# Measuring *in situ* predation by *Mysis relicta* and observations on underdispersed microdistributions of zooplankton

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## Abstract

Described are a method and apparatus that allow *in situ* measurement of predation on zooplankton by *Mysis relicta*. The method, which can be generalized to other predators, involves lowering paired large-volume (30-l) plankton traps to the depth of interest, with subsequent trapping of the ambient zooplankton assemblage in each trap and release of predators into one of the traps. The statistical adequacy of the method was shown by error propagation theory to depend on the percentage of available prey consumed, on the number of prey captured by the traps, and on the distribution of zooplankton within the volume of water captured by the traps. Repeated casts of the apparatus showed that, in contrast to other studies of zooplankton distribution, various zooplankton categories were statistically underdispersed (evenly dispersed in space) or at least not more statistically dispersed (clumped) than was a random distribution at a space scale of 1 m. An error analysis of many replicated feeding experiments showed that the errors obtained were reasonably small and that they conformed with or were less than those predicted by error propagation theory that assumed random distribution of zooplankton. Thus, these results supported the practical application of the method and corroborated the conclusion of random dispersion or underdispersion drawn from the experiment of repeated casts of the apparatus.

## Introduction

In order to understand the significance of a predator like a mysid to the structure of zooplankton communities in lakes, estimates of *in situ* predation rates and prey selectivity are required. Heretofore, direct measurements of *in situ* predation and prey selectivity have not been possible for mysids. In the absence of these direct measurements, investigators have generally relied upon two alternative approaches. The first approach, the gut content method, estimates prey selectivity from gut content analyses and concentrations of prey in the environment (e.g., Rybock 1978; Murtaugh 1981); this approach has been extended to estimate *in situ* feeding rates

from laboratory-determined gut clearance rates (e.g., Rybock 1978). In the second approach, the laboratory feeding method, predation rates are measured in small vessels containing mixtures of zooplankton concentrated from net tows (e.g., Grossnickle 1978; Cooper & Goldman 1980; Murtaugh 1981) or mixtures of both zooplankton and algae (Grossnickle 1978).

These alternative approaches suffer from a number of shortcomings. The gut content method depends on the following critical assumptions that are difficult to verify. First, stomach content must reflect what was actually eaten (e.g., Rybock 1978; Murtaugh 1981). Second, the environmental prey concentrations determined from tows of

plankton nets must be the same as those actually encountered by those predators (e.g., Rybock 1978; Murtaugh 1981). Third, if this approach is used to estimate feeding rates, laboratory-determined gut clearance rates must be assumed to be the same as those for free-living animals (e.g., Windell 1967; Rybock 1978). These gut clearance experiments are extremely laborious and are subject to many of the criticisms we raise below for the laboratory feeding approach.

A major difficulty with the laboratory feeding approach is duplicating environmental conditions and concentrations of zooplankton and other sources of food found in nature. For example, Cooper & Goldman (1980) and Murtaugh (1981) found it necessary to use high concentrations of zooplankton (collected from tows of a plankton net) for selectivity experiments with natural zooplankton assemblages so that significant numbers of each of the different kinds of prey would be represented in the small ($\leqslant$3 l) experimental vessels used. It is posible that not only feeding rates will be affected by prey concentration, but also prey selectivity, since prey selectivity may change with prey concentration (Ivlev 1961; Pastorok 1980). Since mysids also feed on large diatoms (Bowers & Grossnickle 1978; Grossnickle 1978), a meaningful simulation of field conditions for mysids may also require large diatoms.

Another difficulty with laboratory experiments is that the handling required to set up these experiments may injure or affect the physiology of the prey and predator. A serious difficulty we and others (Rybock 1978; Cooper & Goldman 1980) have encountered in working with Cladocera (e.g., *Daphnia* and *Bosmina*), the preferred prey of mysids, is that they are susceptible to being trapped at the water surface during the handling required to set these experiments up. Also, the holding of the predator under various artificial feeding regimes (usually starvation) for various time intervals (usually days) before an experiment will affect its feeding rate (Frost 1972; Cooper & Goldman 1980) and possibly its prey selectivity (Runge 1980; Cooper & Goldman 1980).

Clearly it would be desirable to measure prey selectivity and predation rates *in situ* directly. In this paper, we describe a method to measure *in situ* predation on plankton communities. This method is demonstrated for predation by *Mysis relicta,* but could be applied to other invertebrate and vertebrate predators as well. Paired large-volume (30-l) plankton traps are lowered to the depth of interest, the ambient zooplankton assemblage is captured in each trap, and predators are introduced into one of the traps. The traps remain in place for a suitable time period, after which the zooplankton in each trap are preserved and later enumerated for calculation of clearance rates (Frost 1972), feeding rates, and selectivity coefficients (Vanderploeg & Scavia 1979a, b). The basic idea for our use of the paired-trap method was conceived by Bowers & Vanderploeg (1982) for studying *in situ* predation by *Mysis relicta.* However, Kajak & Rybak (1979) must be credited with first use of the method since one of the approaches they employed to study *Chaoborus* prediction was use of paired 3-l Gliwicz (1968) traps. No discussion was made of the statistical limitations of the method.

