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Bosmina remains in Lake Washington sediments: Qualitative heterogeneity of bay environments and quantitative correspondence to production¹

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Abstract

Bay environments differ in productivity and species composition from open waters. Transects of surface sediments in Lake Washington (Seattle) reveal significant morphological gradients in the small pelagic cladoceran *Bosmina longirostris*. In all bays examined, these bosminids range from shorter featured clones nearshore to longer featured clones offshore. However, because bays constitute such a limited areal extent of the lake (4.9%), only 2.3% of remains in midlake sediments came from bay populations. A core taken from midlake waters indicates nearly uniform long-featured morphology of offshore *Bosmina* over the past 80–125 yr. The localized deposition of remains in bays underscores that biodiversity surveys of large lakes need to include bays in addition to open-water samples.

Clarifying how abundant cladoceran remains are produced, transported to, and preserved in sediments is crucial for interpreting historical sequences. A simple vertical model, derived from molting and death schedules, accurately predicts relative seasonal fluxes for remains at a midlake site ($r = 0.94\text{--}0.95$). However, the absolute flux is low, <7% of the expected rate, suggesting substantial loss through decomposition and fragmentation. Use of abundant cladoceran microfossils to reconstruct species-specific or general secondary production requires careful calibration studies, although the potential dividends are great.

Most of the lakes scattered across vast glaciated regions are discontinuous water bodies that create landscapes analogous to fields of islands. Within these lakes, physical, chemical, and biological interactions (e.g. colonization, predation, and competition) combined to determine the composition of communities through time. Unfortunately,

ly, the strength of past biotic interactions cannot be tested directly from the fossil record. Yet if past species leave a sensitive record of morphology and abundance in lake sediments, that information could be invaluable for paleoecological reconstructions. The data would be lengthy and continuous and could address important questions about present and past relationships between and within lakes, namely species distributions, colonization rates, rates of evolutionary change, and species diversity. Trophic questions could examine production estimates and top-down impacts on food webs (Hrbáček 1969; Kerfoot 1974, 1981; Kitchell and Kitchell 1980; Carpenter and Leavitt 1990).

¹ This paper is dedicated to the memory of Edward Deevey, a pioneer in the study of cladoceran fossil remains.

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Before addressing broader questions we first need to understand certain processes that determine production and distribution of remains. In both large and small lakes, two major concerns of paleoecologists are the spatial sources of remains (i.e. from littoral or pelagic habitats) and the temporal preservation of remains relative to production. Midlake samples from small north-temperate lakes often include high percentages of littoral species because seasonal mixing of the water column causes sediment resuspension and redistribution (e.g. Mueller 1964).

The consequences of scaling up are unclear. In larger lakes we might expect bay and littoral organisms to constitute a smaller fraction of total remains because these environments occupy a smaller spatial area and because remains must be transported over greater absolute distances; however, the higher energy environment of larger lakes increases the potential for large-scale lateral transport.

Another necessary consideration is that of preservation. Remains of relatively few organisms preserve well in lake sediments. Thus, if the fossils in lake sediments record a story, it is censored, with the text altered by several well-known agents: mechanical forces that abrade or redistribute items; chemical gradients that redissolve minerals; planktonic or benthic organisms that consume, fragment, and digest potential remains; bacteria and fungi that decompose whatever escapes macroorganisms. The joint action of these mechanical, chemical, and biological agents usually ensures recycling of most organically produced materials. Only a small fraction of the total organic matter produced in lakes manages to become sealed in bottom sediments.

The yearly loss of organic production to deep sediments was once thought to be more substantial. For example, Livingstone et al. (1958) estimated that ~20% of the total organic production of eutrophic Linsley Pond, Connecticut, became sealed in the sediment. These preliminary findings were slight overestimates for two reasons: resistant allochthonous material (i.e. items manufactured outside the lake, then washed in) may constitute a modest fraction of the organic matter found in small-lake sediments (Mackereth 1966) and redeposition of old sediment in sediment traps often results in spurious, exaggerated estimates of yearly fluxes (Davis 1968, 1973). More recently, detailed studies of North American oligotrophic-mesotrophic lakes suggest that between 11.5 and 16.9% of organic production is lost to the sediment on a yearly basis (Wetzel 1983; Wetzel et al. 1972; Jordan and Likens 1975). Clearly, with this small fraction, only the parts of organisms that are durable enough to withstand normal conditions of diagenesis and sedimentation contribute substance to lake records.

Although biased, the organic fraction in sediments often contains abundant exines of pollen grains, diatom frustules, and the chitinous exoskeletons and mandibles of many microcrustaceans and insects. In the past, this piecemeal information has allowed partial, yet valuable, reconstructions of lake histories. However, many of the attempts at reconstruction are a posteriori inferences suggested by patterns of deposition, not quantitative studies directly calibrated by population dynamics. Detailed quantitative studies of remain production, redistribution, decomposition, and sedimentation are rare (*but see* pollen studies of Davis 1968, 1973; Davis et al. 1984; Pennington 1973; diatom studies of Pennington 1943; cladoceran studies of Deevey 1964; Kerfoot 1981). Unraveling the relationship between production and preservation of remains and calibrating the process seems an essential step toward developing a predictive, experimental approach to paleoecology. Moreover, microfossil records offer cheap,

available historical perspectives on the time-course of ecological and evolutionary events. Toward that end, we must span the gap between production studies of living populations and sediment analysis.

A preliminary approach to the dynamic problem of quantifying fluxes consists of three steps: calculating production rates for remains, comparing these estimates against accumulation rates in sediment collectors suspended near the sediment-water interface or at various depths in the water column, and comparing catchment totals with calculated net accumulation rates from dated sediment cores (Kerfoot 1981). Previous work in Lake Washington (Seattle) suggested that it could be a prime site for investigating bay-open water relationships and flux dynamics. Ecological studies in Union Bay showed that selective removal by predatory copepods in offshore environments favored long-featured clones of the small cladoceran *Bosmina longirostris*, whereas competition and fish foraging in nearshore environments favored short-featured clones. Along the marginal lily pads of the bay, the fish depressed predatory copepod densities, maintaining a gradient in copepod predation (Kerfoot 1975, 1977; Kerfoot and Peterson 1979, 1980). Since *Bosmina* is known to preserve well in sediments (Deevey 1964; Edmondson 1969), this property opened the possibility of sediment studies. During the 1970s and 1980s, Edmondson (Edmondson and Allison 1970; Edmondson 1991) further discovered finely varved sediments in the deep central trough of Lake Washington. The fine laminae of these sediments revealed clay layers, indicating meltwater input during early spring, followed by diatom layers representing late spring and summer plankton. As opposed to prior sediment studies in Frains Lake, Michigan (Kerfoot 1981), Lake Washington offered a deep-water environment in which sedimentation was relatively undisturbed by vertical resuspension, creating an opportunity for detailed historical reconstructions.

In the following account, I examine the spatial and temporal patterns of *Bosmina* remains in Lake Washington sediments. The morphology of remains from inner sediments of bays are contrasted with remains from open-water sites. A simple model, derived from molting and death schedules, predicts the absolute flux of *Bosmina* remains falling through a restricted column of water in the center of Lake Washington. This prediction is then compared with actual fluxes of remains in a deep sediment trap.

