1977, 1980). More in situ experimentation with many diaptomid species will increase the rigor of the empirical relationship described here and hopefully lead to a more representative model of diaptomid grazing in lakes.

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Spatial Distribution of Entrained Fish Larvae in a Power Plant Discharge Canal[1]

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Larval fish were sampled with plankton nets during June and July at 1-, 3-, and 5-m depths at three stations in the 6-m-deep discharge canal of the Monroe electricity-generating plant on western Lake Erie. Of nine species, gizzard shad (*Dorosoma cepedianum*) accounted for 96% of all larval fish collected in June and, along with freshwater drum (*Aplodinotus grunniens*), 78% of those taken in July. Densities of fish larvae at the three depths, and at two of the three stations sampled, were not significantly different. Mean densities of gizzard shad and total fish larvae in June were significantly higher at one station. Fluctuating and significantly lower velocity at that station, causing the flowmeter not to turn while the net was still filtering water, was suspected of causing inflated densities. Generally sizes of larvae were not stratified by depth or station; differences that were found were small. Thus, we concluded that to obtain samples with representative species, densities, and sizes of entrained fish larvae, a stationary net should be positioned where the water has uniform high velocity and is well mixed.

On a prélevé des échantillons de larves de poisson au moyen de filets à plancton au cours de juin et juillet à des profondeurs de 1, 3 et 5 m à trois stations dans le canal de déversement de 6 m de profondeur de la centrale électrique Monroe située à l'ouest du lac Érié. Parmi neuf espèces, l'alose à gésier (*Dorosoma cepedianum*) constituait 96 % de toutes les larves de poisson recueillies en juin et, avec le malachigan (*Aplodinotus grunniens*), 78 % de celles capturées en juillet. La densité des larves de poisson aux trois profondeurs, et à deux des trois stations échantillonnées, ne différait pas de façon significative. La densité moyenne de l'alose à gésier et le nombre total de larves de poisson en juin étaient sensiblement plus élevés à une station. On a soupçonné la variation de la vitesse à cette station, de même qu'une vitesse beaucoup plus réduite, empêchant le débitmètre de tourner pendant que le filet filtrait encore l'eau, d'être les facteurs responsables des densités élevées. De façon générale, il n'y a pas eu stratification de la taille des larves en fonction de la profondeur ou de la station; les différences observées étaient peu importantes. Par conséquent, nous avons conclu que pour recueillir des échantillons où les espèces, la densité et la taille des larves de poisson transportées étaient représentatives, il fallait placer un filet fixe là où la vitesse de l'eau était uniformément élevée et où l'eau était bien mélangée.

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Documenting entrainment losses at electricity-generating plants is an important aspect of evaluating plant impact on fish. Studies are often conducted without sufficient knowledge of whether the sample adequately represents the species, densities, and sizes of entrained fish larvae. Sampler location should be based on criteria such as uniform current velocity and well-mixed water. Failure to do so could lead to a misleading estimation of the number of entrained fish larvae. During an impact study at the Monroe Power Plant located on the western shore of Lake Erie (Jude et al. 1983, available from the authors), we designed a special study to document the spatial distribution of larval fish in the discharge canal of the power plant. We avoided sampling

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