The adequacy of the method depends in large part on each trap capturing within acceptable statistical limits the same large number of zooplankton prey at their ambient concentrations. In this paper we show that the design of our traps conforms to that required for an ideal zooplankton sampler (Patalas 1954; Schindler 1969) so that the ambient concentration of zooplankton is adequately sampled. Requisite for the paired traps to capture nearly equal numbers of zooplankton is that zooplankton be nearly randomly dispersed or at least not badly overdispersed (Cassie 1971), or clumped, within the space scale of the traps. We will demonstrate from an experiment of repeated casts of the paired traps that, contrary to expectation (Cassie 1971; Hutchinson 1967, pp. 792–809), zooplankton were randomly dispersed or statistically underdispersed (evenly spaced) at this scale of microdistribution.

Moreover, we use propagation of error theory to demonstrate the effect of number of prey caught by the traps and the percentage of prey consumed on the accuracy of the results. From the experiment on zooplankton microdistribution and these statistical relations, we suggest that this method is feasible for studying *in situ* predation on zooplankton if the experimenter is careful to control experimental conditions so that a significant fraction of the prey is consumed. This conclusion is reinforced by statistical analyses of data from replicated experiments by Bowers & Vanderploeg (1982) on feeding of *Mysis relicta.*
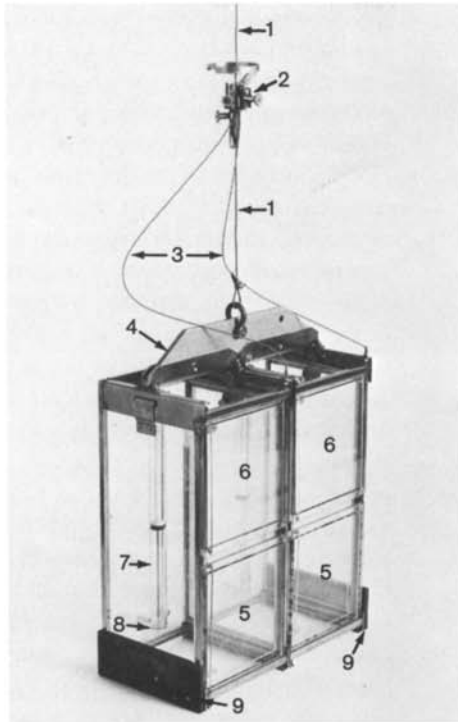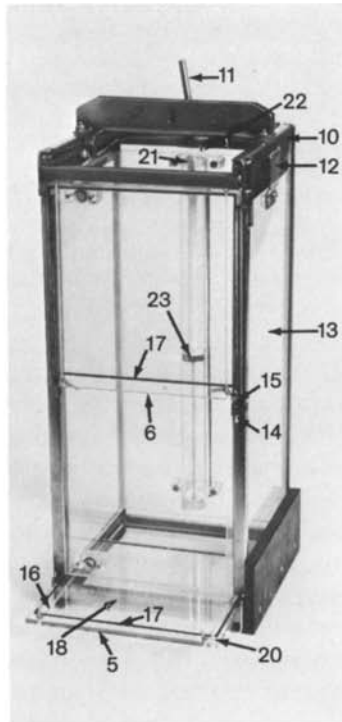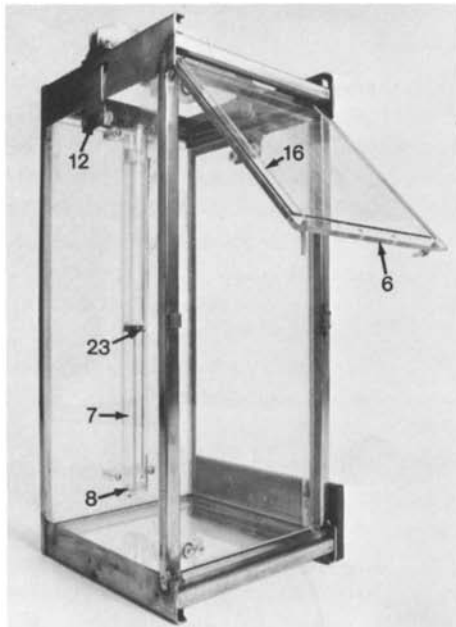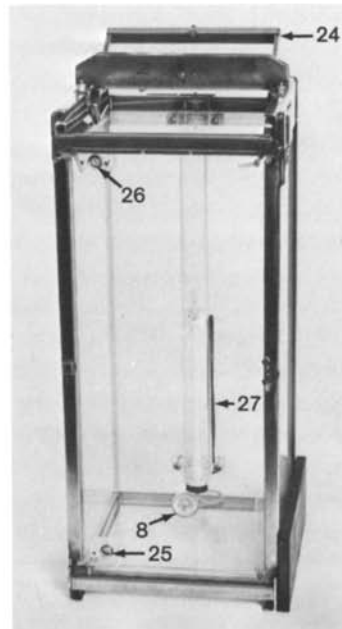
*Fig. 1(a-d).* The experimental apparatus and mechanics of trap closing. Numbered parts on figure are: 1 – hydro wire, 2 – rosette holding cable release push rods, 3 – cable release cord (detachable), 4 – detachable rack, 5 – lower shutter, 6 – upper shutter, 7 – 150-ml dispenser, 8 – dispenser bottom stopper, 9 – detachable brass weight, 10 – main frame (stainless steel), 11 – lifting pin (open position), 12 – Plexiglas box hanger, 13 – Plexiglas box, 14 – lower shutter release catch, 15 – upper shutter release catch, 16 – tension cord (surgical rubber tubing), 17 – rubber 0-ring, 18 – lower pressure frame, 19 – upper pressure frame, 20 – upper shutter trip pin, 21 – dispenser release, 22 – mainspring release, 23 – filling port for dispenser, 24 – mainspring latch handle, 25 – drain port, 26 – air vent port, and 27 – dispenser tension cord (relaxed position).