Methods and materials

The initial investigation focused on two aspects of remains: the spatial patterns of *Bosmina* morphology along transects from bays into open offshore waters and the quantity and quality of exoskeletal remains produced in the central region of the lake. The seasonal morphology of living *Bosmina* populations in Union Bay and at open-water sites has been described previously (Kerfoot 1975; Kerfoot and Peterson 1979, 1980). As a check of morphological representation in sediments, remains were re-

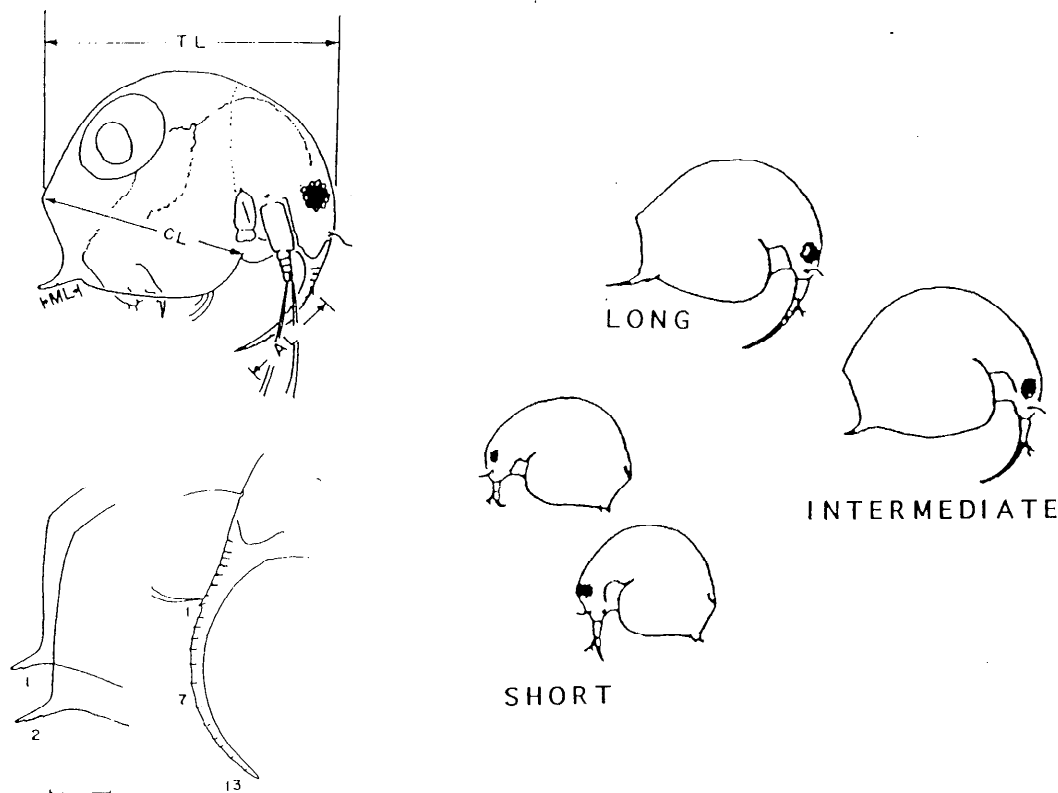


Fig. 1. Morphological measurements of *Bosmina* and clonal appearance. Measured features include carapace length (CL), mucro length (ML) and suture count (below), and antennule length (AL) and segment count (below). To the right are long-featured offshore clones, intermediate length clones, and two varieties of the very short-featured clones found in Union Bay. The hooked antennule variety is termed *cornuta* by Edmondson (1959), whereas the stubby, straight variety is termed *brevirostris*.

moved from short cores. These are the first descriptions of *Bosmina* morphology from Lake Washington sediments, although earlier studies have remarked on the presence and density of remains (Edmondson 1969, 1991).

Bay surface sediments—To compare sediment samples with previously detailed surveys of living populations (1972–1976; Kerfoot and Peterson 1980; Manning et al. 1978), I selected sediment samples taken in summer 1976 along embayment transects. The samples were taken by two methods. In shallow waters, a hand-held Plexiglas coring tube (4.5-cm i.d.) was gently pushed into surface sediments, then corked and extracted. In deeper waters, a 95-mm-diameter automatic piston corer was lowered and released (see Shapiro et al. 1971; Griffiths and Edmondson 1975). The top centimeter of surface sediments was suctioned off by syringe, boiled with 10% KOH in a water bath for 20 min to deflocculate the organic component, centrifuged, and rinsed with water. The supernatant was decanted, 10% HCl was added to neutralize the base, and the entire sample was stained with Eosin Y to highlight chitinous remains. Random fractions were pipetted into 50% glycerin-water drops on a glass slide, then covered with a glass coverslip.

Measurements were taken under a Zeiss Universal at 500 \times . Features measured on all individuals included car-

apace length (because carapaces and head shields disarticulate during decomposition), number of mucro sutures, length of mucro, number of antennule segments, and length of antennule (Fig. 1). The countable variables, sutures and segments, describe the number of cell boundaries along the mucrones and antennules. In Lake Washington, there is a simple, almost linear, relationship between the number of cells that form the structure and the length of the structures in the first instar young (Kerfoot 1975). More detailed descriptions of these characters and measurements are given by Kerfoot (1987).

For continuous variates (carapace, mucro, and antennule lengths), a one-way ANOVA tested the significance of site differences along surface transects and between depth samples in cores. Prior to tests, variates were checked for homogeneity of variance (Bartlett test). Logarithmic transformation was routinely performed in ANOVA tests for comparison with tests using untransformed variables. However, log transformation failed to improve ANOVA results. Tukey's HSD multiple comparisons test was used to designate significant departure groups.

Careful procedures are important when dealing with fossil assemblages and with the range of variate means found in cyclomorphic features. Although many of the variates are distributed normally or log normally, remains

in sediments represent seasonally and spatially integrated samples. Moreover, a simple logarithmic transformation applied to measurements from living populations tends to overcorrect the data (Kerfoot 1988). For detection of heterogeneity, specific descriptive techniques (e.g. box plots) were used to highlight the incidence of outliers. All statistical tests were performed on SYSTAT version 5.0 (Wilkinson 1989).

Certain variables differed more than others in spatial and temporal samples. To quantify and summarize the magnitude of intercharacter responses, I calculated three separate measures: the amount of proportional change (%) along transects, the transect response expressed in standard deviation units, and the F -value in the one-way ANOVA. The ANOVA test indicated the strength of between- vs. within-station variance and was used for significance testing but was necessarily restricted to continuous variates because of statistical test requirements. A χ^2 test of homogeneity was used to determine significant heterogeneity for meristic variables.

Deposition model construction—To investigate production relative to deposition, I constructed a model to predict the number of remains produced per unit time, then compared that predicted estimate with observed counts from sediment traps and cores. The model required knowledge of animal densities and egg ratios, which came from field collections, and of molting schedules, which came from laboratory experiments.

Zooplankton were sampled weekly from the lake with a calibrated Clarke-Bumpus sampler as a part of W. T. Edmondson's long-term zooplankton sampling effort (Edmondson and Litt 1982). Duplicate samples were taken with No. 10 and 20 mesh nets from three continuous depth strata at the central station: 0–10, 10–20, 20–60 m. *Bosmina* and its eggs or embryos were counted in plastic partitioned trays (Edmondson and Winberg 1971) to obtain estimates of densities (expressed as No. liter⁻¹) and egg ratios for each of the sampled strata.

For a cohort, estimating the number of remains produced requires two subtotals because exoskeletons come from two sources—dead individuals and shed exuviae. Hence, the total remains per generation (R_g) equals the sum of the instar-specific mortality (mortality rate M_x times the cohort population size (N_x) to give the dying individuals or corpses per instar increment, where x = instar) and the instar-specific exuvial production (molting or shedding rate S_x times the cohort size to give the molts or shed exuviae per instar), because each individual that survives an instar contributes a single exuvium (Kerfoot 1981):

$$R_g = \sum N_x(M_x + S_x). \quad (1)$$

In practice, assessing precise instar-specific survivorship or mortality schedules for cohorts in natural zooplankton populations is exceedingly difficult. However, crude death rates can usually be calculated from the egg-ratio dynamics of natural populations by the formulas of Paloheimo (1974), and molting rates can be estimated from temperature-dependent schedules.

In the Paloheimo method, emigration and immigration are ignored, age distributions are assumed constant, and population growth is described by the instantaneous equation $N_t = N_0 \exp(rt)$. If the average number of eggs per female (the egg ratio E), the duration of egg development (D), and the observed rate of population growth (r) are all known, then the instantaneous birth (b) and death (d) rates of the population can be calculated because $r = b - d$. Because the components $r = (\ln N_t - \ln N_0)/(t - t_0)$ and $b = [\ln(E + 1)]/D$, then by difference

$$d = \frac{\ln(E + 1)}{D} - \frac{\ln N_t - \ln N_0}{t - t_0}. \quad (2)$$

In nature, the molting rate is closely tied to the developmental duration of eggs and the interval between births, because the exuviae are shed in near synchrony with the birth of young. In this respect, the instantaneous molting rate is essentially equivalent to the solution for an egg ratio of 1

$$S = \frac{\ln(1 + 1)}{D} = \frac{0.693}{D}$$

because each surviving individual produces an exuvium at each instar interval. A short-interval finite approximation, based on laboratory-derived values was used to estimate the instantaneous molting rate of field populations.

