Size-frequency estimates of secondary production by *Mysis relicta* in Lakes Michigan and Huron

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Abstract

Data from five Great Lakes studies of *Mysis relicta* populations were reanalyzed to calculate secondary production estimates using the size-frequency method. Production estimates (P) ranged from 0.25 to 3.2 g dry weight m^{-2} yr^{-1}. Average annual biomass ($\bar{B}$) and mean annual density ($\bar{D}$) were 0.11–1.11 g dry weight/ m^2 and 25–434 animals/ m^2, respectively. P:$\bar{B}$ ratios varied only between 2.2 and 3.3. Maximum and minimum biomass values within a study varied by a factor of 519 for one study but by less than 17 for the others. Highest estimates of P, $\bar{B}$ and $\bar{D}$ were calculated for collections from a 50-m station in Lake Michigan despite the larger populations suspected to be present at greater depths sampled in the other studies. These conservative estimates provide a basis for scaling trophic interactions involving *M. relicta* and emphasize findings by previous workers that night-time sampling with vertical net hauls is the best available technique for quantitative studies of *M. relicta* populations in the Great Lakes.

Introduction

Mysis relicta is an important component of the food chain in the Great Lakes and in other northern lakes. The importance of *Mysis* in the diets of many Great Lakes fishes has been well documented (Wells & Beeton 1963; Morsell & Norden 1968; Foltz & Norden 1977; Janssen & Brandt 1980). *Mysis* has also been shown to be a voracious predator on zooplankton (Lasenby & Langford 1972; Grossnickle 1978; Cooper & Goldman 1980) and on *Pontoporeia hoyi* (Parker 1980). The introduction of *M. relicta* into lakes as prey for fish has been linked to dramatic alterations in zooplankton communities (Zyblut 1970; Northcote 1972; Richards *et al.* 1975; Morgan *et al.* 1978; Goldman *et al.* 1979). Furthermore, *Mysis* is capable of filter-feeding at high rates on colonial and single-celled phytoplankton (Grossnickle 1978) and has been shown to feed at night during summer stratification on phytoplankton in the deep chlorophyll maximum of Lake Michigan (Bowers & Grossnickle 1978; Grossnickle 1979). Ferrante & Parker (1978) suggest that *Mysis* has an important influence on silicon cycling in Lake Michigan as a result of its feeding on diatoms. *Mysis* may be a detritivore by day (Lasenby & Langford 1972) or during periods of low plankton abundance (Grossnickle 1978). Knowledge of mysid production rates would aid understanding of the quantitative relationships between these dynamic processes.

Most methods for calculating secondary production of invertebrates require identifying and tracking cohorts. This is true for the removal-summation, increment-summation, instantaneous growth rate, and Allen curve methods (Waters 1977). The size-frequency method (Waters & Hokenstrom 1980; Hynes 1980), formerly known as the Hynes or Hynes/ Hamilton method (Hynes & Coleman 1968; Hamilton 1969), does not require identifying cohorts. Size-frequency production estimates have been made for a variety of aquatic invertebrates

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including insects (Hynes & Coleman 1968; Waters & Crawford 1973; Benke 1976; Krueger & Martin 1980), gastropods (Eckblad 1973), and amphipods (Martien & Benke 1977; Welton 1979; Waters & Hokenstrom 1980). The size-frequency method is an appropriate one for calculating secondary production of *Mysis relicta* in the Great Lakes because some reproduction within these populations occurs throughout the year and cohorts can not be easily followed (Morgan & Beeton 1978). Size-frequency production estimates will be presented here for *Mysis relicta* using five existing Great Lakes data sets. Furthermore, the conceptual framework for calculating production estimates will be used to compare density and biomasss data drawn from Great Lakes studies.

Methods

Unless otherwise indicated, measures of body length will be given as the distance from the tip of the rostrum to the tips of the telson. The length-weight conversion used for all data except Morgan's (discussed below) was derived from *Mysis relicta* specimens collected at a 100-m station in Lake Michigan west of Grand Haven, Michigan. Sampling was conducted on 7 November 1980 using a benthic sled during daylight hours and animals immediately preserved in 10% formalin. Animals were measured to the nearest 0.254 mm within 24 hours of collection for total body length and placed on aluminum foil boats. Specimens were then dried at 55 °C for 48 hours in a drying oven, transferred to a desiccator containing silica gel, and weighed individually on a Cahn Electrobalance® Model 4400. Dry weight was chosen, rather than wet weight, for use in production estimates discussed here because of inaccuracies due to evaporation while estimating wet weights of small invertebrates.