## Description of apparatus

Figure 1a shows the experimental apparatus, consisting of two 30-l plankton traps (each 23.4 × 23.4 × 54.4 cm inside dimensions) held together by a rack (4) at the top and a bolt at the bottom. In a typical experiment the apparatus, similar in principle to paired Gliwicz (1968) or Haney (1971) traps, is lowered to the depth at which the predator feeds, with the top and bottom of each of the traps open. A messenger striking the cable release push rods (2) causes the shutters (5 and 6), which lie close against the side of each trap when it is lowered, to seal off the top and bottom of each trap. Upon sealing the trap, predators are released from the 150-ml dispenser (7) into one of the pair of traps.

The ideal plankton trap (Patalas 1954; Schindler 1969) should have a large volume, be constructed of clear materials, move through the water without creating a great deal of turbulence, and close soon after reaching the sampling depth. The volume and dimensions of our trap, its general clarity, and the open top and bottom when lowered are similar to Schindler's (1969) ideal design for capturing zooplankton. A further stringent requirement of our trap was that the closed traps should have a perfectly watertight seal. This was required for our application because of the many hours the traps had to remain *in situ*. A water-tight seal would also be required if the traps were to be used for experiments with radioactively-labeled food (e.g., Haney 1971).

The mechanics of trap closing and sealing are revealed in Fig. 1b-d. The messenger first releases the lower shutter of a trap by opening a lower shutter release catch (14), which is barely visible in Fig. 1b. Upon release, the tension cord (16) on the outside surface of the shutter forces it to swing in an arc downward away from the lower shutter release and be drawn in between the space between the Plexiglas box (13) and lower pressure frame (18). In Fig. 1b the lower shutter is being drawn in between the space between the Plexiglas box and lower pressure frame by its tension cord (16). At this time there is ample space (~3 mm) between the Plexiglas box and pressure frame for low-friction sliding of the shutter. Upon closing of this shutter, the upper door trip pin (20) activates the upper shutter release catch (15), allowing the upper shutter to move through an arc as shown in Fig. 1c and be drawn in by its tension cord in a fashion similar to that

described for the lower shutter. Upon reaching the end of its travel, the upper shutter strikes the dispenser release (21) and mainspring release (22), which are most easily seen in Fig. 1b, emptying the 150-ml dispenser and releasing the mainspring. Figure 1d shows the mainspring latch handle (24) in its released position. At this time the trap is completely sealed because the mainspring is pressing the pressure frames, which in turn press the shutters against the Plexiglas box. A tight seal between the box and shutters is provided by 0-rings on the shutters. Figure 1d shows that the contents of the dispenser have been forced out by the plunger, which is driven by its tension band (27). The bottom stopper (8) of the dispenser can be seen lying at the bottom of the trap.

The above sequence of trap closing was necessary to assure that the contents of the dispenser would not be released before both doors were closed. The design of the traps is such that they will close even under conditions of considerable vertical motion caused by ship motion in waves. Under these conditions, the lower shutter door closes on the upswing of the trap and the upper shutter on the following downswing or on the pause before downswing. From a stable platform or in calm seas the trap closing sequence takes about 2 s after the messenger strikes the cable release push rods (2). Under conditions of vertical motion on the order of a meter per second or more an extra second may be added to the time required for the closing sequence. The
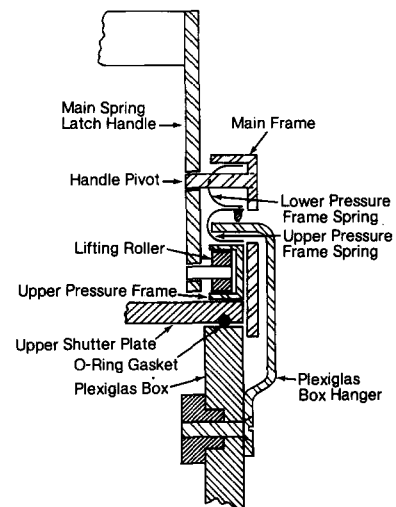


*Fig. 2.* Sectional schematic of trap pressure closing mechanism.

traps have been deployed from a small (20-m long) research vessel in wave heights up to 1.6 m. Although the traps will seal under conditions of considerable vertical motion, they will not seal if the ship drifts quickly, since towing of traps exerts a constant downward pressure on the upper shutter that prevents its closing. The trap closing sequence was monitored by feeling the vibrations sent up the hydro wire by the closing shutters. The shutters on both traps of a pair close almost exactly at the same time.