In the laboratory, culture experiments provided the temperature-dependent molting schedules and the estimate of developmental duration for egg hatching. The bosminids were brought into the laboratory from plankton tows, placed in individual small beakers or depression cells in a Scherer environmental chamber (14:10 L/D cycle) and fed *Chlamydomonas*. The average instar duration was determined by fitting a least-squares regression line to the log-log plot of these and similarly derived data (see figure 9 of Kerfoot and Peterson 1979 and figure 7 of Kerfoot 1981). The specific regression used here was

$$\log_{10} D = -1.618 \log_{10} T + 2.432. \quad (3)$$

D and T are molting duration and temperature.

Temperature, *Bosmina* density, instar duration, and molting and death rate estimates were tabulated for weekly intervals through 1972. Of the two demographic estimates (i.e. d , r), death rate was the least precise, largely because of indirect calculation. Death rate estimates were derived by difference and are known to be extremely sensitive to small sample sizes (DeMott 1980; Keen and Nassar 1981; Taylor and Slatkin 1981).

Because temperature varies with depth in the water column, the total production of remains was calculated two ways: as a function of mean *Bosmina* density and mean temperature for the entire water column, appropriate for individuals that migrate between strata (average individual method), and as a summation of production for the three depth strata (0–10, 10–20, 20–60 m), appropriate for individuals that stay in the water column (nonmigratory individual method).

The production model contained several other assumptions. The model assumed that preservation was

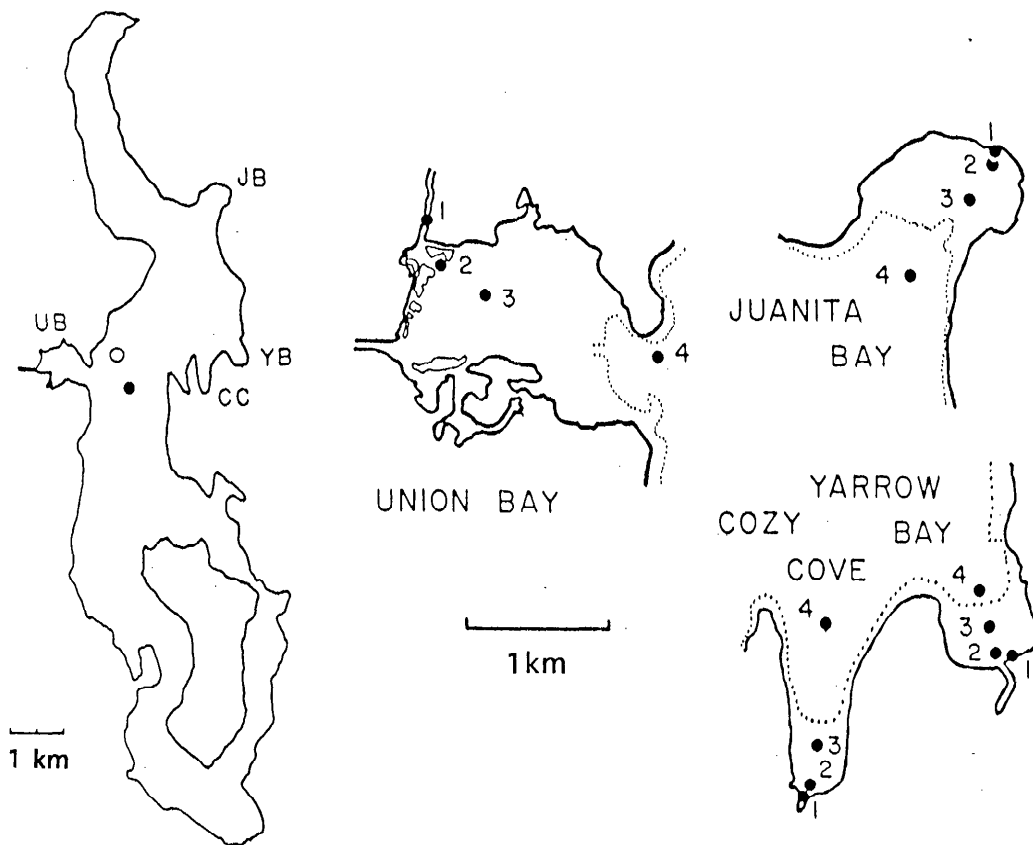


Fig. 2. Sediment sampling sites in Lake Washington. Outline map of the lake indicates positions of bays (Union Bay—UB; Juanita Bay—JB; Yarrow Bay—YB; Cozy Cove—CC), Evergreen Bridge sediment traps (●), and Webster Point core (O). Enlargements of the bays with the sites of surface sediment samples along transect lines are shown on the right. Dotted depth contour is ~6 m.

complete; that there was no supplemental horizontal or vertical influx (from density currents, resuspension); that molting schedules in nature matched laboratory-determined rates; that all categories of remains (carapaces, head shields, exuviae, and dead animals) settled rapidly, i.e. that exuviae (molted exoskeletons) settle in the same way as dead individuals; and that sediment traps were 100% efficient at capturing items. Under these conditions, true quantitative preservation could be evaluated by comparing estimated weekly production against the observed trap catches.

In terms of sediment dynamics, Lake Washington has two major advantages over a previous attempt at calibration (Frains Lake, Michigan, Kerfoot 1981). Resuspension of sediments, a problem in Frains Lake, is minimized by two properties of Lake Washington: the central basin is deep with steep walls, so that mixing resuspends and redistributes little sediment, and shallow bays make up a small fraction of the bottom surface (Gould and Budinger 1958).

An important additional consideration in Lake Washington is that zooplankton population dynamics have been studied for an extensive period of time. Edmondson and his associates have monitored zooplankton abundances and maintained sediment traps for >30 yr, providing one of the best long-term records in North America (e.g. Ed-

mondson and Litt 1982). Although my eventual intent is a long-term study, I focus here on a single year in the sequence 1972 to illustrate and explore what can be calculated.

Sediment trap records—Remains and sediment were collected in inverted small-neck polyethylene bottles (height-to-trap diameter aspect ratio equaled ~2.8). The bottle bottoms were removed and two bottles each were inverted and hung from wires at 30- and 50-m depths from the Evergreen Point Bridge (Fig. 2, see also Edmondson and Allison 1970). The 4-liter polyethylene bottles tapered to a small neck and screwcap. Every 7–14 d, depending on the series, the bottles were hauled gently to the surface, their caps removed, and the contents drained and washed into collection vessels. The empty bottles were then returned to the water. In this manner, a continuous, albeit quantized, record of sediment accumulation was kept throughout the year. Here, the reported counts come exclusively from one of the two 50-m trap sets (50-1)—a set that contained a complete record throughout the year.

Once in the laboratory, the contents of the polyethylene bottle traps were allowed to settle, then the total in a single trap was split into two approximately equal fractions. One fraction was analyzed for weights and chem-

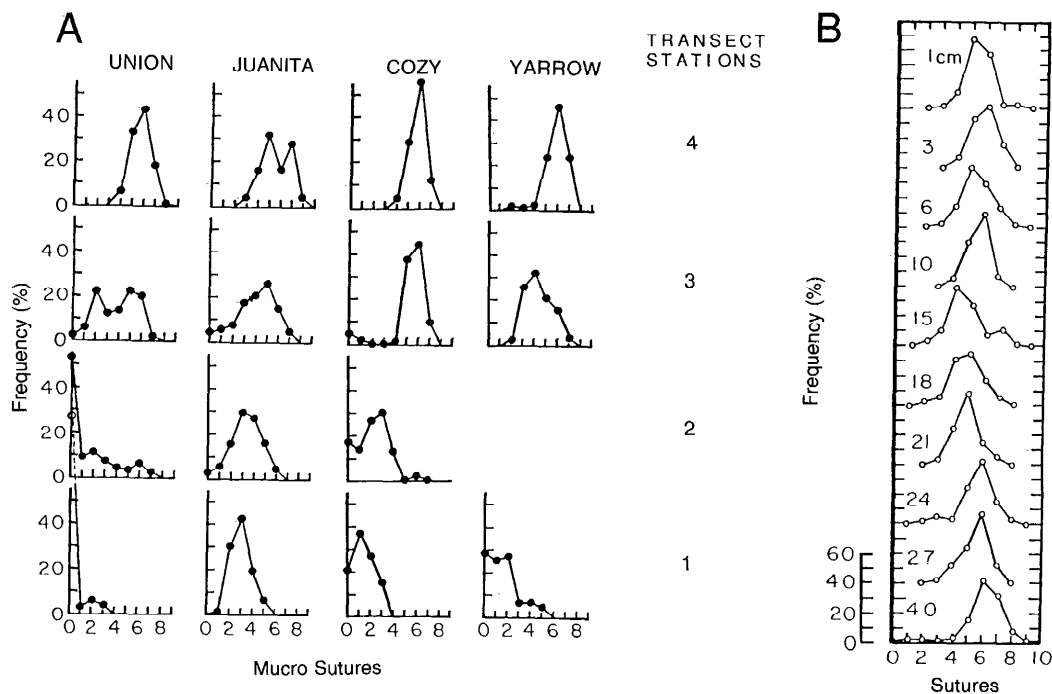


Fig. 3. Morphology of countable characters at bay transect and midlake core sites. A. Frequency distributions for micro suture counts from inner bay (Sta. 1, bottom) to outer bay sites (Sta. 4, top). Unfortunately, no surficial sediments were recovered at YB station 2. B. Frequency distributions for micro suture counts in the Webster Point core plotted vs. depth. The means, ranges, and standard deviations for samples are listed in Table 1.

istry (Edmondson and Winberg 1971), and, the other was scanned under a binocular scope ($100\times$) for *Bosmina* carapaces and head shields, *Diaphanosoma* mandibles, and other zooplankton remains. Here, results from only the *Bosmina* remains are considered.

Sediment cores—Deep-water remains were examined primarily in core 81-D, taken at 57-m depth east of Webster Point on 4 October 1976 (Fig. 2). The core was taken with a 95-mm-diameter automatic piston corer (see Shapiro et al. 1971; Griffiths and Edmondson 1975). Extruded sediment was cut into 1-cm slices and treated the same as surface sediments (see bay surface sediments). Preliminary subsampling consisted of stirring the sample, then pipetting between 1/100 and 1/10 of the suspended material onto a counting tray grid for tabulation of intact carapaces and head shields. However, for actual morphological measurements and fragmentation studies, pipetted subsamples of known volume were transferred to 50% glycerin/water solution on a glass slide, covered with a coverslip, and scanned under $125\times$ (Zeiss Universal compound microscope). A few unprocessed samples were also scanned at $60\times$ to compare with the dissection scope magnification. Measurements also followed identical procedures for surficial samples. Remains in two additional deep-water cores (one east of Madison Park, another west of Yarrow Bay) were also checked for *Bosmina* morphology, although not with the detail devoted to 81-D. Some samples from the Madison Park core are included in the tables.

Results

Spatial patterns: Bay surface transects—The transects ran down the middle of four of the largest bays in Lake Washington (Fig. 2; Union Bay, Juanita Bay, Cozy Cove, and Yarrow Bay). In all of these bays, *Bosmina* exhibited highly significant morphological gradients that ranged from shorter featured forms near shoreline lily pads (Sta. 1) to longer featured forms found in deeper, open waters (Sta. 4). Differences in the morphological gradients were evident between bays. Carapace length gradients were weak in Union and Yarrow Bays, whereas gradients for micro and antennule lengths were most pronounced in Union Bay and Cozy Cove (Table 1, Figs. 3 and 4). Body length was the least sensitive variable, with transect increases ranging between 9 and 55% (0.4–2.5 SD), whereas micro length (43–217%; 1.7–4.7 SD), micro sutures (80–2,058%; 1.8–4.5 SD), antennule length (30–139%; 1.3–4.6 SD), and antennule segments (17–49%; 1.1–3.2 SD) all showed substantially greater increases.

When a simple one-way ANOVA (within-station vs. between-station variance) was applied, all continuous characters (carapace, micro, and antennule lengths) showed highly significant increases in feature lengths from the inner shallow to the outer deep bay margins, although carapace length increases were less than those of micro or antennule lengths. *F*-values ranged from 4.9 to 47.1 for carapace length, 14.7 to 214.5 for micro length, and 19.0 to 209.5 for antennule length. The results of Tukey's HSD pairwise comparisons (continuous variates) for spe-

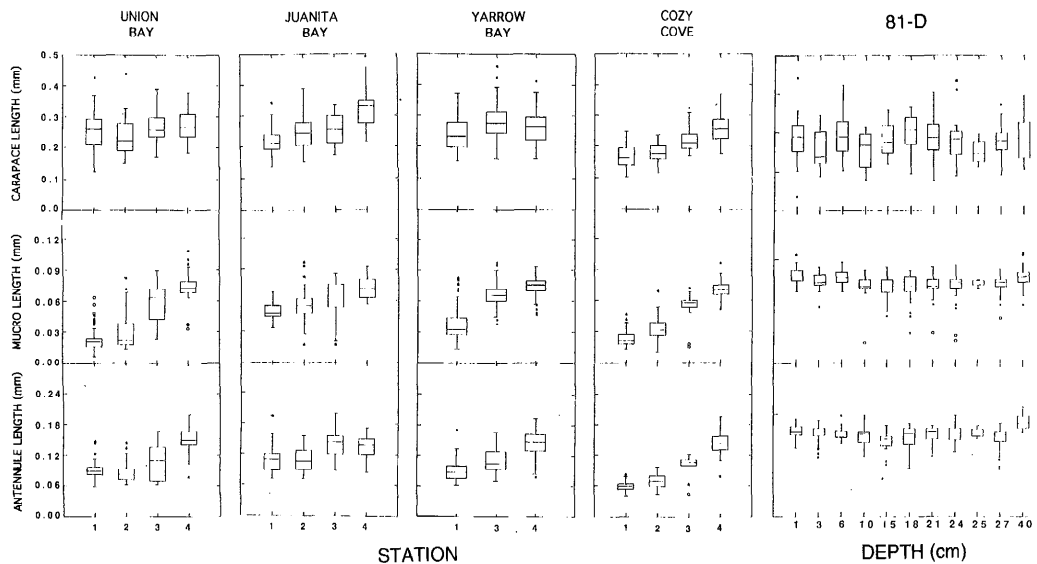


Fig. 4. Morphology of continuous variables at bay transect and midlake core sites. Box plots describe trends for carapace, micro, and antennule lengths. The box plot gives the median, first and third quartiles, "adjacent" and outside observations. The adjacent (●) values lie within four quartiles of the median, whereas outside (○) values lie beyond four quartiles (Olson 1987). Values for carapace, micro, and antennule lengths are also plotted for selected strata down to 40-cm depth. The means, ranges, and standard deviations for stations are given in Table 1.

cific transects and characters are shown in Table 1. Box plots emphasize the greater normality of carapace length and show several outliers for micro and antennule lengths (Fig. 4).

χ^2 tests of homogeneity on meristic characters (micro sutures, antennule segments) also confirmed strong patterns. Significant departures from homogeneity ($P < 0.05$) were found for micro suture counts along all bay transects ($P < 0.000$). Antennule segment counts also showed significant departures (Cozy Cove, $P < 0.000$; Juanita Bay, $P < 0.015$; Union Bay, $P < 0.000$; Yarrow Bay, $P < 0.000$).

A final consideration is dispersion. Because remains are subject to seasonal integration and perhaps lateral transport, are the morphological characters in remains more heterogeneous than those sampled from natural populations? A first step in answering this question involves comparing coefficients of variation (where $C.V. = \text{sample SD}/\text{mean}$).

Coefficients of variation from 24 seasonal population samples in Union Bay were compared with those from surficial sediment samples. Coefficients of variation for carapace length (range 13.9–30.0%) and micro length (24.2–61.3%) from living populations fell close to values from sediments (CL, 18.3–23.3%; ML, 28.8–56.6%), whereas those for antennule length (8.4–20.2%) from living populations were lower than those from sediment (17.6–33.3%).

In summary, the station sediment samples document strong morphological gradients for remains along all the embayment transects. The sample mean and dispersion tests suggest that the spatial morphological gradients found in natural populations of *Bosmina* are preserved faithfully in the sediments.

Webster Point core record—Remains from an open-water sediment core (81-D, Webster Point) revealed predominantly long-featured morphology both at the surface and deeper. Almost all remains came from long-featured individuals and there was generally great uniformity throughout the core (Figs. 3 and 4; Table 1). Almost all carapaces and head shields had the long mucrones and antennules characteristic of present open-water populations (Kerfoot 1975). Moreover, the mean and modal lengths of mucrones and antennules corresponded closely with offshore phenotypes. Because estimates of deposition rates average between 3.2 and 5.0 mm yr⁻¹ (Griffiths and Edmondson 1975), the interval probably covered a span of 80–125 yr.