Figure 2 is a schematic drawing showing the relationship between mainsprings, pressure frame, shutters, and Plexiglas box. Note that the upper pressure frame spring, which has a lower spring constant than the lower pressure frame spring, is first compressed when pressing the mainspring latch handle, thus releasing the pressure on the upper shutter of a sealed trap first. Further depression of the mainspring latch handle lifts the Plexiglas box hanger (also shown in Fig. 1b and c) and compresses the lower pressure frame spring, thus releasing the bottom shutter. This design allows the investigator to open the top of a filled trap and add chemicals or predators, or do other manipulations without losing the contents of the trap through the bottom.

## Statistical considerations and direct evidence for underdispersed microdistribution of zooplankton

As noted above, the success of predation experiments of the kind advocated here depends strongly on the spatial distribution of zooplankton within the volume sampled by the traps. Distributions that fall within this space scale ($\sim$1 m) may be properly described as microdistributions (Cassie 1959). It also strongly depends on the proportion of available prey that the predator consumes in the experimental trap. Assuming for the moment that zooplankton are randomly distributed in space, we can make use of simple propagation of error theory (e.g., Bevington 1969) and Poisson (random distribution) statistics to show that we must allow the predators to eat a large fraction of the prey to obtain statistically meaningful results. Clearance rate is the parameter of interest because it is not only calculated routinely, but is also used to calculate feeding rate (Frost 1972) and selectivity coeffi-

cients (Vanderploeg & Scavia 1979a, b), the other parameters of interest.

Clearance rate is given by the expression modified from Gauld (1951):

$$F = Vln(C/Z)/tn \qquad (1)$$

where V = volume of the experimental container (30 l),

C = total number of zooplankton in the control trap (without predators) at the end of the experiment,

Z = total number of zooplankton in the experimental trap (with predators) at the end of the experiment,

t = time duration of the experiment, and

n = number of predators in the trap.

From propagation of error theory (e.g. Bevington 1969), the standard deviation of the clearance rate, $\sigma_F$, is

$$\sigma_F \cong V(\sigma_C^2/C^2 + \sigma_Z^2/Z^2)^{1/2}/tn, \qquad (2)$$

which implies that the coefficient of variation ($\sigma_F/F$) is

$$\sigma_F/F \cong (\sigma_C^2/C^2 + \sigma_Z^2/Z^2)^{1/2}/ln(C/Z). \qquad (3)$$

The assumption of Poisson statistics allows us to substitute C and Z, respectively, for $\sigma_C^2$ and $\sigma_Z^2$, resulting in

$$\sigma_F/F \cong (1/C + 1/Z)^{1/2}/ln(C/Z). \qquad (4)$$
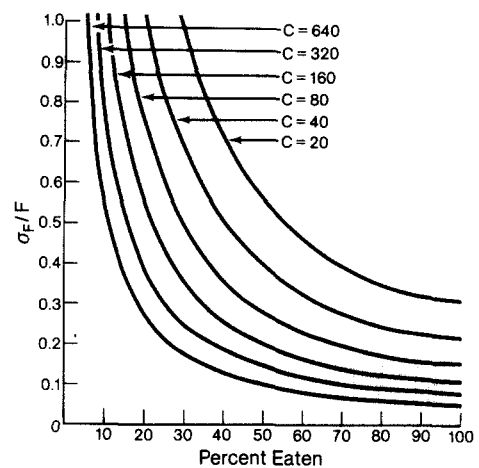


Fig. 3. Predictions of $\sigma_F/F$ as a function of percentage of prey eaten and number (C) of prey in control container. When C is interpreted as total count in a single control trap, $\sigma_F$ is standard deviation; if C is interpreted as total count in all N control traps in a replicated experiment, $\sigma_F$ is standard error.

*Table 1.* Comparison of paired traps A and B for 10 replicate casts made at the 5-m depth between 1100 and 1400 EDT on 25 September, 1979 from an unanchored ship 9.6 km west of Grand Haven, Michigan. The weather was calm and bright. All $\chi^2$ among cast values are higher than the P = 0.005 value. All $\chi^2$ within cast values are not significantly lower (P > 0.1) than expected for random distribution.