Only rarely did the sediment samples include distinctive types of head shields assignable to inner bay populations (e.g. ones with stubby mucrones or the hooked *cornuta* antennules of some individuals characteristic of lily pad margins in Union Bay, Fig. 1). These occasional morphological measurements fell outside the spread expected from strictly normally distributed variates (outliers in box plots, Fig. 4). The most extreme cases were short micro carapaces found primarily at middepth. Of 692 remains examined in core 81-D, only 16 (2.3%) were clearly of inshore morph derivation.

Detailed comparisons between remains from the upper 40-cm sections indicate the relative consistency of offshore morphology (Fig. 4). In the ANOVA test, F -ratios for characters were very low relative to transect values: carapace 1.6, micro 5.5, and antennule 5.7. Carapace length differences were not significant between layers, but micro and antennule variables were significant, but weak (Table 2). χ^2 tests on micro suture tallies from both cores (Webster Point, Madison Park) showed significant het-

Table 1. Morphology across bay transects and in cores 81-D and Madison Park. Significance ($P \leq 0.05$) of continuous variates indicated by Tukey's HSD multiple comparison test. Entries give mean (SD), range, and sample size. Core samples arranged by depth in centimeters.

Sta. or depth	Carapace length	Mucro		Antennule	
		length	sutures	length	segments
Cozy Cove					
No. 1	0.167(0.035) 0.11-0.25 56	0.023(0.007) 0.01-0.05 56	1.4(0.9) 0-3 56	0.059(0.009) 0.04-0.08 41	9.4(1.0) 7-12 41
No. 2	0.175(0.027) 0.12-0.24 52	0.031(0.011) 0.01-0.07 53	2.2(1.4) 0-6 53	0.068(0.014) 0.04-0.10 40	10.2(1.2) 8-14 40
No. 3	0.220(0.036) 0.17-0.32 32	0.056(0.012) 0.02-0.07 32	5.3(1.4) 0-7 32	0.099(0.027) 0.04-0.12 9	12.1(2.1) 9-15 9
No. 4	0.259(0.049) 0.18-0.37 22	0.070(0.010) 0.05-0.10 35	5.6(1.0) 3-8 36	0.141(0.021) 0.08-0.20 45	14.1(1.4) 12-17 22
Juanita Bay					
No. 1	0.218(0.040) 0.14-0.34 57	0.051(0.009) 0.03-0.07 57	3.0(1.0) 1-5 57	0.109(0.025) 0.07-0.19 40	11.6(1.6) 9-16 42
No. 2	0.0251(0.057) 0.16-0.39 51	0.056(0.014) 0.02-0.10 51	3.4(1.4) 0-6 51	0.108(0.022) 0.07-0.16 44	11.6(1.7) 8-17 42
No. 3	0.257(0.049) 0.17-0.34 51	0.063(0.018) 0.02-0.09 51	4.1(1.7) 0-7 51	0.140(0.027) 0.09-0.20 50	12.8(1.9) 9-17 49
No. 4	0.326(0.074) 0.22-0.49 17	0.073(0.011) 0.06-0.09 19	5.4(1.2) 4-7 18	0.136(0.023) 0.09-0.17 17	13.6(2.4) 9-16 13
Union Bay					
No. 1	0.251(0.055) 0.13-0.42 111	0.023(0.010) 0.01-0.06 109	0.4(0.9) 0-4 108	0.091(0.016) 0.06-0.15 79	10.0(1.2) 8-15 79
No. 2	0.236(0.055) 0.15-0.43 52	0.030(0.017) 0.01-0.08 52	1.0(1.7) 0-7 52	0.086(0.019) 0.06-0.14 38	10.2(1.5) 8-15 37
No. 3	0.268(0.049) 0.17-0.39 47	0.059(0.017) 0.02-0.09 47	3.9(1.8) 0-7 47	0.108(0.037) 0.06-0.17 15	12.8(2.3) 9-16 15
No. 4(MP1)	0.274(0.052) 0.19-0.38 34	0.073(0.014) 0.03-0.11 42	5.8(0.6) 5-7 42	0.151(0.021) 0.08-0.20 46	13.9(1.5) 10-16 39
Yarrow Bay					
No. 1	0.240(0.048) 0.16-0.37 70	0.039(0.017) 0.01-0.08 70	1.8(1.8) 0-8 70	0.091(0.023) 0.06-0.17 42	10.3(1.4) 8-14 40
No. 3	0.282(0.058) 0.16-0.46 69	0.067(0.011) 0.04-0.10 77	4.1(1.1) 2-7 77	0.112(0.024) 0.07-0.17 28	12.3(1.7) 9-15 28
No. 4	0.262(0.053) 0.16-0.41 124	0.074(0.009) 0.05-0.09 151	5.4(1.1) 2-8 150	0.145(0.025) 0.08-0.19 112	14.0(1.7) 9-18 110
Core 81-D					
1	0.284(0.054) 0.14-0.44 36	0.085(0.007) 0.07-0.10 42	5.6(0.8) 4-8 42	0.167(0.013) 0.14-0.19 28	14.4(1.4) 12-18 38
3	0.256(0.047) 0.19-0.34 32	0.080(0.007) 0.06-0.09 33	5.6(0.9) 4-7 33	0.164(0.016) 0.12-0.19 44	13.9(2.1) 6-18 55

Table 1. Continued.

Sta. or depth	Carapace length	Mucro		Antennule	
		length	sutures	length	segments
6	0.296(0.055)	0.083(0.006)	5.7(1.0)	0.162(0.011)	14.8(1.4)
	0.20-0.42	0.07-0.10	4-8	0.14-0.20	12-18
	29	48	49	35	50
10	0.257(0.044)	0.075(0.013)	5.7(1.3)	0.155(0.020)	13.7(2.0)
	0.18-0.31	0.02-0.09	0-7	0.12-0.20	8-17
	20	25	25	17	31
15	0.284(0.048)	0.075(0.012)	4.8(1.3)	0.148(0.020)	14.2(1.6)
	0.22-0.36	0.05-0.09	2-8	0.10-0.18	11-17
	9	31	31	21	29
18	0.296(0.058)	0.074(0.013)	4.7(1.4)	0.156(0.021)	14.4(2.1)
	0.20-0.37	0.03-0.09	0-7	0.10-0.18	9-18
	11	34	34	29	42
21	0.288(0.055)	0.076(0.012)	5.0(1.3)	0.160(0.017)	14.3(2.1)
	0.18-0.40	0.03-0.09	0-7	0.12-0.18	6-17
	15	30	30	23	37
24	0.281(0.066)	0.075(0.014)	5.6(1.7)	0.162(0.018)	14.9(1-7)
	0.19-0.43	0.02-0.10	0-8	0.13-0.20	10-18
	25	38	39	27	36
25	0.250(0.036)	0.078(0.003)	5.6(0.5)	0.164(0.011)	14.2(1.6)
	0.21-0.30	0.07-0.08	5-6	0.15-0.18	12-16
	4	7	7	4	6
27	0.277(0.045)	0.078(0.009)	5.8(1.1)	0.152(0.025)	14.1(1.9)
	0.19-0.37	0.04-0.09	3-9	0.09-0.18	10-18
	30	53	53	22	37
40	0.284(0.056)	0.084(0.009)	6.3(1.2)	0.186(0.015)	15.5(1.2)
	0.21-0.40	0.06-0.11	2-8	0.16-0.21	13-18
	22	41	41	16	29
Madison Park core					
1	0.274(0.052)	0.073(0.014)	5.8(0.6)	0.151(0.021)	13.9(1-5)
	0.19-0.38	0.03-0.11	5-7	0.08-0.20	10-16
	34	42	42	46	39
2	0.286(0.036)	0.084(0.010)	5.0(0.7)	0.178(0.012)	15.2(1.3)
	0.25-0.32	0.07-0.10	4-6	0.17-0.20	13-16
	4	5	5	5	5
4	0.214(0.038)	0.058(0.007)	5.8(0.8)	0.121(0.011)	14.6(1.4)
	0.11-0.31	0.04-0.08	5-7	0.10-0.14	12-17
	52	52	52	26	24
13	0.306(0.050)	0.063(0.009)	4.6(1.2)	0.140(0.025)	13.8(2.2)
	0.26-0.36	0.05-0.08	2-7	0.10-0.20	11-20
	4	24	30	21	16
40		0.065	4.5	0.132(0.009)	13.2(0.84)
		0.06-0.07	4-5	0.12-0.15	12-14
		2	2	5	5

erogeneity ($P < 0.000$), whereas comparable calculations on antennule segments showed insignificant departures (81-D, $P < 0.533$; MP, $P < 0.106$). Almost all significant pairwise comparisons involved divergence of the lowermost sample (40-cm depth) from overlying strata or the topmost sample (1 cm) from underlying strata (Fig. 4, Table 1).

One general conclusion is that although significant differences exist between some strata, these differences are minor. Open-water populations have been long featured for a considerable time, maintaining their relatively uniform morphology despite major changes in the trophic status of the lake.

Samples from the more inshore Madison Park core show essentially the same pattern (i.e. all long-featured forms with some subtle indications of slightly decreased feature lengths with depth, Tables 1 and 2). F -values were still low, but substantially higher than those from core 81-D.

Sediment traps: Predicted production and observed flux—The actual number of remains that accumulate yearly in the sediment represents a net flux (Kerfoot 1974, 1981), the end result of a rather complex interplay between gains and losses from several sources. Important processes include production of remains by either molting or death;

Table 2. One-way ANOVA results from bay transects and core samples (df—degrees of freedom for site and individual comparisons; ss—sum of squares; ms—mean squares; *f*—*F*-value; *P*—probability of null hypothesis from *F*-test). Italicized values are Bartlett's test for homogeneity of variances. Carapace lengths generally show homoscedasticity; antennule lengths show some significant departures from homogeneity, whereas mucro lengths typically depart significantly from homogeneity of variance.

Site	Carapace length (mm)					Mucro length (mm)					Antennule length (mm)				
	df	ss	ms	<i>f</i>	<i>P</i>	df	ss	ms	<i>f</i>	<i>P</i>	df	ss	ms	<i>f</i>	<i>P</i>
Union Bay	3	0.042	0.014	4.9	0.003	3	0.101	0.034	176.1	0.000	3	0.126	0.042	102.9	0.000
	240	0.691	0.003			246	0.047	0.000			174	0.071	0.000		
			<i>0.820</i>					<i>0.000</i>					<i>0.000</i>		
Juanita Bay	3	0.158	0.053	19.9	0.000	3	0.008	0.003	14.7	0.000	3	0.034	0.011	19.0	0.000
	172	0.454	0.003			174	0.032	0.000			147	0.089	0.001		
			<i>0.006</i>					<i>0.000</i>					<i>0.646</i>		
Cozy Cove	3	0.175	0.058	47.1	0.000	3	0.061	0.020	214.5	0.000	3	0.175	0.058	209.5	0.000
	158	0.196	0.001			172	0.016	0.000			131	0.037	0.000		
			<i>0.006</i>					<i>0.003</i>					<i>0.000</i>		
Yarrow Bay	2	0.062	0.031	10.9	0.000	2	0.062	0.031	210.2	0.000	2	0.095	0.048	79.8	0.000
	260	0.734	0.003			295	0.043	0.000			179	0.107	0.001		
			<i>0.320</i>					<i>0.000</i>					<i>0.875</i>		
Core 81-D	10	0.044	0.004	1.6	0.113	10	0.006	0.001	5.5	0.000	10	0.017	0.002	5.7	0.000
	222	0.622	0.003			371	0.039	0.000			255	0.078	0.000		
			<i>0.697</i>					<i>0.000</i>					<i>0.003</i>		
Madison Park core	3	0.101	0.034	17.4	0.000	3	0.007	0.002	22.4	0.000	4	0.022	0.005	14.5	0.000
	90	0.175	0.002			119	0.013	0.000			98	0.037	0.000		
			<i>0.282</i>					<i>0.000</i>					<i>0.001</i>		

loss by fragmentation, decomposition, or digestion; horizontal transport in the water column (e.g. along the thermocline by internal waves or currents) or at the mud-water interface (e.g. profile-bound density currents); and vertical movement through resuspension and redeposition (e.g. primarily during overturn).

In the open waters of the lake, expected production of remains was very sensitive to *Bosmina* density and increasing lake temperatures (Fig. 5). In 1972, the number of eggs carried per individual rose in early May, followed by a positive population response in late May to early June. The negative death rates in April are spurious, probably a consequence of resting egg recruitment. The density of *Bosmina* peaked in early June. Together, the per capita instantaneous birth and death rates rose sharply—largely as a consequence of warming temperatures. Thereafter, population density declined throughout late June, July, and August.

Expected settling rates for molts and corpses were calculated on a weekly basis. Negative death rates were reset to zero. To illustrate the calculation of expected settling rates from weekly tabled data, consider the week of 15–21 June. During this week, there were 2.64 *Bosmina* liter⁻¹ in the 825 liters of the water column above the 50-m Evergreen Point Bridge sediment trap. If we express these concentrations in terms of cubic centimeters and substitute into Eq. 2 and 3, deaths and molts gave an estimated production of 5,836 remains. Dividing this estimate by the trap bottom area (165 cm²) gave 35.4 remains cm⁻² week⁻¹.

Expected production of remains, expressed as total remains and its two components (exuviae, deaths), was

highly correlated with density ($r = 0.83$) and predicted a sharp June peak (Fig. 6). The curves of expected exuviae, total remains (exuviae + dead animals), and observed accumulation rates were nearly synchronous and roughly similar in basic shape. Because of the population peak, enhanced death rates, and temperature-dependent molting, 53.3% of remains were predicted to be produced in June. The two ways of calculating production—mean individual vs. weighted stratum—gave almost identical results ($r^2 = 0.998$ for weekly values).

As expected, observed trap catches were highly correlated with *Bosmina* density (carapaces, $r = 0.79$; head shields, $r = 0.78$), but the match improved with the death rate—molting rate model (carapaces, $r = 0.94$; head shields, $r = 0.95$). Despite disarticulation, weekly totals for head shields and carapaces were highly correlated ($r = 0.99$) and similar. However, there was a slight and significant bias toward carapaces (the regression of head shield on carapaces; $n = 52$, $y = -4.71 + 0.867x$; $P < 0.01$), as head shield tallies were only 87% of carapace tallies. Otherwise, the pattern of observed trap catches closely followed the predicted seasonal production pattern, including the strong peak in June. Regression analysis of observed vs. expected total remains illustrated the very high relative correspondence (carapaces week⁻¹, $y = 13.88 + 0.051x$, $R^2 = 0.843$; head shields week⁻¹, $y = 6.38 + 0.04x$, $R^2 = 0.864$).

The observed catchment values, however, did not follow the absolute magnitude of expected production (Fig. 6). Predicted contributions from molting (R_m) and death (R_d) are shown separately, so that $R_m + R_d = R_w$. The absolute accumulation rate of remains in sediment traps

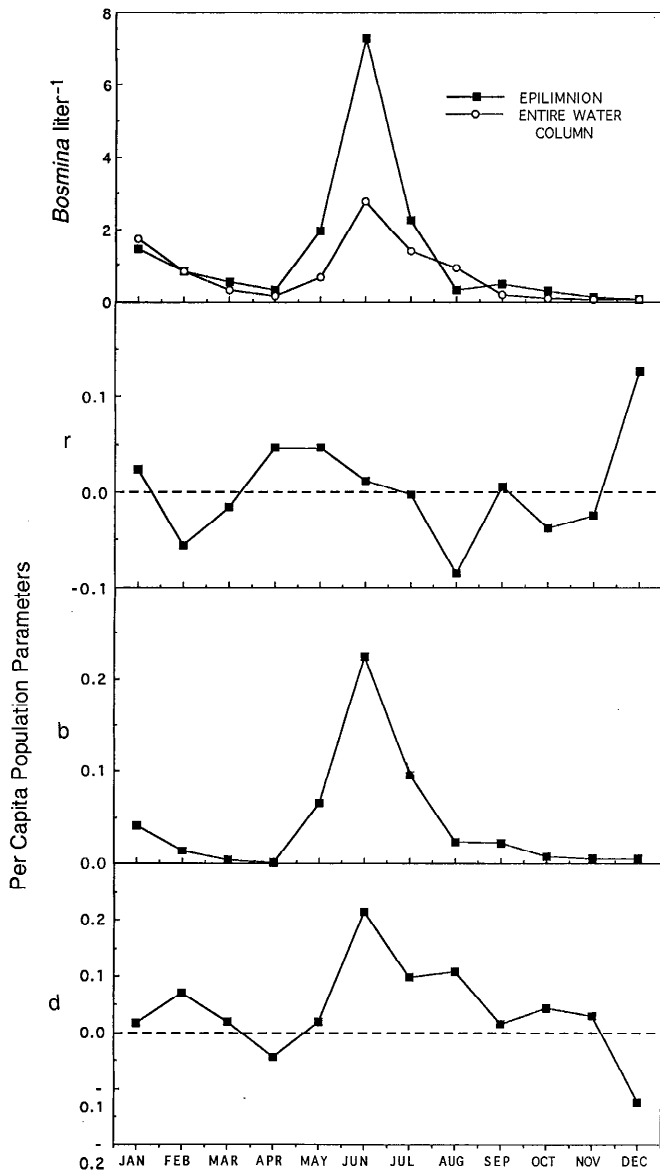


Fig. 5. Monthly densities and per capita rates of population growth (r), birth rate (b), and death rate (d) for *Bosmina* populations in Lake Washington in 1972. Here, the monthly values are based on averages of the basic weekly calculations within months; hence the values may not correspond exactly to between monthly calculations.