| Cast number | Calanoid adults | | Calanoid copepodids | | Cladocera | | Cyclopoid adults | | Cyclopoid copepodids | | Nauplii | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B |
| 1 | 111 | 128 | 380 | 369 | 110 | 98 | 91 | 85 | 225 | 191 | 807 | 789 |
| 2 | 21 | 15 | 75 | 101 | 31 | 42 | 25 | 32 | 155 | 170 | 239 | 227 |
| 3 | 19 | 26 | 229 | 240 | 114 | 121 | 33 | 40 | 307 | 285 | 425 | 420 |
| 4 | 30 | 34 | 220 | 210 | 87 | 95 | 25 | 20 | 185 | 210 | 330 | 335 |
| 5 | 80 | 74 | 327 | 311 | 152 | 147 | 81 | 84 | 140 | 160 | 718 | 736 |
| 6 | 26 | 39 | 130 | 116 | 58 | 65 | 37 | 44 | 222 | 233 | 278 | 301 |
| 7 | 35 | 30 | 201 | 219 | 92 | 101 | 31 | 40 | 170 | 160 | 304 | 327 |
| 8 | 40 | 35 | 235 | 240 | 123 | 117 | 45 | 39 | 205 | 207 | 340 | 320 |
| 9 | 42 | 37 | 120 | 125 | 113 | 109 | 35 | 22 | 196 | 209 | 232 | 259 |
| 10 | 40 | 43 | 145 | 140 | 120 | 113 | 30 | 27 | 135 | 121 | 235 | 209 |
| $\bar{X}$ | 44.4 | 46.1 | 206.2 | 207.1 | 100.0 | 100.8 | 43.3 | 43.3 | 194.0 | 194.6 | 390.8 | 392.3 |
| SE | 9.2 | 10.3 | 29.9 | 27.9 | 11.0 | 9.3 | 7.4 | 7.3 | 16.1 | 14.4 | 65.0 | 64.6 |
| $\chi^2$ among | 171.6 | 207.1 | 390.2 | 338.3 | 108.9 | 77.2 | 113.8 | 110.8 | 120.2 | 95.9 | 973.0 | 957.4 |
| $\chi^2$ within | 7.52 | | 6.70 | | 4.25 | | 8.05 | | 8.95 | | 6.16 | |

To illustrate the importance of letting the predators consume a large fraction of the zooplankton, the coefficient of variation ($\sigma_F/ F$) has been plotted as a function of the percentage of food eaten for different values of C in Fig. 3. C may also be interpreted at total counts in all control traps of a replicated experiment. In this case, $\sigma_F$ is the standard error. As can be seen from Fig. 3, the percent eaten must be greater than 50% at the lower values of C to get reasonable $\sigma_F/ F$ values. Note that it is theoretically possible to improve the $\sigma_F/ F$ ratio by replicating the experiment or increasing the size of the container. Replication is a better solution since it does not rely on the assumption of random distribution of zooplankton and because errors introduced from other sources, such as equipment failure and experimenter error, would be smoothed out by replication or would be at least revealed.

Heretofore, no experiments had been performed with large paired plankton traps to determine if the microdistribution of zooplankton is random. However, studies of Lauff (1953, cited in Cassie 1959) and Cassie (1959), which sampled small volumes of water (0.02 l and 1 l, respectively) over centimeter and meter space scales, suggested that zooplankton are clumped, that is, statistically overdispersed. Hutchinson (1967, pp. 792–809) in a review of data on horizontal distribution of zooplankton noted

there were few cases (e.g., Naber 1933; Langford 1938) of random distribution of zooplankton at any space scale. Most of these data were obtained from repeated casts of a single water bottle or plankton trap. If overdispersion is the case, variation in counts between our traps would be worse than predicted by Poisson statistics. That is, sample variance ($s^2$) between the two traps would be higher than the mean counts for the pair.

We therefore did a series of 10 casts of the apparatus to determine the size of $s^2$ relative to mean counts. The raw data from the replicate casts are shown in Table 1. All organisms captured in the traps were counted to avoid subsampling errors. Methods of concentrating and preserving the animals are described by Bowers & Vanderploeg (1982). Although the traps were usually used for experiments at night and at a depth greater than 10 m, we did the replication experiment under conditions of relatively high light intensity at 5 m. We reasoned this would be a more rigorous test of the apparatus since the zooplankton could use the visual as well as mechanical cues at this time. Examination of the data shows that, although concentration of captured zooplankton varied with time over the 3-h sampling period, counts in each trap for a given cast were quite close. Figure 4 shows, for each prey category, the sample variance of each pair in a
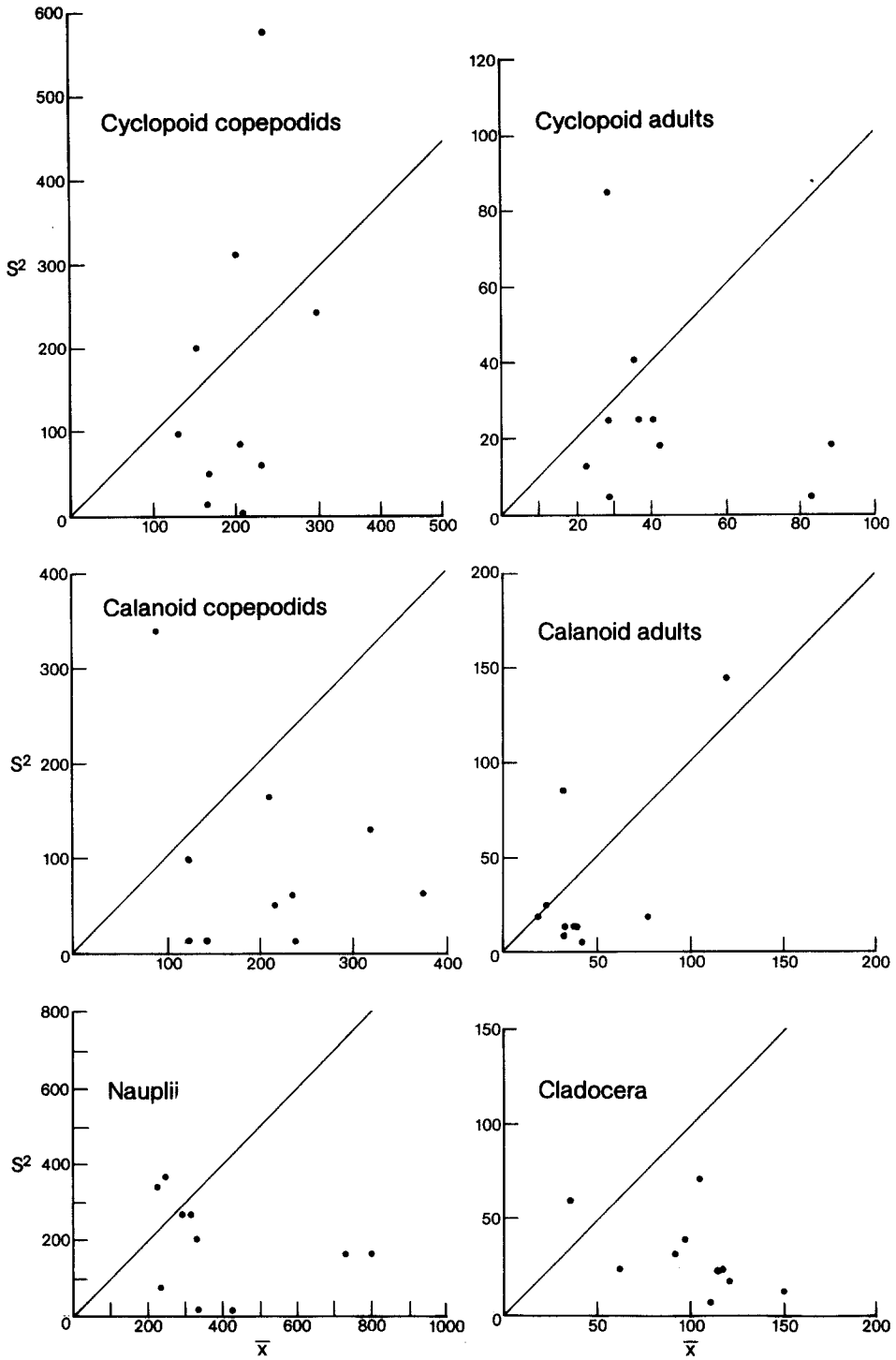
*Fig. 4.* Plots of s² vs. X̄ for different zooplankton groups.

cast plotted against its mean count. On the graphs for each group a line passing through the origin and having a slope of 1 is drawn in. Thus, points falling above the line represent overdispersion ($s^2 > \overline{X}$) and points falling below represent underdispersion ($s^2 < \overline{X}$). Since most of the points fall below the line, it appears that the zooplankton are underdispersed. This general underdispersion is especially evident for nauplii, Cladocera, and calanoid copepodids.

To evaluate these results further, $\chi^2$ tests of equality of variance and mean were preformed. A $\chi^2$ test (9 degrees of freedom) showed that variances between the paired traps were less than their means, but not significantly ($P > 0.1$), for all prey categories (see $\chi^2$ within, Table 1). To perform this test, $\chi^2$

for each cast of a pair of traps was calculated and the $\chi^2$ values summed (e.g., Snedecor & Cochran 1967, pp. 228–230). In contrast, $\chi^2$ values (9 degrees of freedom) obtained for the 10 separate casts of the traps indicated that the variance was very much higher (significant at the $P < 0.005$ level) than the mean (see $\chi^2$ among, Table 1). These data suggest existence of randomly dispersed or underdispersed zooplankton (at ~1-m space scale) within large patches. The variance among casts could have been caused by vertical migration or the ship's drifting.

## Statistical analyses of feeding experiments

Details on methods of deployment and use of the traps for studying *in situ Mysis* predation are given

*Table 2.* Percentage of prey eaten, clearance rates (F), and W's determined for two sets of traps activated at the 20-m depth at noon on September 27, 1979. Mysids were allowed to feed in the dark in an incubator set to ambient temperature (7 °C); $\sigma_F^- / \overline{F}$, which may be compared with SE/$\overline{X}$ of F, was calculated from average percentage eaten and total number of prey in both control traps using Eq. (4). Asterisks indicate indeterminate values.