is considerably smaller than expected. For the sediment trap, the expected production averaged 7.25 carapaces $\text{cm}^{-2} \text{week}^{-1}$, with a peak of 86.1, whereas the observed settling rates averaged 0.45 whole carapaces $\text{cm}^{-2} \text{week}^{-1}$ with a peak at 5.0. Numerical integration of the expected gave 62,208 whole carapaces for the trap or 377.0 carapaces $\text{cm}^{-2} \text{yr}^{-1}$, whereas the corresponding figures for the observed were 3,882 or 23.4, an average catchment of only 6.2% of the expected production. Hence, there are 16.6 \times more expected than observed carapaces. Slopes of the previous regression analyses gave even lower values—between 4 and 5%.

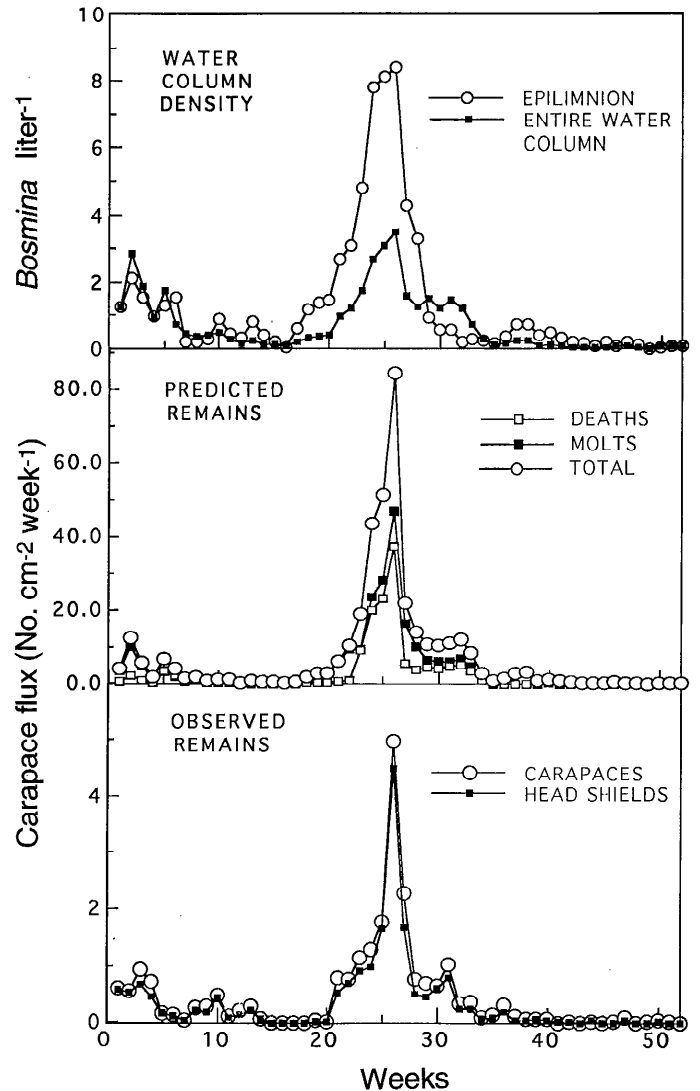


Fig. 6. Expected production vs. observed catchment in the 50-m sediment trap. Seasonal density of *Bosmina* is shown in the upper panel. Lower panels contrast predicted production of remains with observed trap capture. Note that the axes for production and trap capture differ by a factor of 15 \times .

The disparity between predicted trap catchment and observed absolute flux could be attributed to various processes or violations of assumptions (e.g. trap capture efficiency, differential transport, etc.). However, two phenomena that seem responsible for much of the quantitative mismatch are simply decomposition and fragmentation. Various stages of these attrition processes show up with magnification of trap and surficial sediments. During the decomposition and fragmentation process, the head shield and carapace disarticulate, the two halves of the carapace separate, and the antennules and mucrones break off.

Between 16.5 and 68.0% of the remains encountered in most surficial and core sediments are fragments, pieces of carapaces with mucrones, and antennules separated

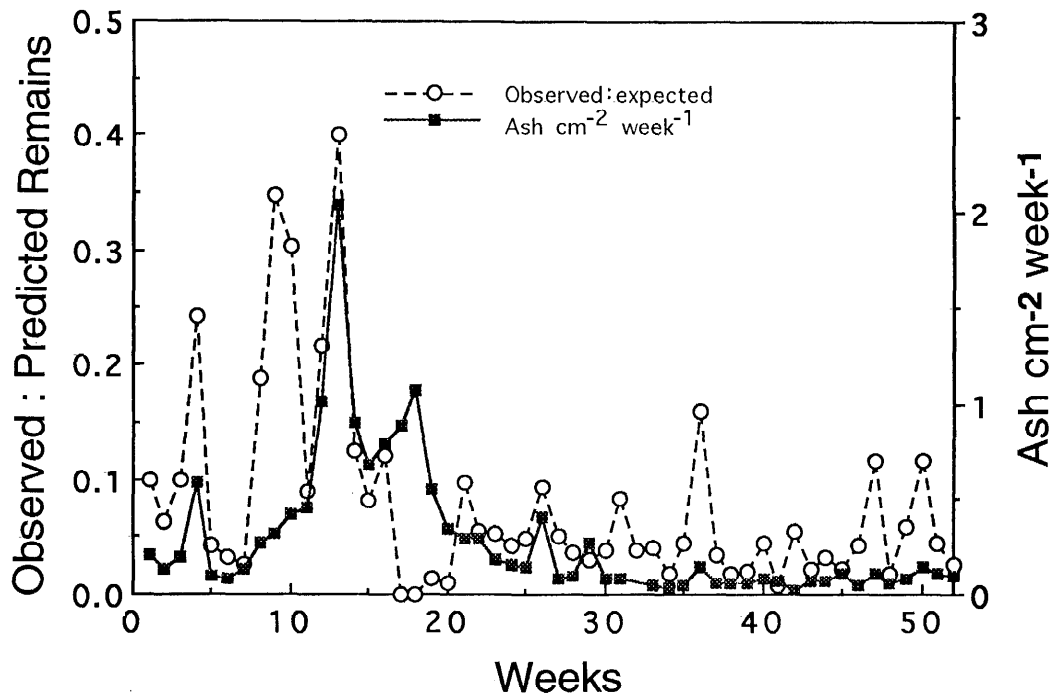


Fig. 7. Weekly changes in ratio of observed to expected production (o : e) plotted with inorganic sedimentation into trap 50-1. Notice elevated values during first 4 months.

from head shields. Even in sediment trap material, fully articulated carapaces and head shields amount to only 29.3% of the settling carapaces. However, this observation indicates that at least 29% of the carapaces are from dying individuals, because head shields and carapaces usually disarticulate during molting. Most of the smaller fragments were not tabulated during the original staining and scanning technique on sediment trap remains because that procedure emphasized only whole carapaces and head shields (*see methods*). In the deep-water core, entire carapaces with both mucrones made up between 31.9 and 93.8% of total carapaces at various depths, whereas half-carapaces (broken apart) with a mucro made up 3.1–27.0%. Microscope scans at higher magnification (400–500 \times) increased mucro and antennule totals through addition of pieces. Whether the fragmentation is due primarily to physical factors, predation, action of benthic detritivores, or natural decomposition is uncertain.