| Prey group | C (Number · (30 l)⁻¹) | Z (Number · (30 l)⁻¹) | % eaten | F (1 · day⁻¹) | | W'$\sigma_F^-$/$\overline{F}$ |
|---|---|---|---|---|---|---|
| **Cladocera** | | | | | | |
| Set 1 | 186 | 101 | 46 | 14.66 | 1.00 | |
| Set 2 | 226 | 98 | 56 | 20.05 | 1.00 | |
| $\overline{X} \pm$ SE | 206.0 ± 20.0 | 99.5 ± 1.5 | 51.0 ± 5.0 | 17.36 ± 2.70 | 1.00 ± 0.00 | |
| SE/$\overline{X}$ | 0.10 | 0.02 | 0.10 | 0.16 | 0.00 | 0.12 |
| **Calanoid adults** | | | | | | |
| Set 1 | 31 | 36 | 0 | 0.00 | 0.00 | |
| Set 2 | 41 | 43 | 0 | 0.00 | 0.00 | |
| $\overline{X} \pm$ SE | 36.0 ± 5.0 | 39.5 ± 3.50 | 0.0 ± 0.0 | 0.00 ± 0.00 | 0.00 ± 0.00 | |
| SE/$\overline{X}$ | 0.14 | 0.09 | * | * | * | ∞ |
| **Cyclopoid adults** | | | | | | |
| Set 1 | 23 | 15 | 35 | 10.26 | 0.70 | |
| Set 2 | 19 | 20 | 0 | 0.00 | 0.00 | |
| $\overline{X} \pm$ SE | 21.0 ± 2.0 | 17.5 ± 2.5 | 17.5 ± 17.5 | 5.13 ± 5.13 | 0.35 ± 0.35 | |
| SE/$\overline{X}$ | 0.10 | 0.14 | 1.00 | 1.00 | 1.00 | 1.26 |
| **Nauplii** | | | | | | |
| Set 1 | 336 | 265 | 21 | 5.70 | 0.39 | |
| Set 2 | 341 | 280 | 18 | 4.73 | 0.24 | |
| $\overline{X} \pm$ SE | 338.5 ± 2.5 | 272.5 ± 7.5 | 19.5 ± 1.5 | 5.22 ± 0.49 | 0.32 ± 0.08 | |
| SE/$\overline{X}$ | 0.01 | 0.03 | 0.08 | 0.09 | 0.25 | 0.27 |
| **Calanoid copepodids** | | | | | | |
| Set 1 | 210 | 168 | 20 | 5.36 | 0.37 | |
| Set 2 | 195 | 172 | 12 | 3.01 | 0.15 | |
| $\overline{X} \pm$ SE | 202.5 ± 7.5 | 170.0 ± 2.0 | 16.0 ± 4.0 | 4.19 ± 1.18 | 0.26 ± 0.11 | |
| SE/$\overline{X}$ | 0.04 | 0.01 | 0.25 | 0.28 | 0.42 | 0.42 |
| **Cyclopoid copepodids** | | | | | | |
| Set 1 | 165 | 151 | 8 | 2.13 | 0.15 | |
| Set 2 | 179 | 129 | 28 | 7.86 | 0.40 | |
| $\overline{X} \pm$ SE | 172.5 ± 7.00 | 140.0 ± 11.0 | 18.0 ± 10.0 | 5.00 ± 2.87 | 0.28 ± 0.13 | |
| SE/$\overline{X}$ | 0.04 | 0.08 | 0.56 | 0.57 | 0.46 | 0.39 |

by Bowers & Vanderploeg (1982). In this section we do an error analysis of their feeding experiments. This analysis will be useful for testing the assertions derived from propagation of error theory and imposition of Poisson statistics. Two pairs of traps, deployed within 10 min of each other, were used for all experiments. The concentrations of prey in the control traps of the two pairs were fairly close (Bowers & Vanderploeg 1982). Thus, observed errors between the pairs can be compared with predicted errors.

Table 2 shows the results from a midday experiment with two sets of traps. Negative filtering rates, which are probably statistical artifacts in these experiments, were assigned zero values (Table 2: calanoid adults, set 2 cyclopoid adults). Note that it is theoretically possible for negative filtering rates to occur by *Mysis* feeding on other predators, causing an increase in certain prey in experimental containers. We assume this indirect effect is small because of great biomass of added *Mysis* relative to that of other zooplankton predators found in the traps and because of the short duration ($\sim$5 h) of the experiments. Selectivity was expressed by the selectivity coefficient W′, which was calculated by dividing the clearance rate for a prey by the highest clearance rate observed in that experiment. W′ is preferable to other commonly used selectivity coefficients because it is not biased by varying relative abundances of prey, amount of prey consumed, or number of prey categories (Vanderploeg & Scavia 1979a, b; Vanderploeg 1981). Moreover, when examining the relation between ingestion rate and food concentration, W′ is the weighting factor used for converting total food concentration to effective food concentration (Vanderploeg & Scavia 1979a).

Cladocera, having a W′ of 1.0, were definitely the preferred prey. The nauplii, cyclopoid copepodids, and calanoid copepodids all had values of W′ near 0.3. The calanoid adults, having a W′ of 0.00, were the least preferred prey. The W′ ± SE values of 0.35 ± 0.35 obtained for cyclopoid adults make it impossible to conclude from these data whether these prey are or are not preferred. To improve statistical results further, experiments of this kind were usually run for 3 or 4 days in succession. Clearance rates from one day to the next were usually quite close (Bowers & Vanderploeg 1982), and concentrations of zooplankton were not greatly different.
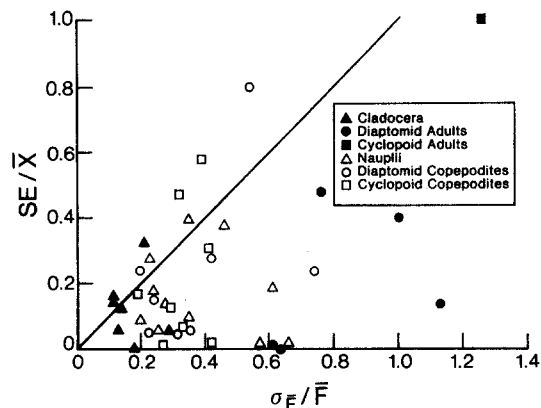


*Fig. 5.* Plots of SE/$\bar{X}$ vs. $\sigma_F/\bar{F}$ predicted from error propagation.

The values of SE/$\bar{X}$ for filtering rates generally reflect the trends predicted by $\sigma_F/\bar{F}$ (Table 2). It is obvious from Fig. 3 that the high SE/$\bar{X}$ values for clearance rates of cyclopoid adults result from low values of C. Interestingly, SE/$\bar{X}$ values of nauplii and calanoid copepodids were considerably lower than corresponding $\sigma_F/\bar{F}$ values. This may be caused by the underdispersion of these categories that was suggested by Fig. 3.

In Fig. 5, SE/$\bar{X}$ for filtering rates is plotted as a function of $\sigma_F/\bar{F}$ predicted by error propagation (Eq. 4) for all feeding experiments by Bowers & Vanderploeg (1982). Since most of the data fall below the 45° line, $\sigma_F/\bar{F}$ usually was an overpredictor of SE/$\bar{X}$. This pleasing result shows that the paired trap technique has broad practical utility since the errors were quite reasonable. Some of the overprediction could have resulted from approximations inherent in the propagation of error technique. Best results would be expected for small errors about the independent variables, that is, for small coefficients of variation. Since the coefficient of variation of C and Z are, respectively, 1/C and 1/Z (see Eqs. 3 and 4), best predictions from Eq. (4) would be expected for high zooplankton counts. Practically speaking this implies that predictions at lower values of $\sigma_F/\bar{F}$ would be more accurate. Since this model assumes Poisson statistics, these results corroborate the inference of random or underdispersed distributions we drew from the 10 casts of the paired traps. Without question, we would not have obtained these reasonable errors on clearance rates if there were appreciable overdispersion of zooplankton at the 1-m space scale.

## Discussion and conclusions

We have demonstrated that the plankton traps have the general features of an ideal plankton sampler and that each trap in a pair samples, within reasonable statistical limits, the same number of zooplankton. By means of the statistical tests, propagation of error, and the error analysis of the *Mysis* feeding experiments, we have shown that our method is feasible for measuring *in situ* predation in Lake Michigan.

Assuming that zooplankton in all lakes are not clumped within a space scale of ~1 m, the ultimate limiting factor of this method is the number of prey captured by the traps (Fig. 3), because amount of predation in the traps can be controlled by manipulation of the number of predators. The number of prey captured depends on the concentration of prey and volume of the traps. Paired Gliwicz (1968) or Haney (1971) traps would not have been suitable for experiments in Lake Michigan because their basic designs limit their volumes to ~5 l, which would not have contained enough zooplankton to get statistically reliable results. This same criticism would also apply to the original use of the Haney trap (1971) for measuring *in situ* feeding by herbivorous zooplankton with radioactively-labeled food. It is reasonable to conclude that our method, employing 30-l traps, would be suitable for lakes varying between eutrophy and oligo-mesotrophy. Still larger traps may be required for ultra-oligotrophic lakes like Lake Tahoe.

As noted above, our observations on underdispersed zooplankton run counter to the generalization that zooplankton will be overdispersed at all space scales (Cassie 1959, 1971; Hutchinson 1967). Cassie's conclusion for overdispersion of microdistributions of zooplankton was drawn only from the results of Cassie (1959) and Lauff (1953). The experiments of Cassie (1959) and Lauff (1953) differ from ours in two important respects. First, they used much smaller samplers, which may have introduced artifacts from zooplankton escapement or orientation to the sampler. Second, their experiments were not performed in an open-water, relatively featureless environment as ours were, where there would be few small-scale environmental cues for plankton orientation other than vertical gradients in light intensity. Cassie's (1959) experiment was done at the sea surface, and Lauff's in a pond.

The results of our experiments of 10 replicate casts of the paired traps are in a sense analogous to Landford's (1938) results for a comparison of 10 replicate casts of a single water bottle at one station with single casts made at each of 10 stations along a 1.2 km line. These two cases are described in Hutchinson's (1967) analysis as 'close' and 'distant.' The plankton was less ovedispersed at the single station than over the space scale of the separate stations. In the case of our experiment with the paired traps, the pair of traps within a cast sampled the same small volume of water while the separate casts sampled more widely separated water volumes. Our data suggest that it is possible that others have not often observed random or underdispersed distributions of zooplankton from repeated casts of a single large sampler at a single station because they were probably sampling widely spaced parcels of water during the sampling interval. Considering the excellent replication between paired traps that was maintained under conditions of great variability among casts and the low standard errors obtained for clearance rates, it seems likely that random dispersion or underdispersion may be a common phenomenon for space scales of ~1 m. This conclusion should be tested by further work with paired or multiple traps.

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