The surprisingly good agreement between seasonal *Bosmina* production and catchment suggests little horizontal sediment flux and relatively minor resuspension. However, some seasonal deviations merit comment. During the prolonged winter period of mixing (January–April) for this monomictic lake, the observed-to-expected (o : e) ratios are higher than for the rest of the year. Figure 7 superimposes the yearly pattern for inorganic sedimentation, as measured by ash weight, on the weekly o : e ratios. The correlation between ash weight and o : e ratios is significant ($N = 52$, $r = 0.698$, $P < 0.05$), although the agreement of peaks is poor. The higher o : e ratio of remains in the early months may represent resuspended sediments added to catchment totals or to less decom-

position or fragmentation (e.g. from invertebrate predation) during colder months.

Discussion

Preliminary examination of the morphology and production of *Bosmina* remains in Lake Washington sediments is beginning to reveal how spatial and temporal morphological patterns are preserved in the long-term sedimentary record. When remains from coves and bays are compared with remains from the central basin, there are marked differences. All examined embayments showed a significant gradient from short-featured forms off near-shore lily pads to long-featured forms characteristic of open waters. Thus, the remains in surficial embayment sediments preserve a sensitive record of *Bosmina* morphology and hence of copepod predation gradients in the bay sediments. Remains appear to stay in place in bays, reflecting the morphological character of overlying living populations. However, only 2.3% of remains found in core samples from midlake sediments were from bay populations, in part also reflecting the limited areal extent (4.9% surface area) of bays relative to the open-water portions of the lake. The relatively low representation of bay remains in midlake surface samples emphasizes that diversity surveys of large lakes should require grid sampling of bay sediments. A single midlake sample is probably insufficient to fully characterize biological heterogeneity and diversity.

The sedimentary record clears up one historical issue. Scheffer and Robinson (1939) reported *Eubosmina longispina* from Lake Washington in 1933, whereas *B. lon-*

girostris was the dominant bosminid in 1950 (Edmondson 1969). Rather than a replacement, Kleckner (1967) and Edmondson (1969) thought that the original classification was in error, and that *B. longirostris* had persisted throughout the reported interval. My investigation confirms Kleckner's findings. In terms of morphology, offshore bosminid populations remained relatively unchanged during eutrophication in the lake, with only a slight reduction in feature lengths, and the remains are referable to *B. longirostris*.

As this question was settled, electrophoretic information raised new questions about genetic heterogeneity between some bay and open-water populations. Electrophoretic surveys of *Bosmina* from Lake Washington and surrounding lakes uncovered evidence for sibling species complexes within *B. longirostris* (Manning et al. 1978; Kerfoot and Peterson 1980). The studies suggested that short-featured inner bay populations of *B. longirostris* in Union Bay currently are not exchanging genes with offshore populations, although the two populations converge in phenotype across the bay. In contrast, populations characterized in other bays did not show such electrophoretic heterogeneity (Manning et al. 1978).

Historical differences may underlie some of the contrast between particular embayments, although the details raise more questions than they resolve. Union Bay is the largest bay in the lake and occupies a depression formerly connected to the lake through an elevated sill of glacial sediments. Beginning around 6000 B.P., an extensive peat layer was deposited in the bay, indicating lower water levels (McManus 1963). Is it possible that the short-featured clones colonized the bay during the low-water stage before the bay reconnected with the lake? Having the two populations separated in two adjacent lakes could explain the biological contrast with the other embayments. A second alternative explanation is that invasion by short-featured genotypes is relatively recent, i.e. that it coincides with the 3-m lowering of lake level by the Army Corps of Engineers (Lake Washington Ship Canal construction) in 1916. A third alternative is that the contrast is a simple consequence of scale. Because Union Bay is the largest bay, the vast extent of its relatively shallow interior waters, laden with macrophytes, might support populations of two parapatric sibling species. Longer cores of Union Bay sediments should provide answers to these questions.

The spatial distribution of morphological remains in sediments describes patterns, but what about dynamics? To get at fundamental processes, a simple vertical model, derived from molting and death schedules, predicted the flux of *Bosmina* remains through a restricted column of water in the center of the lake. The model was very simple in that it neglected terms for horizontal movement and resuspension. The predictions from the vertical model were compared with actual flux observations of remains from sediment traps.

The seasonal correlation between expected production and observed trap catchment was high ($r = 0.94-0.95$). Moreover, very few shallow bay remains settled into traps. However, the absolute deposition rates of intact, large remains were low—less than the general estimates of total

carbon loss to sediments in the lake (i.e. 7–17%; Griffiths and Edmondson 1975). A major part of the discrepancy appears attributable to active decomposition and fragmentation. A substantial proportion of the remains from open-water sediments are fragmented to a degree.

Deevey (1964, 1969) originally postulated quantitative preservation of *Bosmina* carapaces and head shields. Unfortunately, this is not the case. Estimates of direct flux from sediment trap studies in Lake Washington suggest <4–6% preservation for whole head shields and carapaces. Previous estimates of deep burial fluxes from cores in Frains Lake, a smaller (6 ha) water body, gave estimates of ~7% (Kerfoot 1981). Underrepresentation probably originates from several sources, but the simplest are decomposition and fragmentation in the water column and at the mud–water interface. Benthic crustaceans such as *Hyalella* and *Diporeia* (*Pontoporeia*) are known to break diatoms into small pieces, so the same fate might await dead *Bosmina*. Predatory copepods are also known to fragment exoskeletons during feeding (Kerfoot 1975). Do remains from dead individuals suffer the same fate as remains produced by molting because the two have radically different settling velocities? The latter possibility requires further research.

Certain microfossils preserve much better than *Bosmina* remains but rarely are there direct tests of expected vs. observed flux. For example, the resistant exines of most pollen grains appear to preserve quantitatively in freshwater sediments. Resistant silicious tests of diatom species in small lakes may approach 50% representation (Tutin 1955), yet dissolution can dramatically lower preserved concentrations in large lakes (Schelske 1985). By contrast, the chitinous remains of invertebrates are much more susceptible to abrasion, digestion, and decomposition (Deevey 1964; Tsukada 1972; Kerfoot 1981). Because of their numerical abundance and potential importance in reconstructing zooplankton community changes, investigations of production and deposition dynamics would seem necessary for more precise inferences.

Among the invertebrate remains, those of the cladocerans *Bosmina*, *Eubosmina*, and various chydorids are abundant enough in lake sediments to prompt the belief by some (e.g. Alhonen 1967) and the conviction by others (Deevey 1942, 1955, 1969; Frey 1961) that they provide a history of lake productivity. Even for a secondary production caution with this generality comes from two sources: certain zooplankton species preserve poorly (with a consequent loss of absolute record), and competition or predation may shift the community composition from well-preserved species to poorly preserved species or vice versa, giving a false impression of a fluctuating resource base.

For example, certain important components of lake communities, chiefly protozoans, copepods, and rotifers, fail to preserve well in sediments. If the lake community were to shift from an assemblage of relatively well-preserved species, such as *Bosmina* and *Chaoborus*, to one of poorly preserved species, the sediment would falsely predict a general reduction in lake productivity. Although this point usually is not ignored (Livingstone et al. 1958;

Goulden 1964; Harmsworth and Whiteside 1968), it is often unheeded. Kerfoot (1974, 1981) treated a situation where a midcore increase in poorly preserved *Daphnia* remains coincided with a major decrease in *Bosmina* remains, presumably because *Daphnia* gathered more of the shared resources. Under these circumstances, use of *Bosmina* remains alone to indicate community secondary production would overlook the resources consumed by the more poorly preserved *Daphnia*.

Despite these reservations, the preliminary results in Lake Washington seem to encourage more accurate calibration studies. Detailed inspection of weekly patterns between production and trap catchments reveals only minor evidence for redeposition effects during the period of monomixis. Moreover, recent community shifts in the lake (late 1970s–1980s) included major changes in pelagic cladoceran populations from *Bosmina* to *Daphnia*. Because Edmondson and his colleagues have so thoroughly documented historical changes (e.g. Edmondson and Litt 1982), including estimates of key demographic parameters, Lake Washington is an exceptional candidate for further tests of matches between core flux rates and observed production dynamics as well as efforts to reconstruct community composition and species production from sedimentary remains.

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