Menzie's (1980) formulation of the size-frequency method was used to calculate secondary production. This formulation incorporates both Benke's (1979) cohort production interval (CPI), which is a modification for voltinism, and Hamilton's (1969) correction for development times. Menzie (1980) suggests calculating numbers of individuals growing into size category j (N_j), here expressed in number $m^{-2}\ yr^{-1}$:

$$N_j = i\,\bar{n}_j\,(e_j/a_j)\,(1/\mathrm{CPI}) \qquad (1)$$

where i is the number of size categories, $\bar{n}_j$ is the average annual density (numbers/ m^2) of animals in size category j, all e_j terms are equal to 1/i, a_j is the actual proportion of the life span spent in size category j, and CPI is the life span (yr) as defined by the time from release from a brood to death in the largest size category. By substituting 1/i for e_j, equation (1) may be rewritten:

$$N_j = \bar{n}_j / D_j \qquad (2)$$

where $D_j = a_j$ CPI, the development time (yr) spent in size category j. The hypothetical relationship between total body length and age shown in Fig. 1, derived from Reynolds & DeGraeve's (1972) and Morgan & Beeton's (1978) characterization of 1 mm/ month average growth rates for *Mysis relicta* in the Great Lakes, was used to estimate D_j. Use of a single length-age relationship compensates for differences among studies in the definition of size classes and assumes that growth is the same at all study sites. Further consequences of assumptions about growth rates are discussed below. Losses between numbers of animals growing into size categories were then converted into biomass as an estimate of production, P (Menzie 1980):

$$P = \sum_{j=1}^{i} (N_j - N_{j+1}) \quad (W_j\,W_{j+1})^{1/2} \qquad (3)$$

where W_j is the mean weight of an individual in size category j. Krueger & Martin (1980) suggest the use of geometric mean weights of size category average weights, $(W_j\,W_{j+1})^{1/2}$, to estimate the weights of individuals lost.

Fig. 1. Hypothetical relationship between total body length (in mm) and age (in months) used in production calculations to estimate the time spent in size categories. Of the five Great Lakes studies, only Reynolds & DeGraeve (1972) observed mysids larger than 22 mm, corresponding here to an age of 19 months (dotted line).

Table 1. Summary of sampling methodology used in five Great Lakes studies of *Mysis relicta.* This summary represents the restricted subsets of data from the original studies which were used to calculate production estimates. Studies are arranged in approximate order by station depths examined.

	Grossnickle	Reynolds & DeGraeve	Beeton	Morgan	Carpenter *et al.*
Sampling years	1975–1976	1970–1971	1954	1975–1976	1971
No. dates	17	10	6	11	7
Lake	Mich.	Mich.	Mich.	Mich.	Huron
Station depth (m)	50	45–73	74	115	90–210
Gear	Vert. Haul	Sled	C-B Horiz.	Sled (flowmeter)[a]	Vert. Haul
Net mouth (m^2)	0.44	1.0	0.02	1.0	1.0
Net mesh (mm)	0.570	0.656	0.366	0.570	0.505
Sampling time	Night	Day	Night	Day	Night (& day)
No. animals measured	6200[b]	4500	2850	1350	7300
Measurement used	TBL[c]	TBL[c]	ASL[d]	BL[e]	TBL[c]

[a] Flowmeter used at surface in conjunction with sled tows.

[b] Measured in the present study.

[c] Total body length – distance from tip of rostrum to tips of telson.

[d] Antennal scale length.

[e] Body length – distance from tip of rostrum to cleft of telson.

Sampling times, depths, and collecting methods used in the five studies are summarized in Table 1. Details of the original methodology and restrictions imposed upon the data in the present study follow.

Beeton's 1954 data

Dr. A. M. Beeton provided unpublished size data from his study of the vertical migration of *M. relicta* (Beeton 1960). The data used here were collected in 1954 on six sampling dates from a 74 m depth station (Station 13) in Lake Michigan using horizontal tows of a calibrated Clarke-Bumpus sampler at 10 m depth intervals from 10 to 40 m. Although series of tows were made at several times on each sampling date, only the two series of Clarke-Bumpus tows preceding midnight were used here as this was the time mysids were highest in the water column and available to the sampler. The volumetric estimates (numbers/m^3) of mysid densities obtained from the Clarke-Bumpus samples were converted into areal densities (numbers/m^2) by a simple integration of depth strata. Volumetric densities of mysids in surface, 10, 20, 30, and 40 m tows were assumed to be representative of the water column intervals 0–5, 5–15, 15–25, 25–35, and 35–74 m, respectively. All animals in a tow (except five tows which were sub-sampled) were measured by Beeton for antennal scale length to the nearest 0.125 mm. Grossnickle & Beeton (1979) have shown antennal scale length to be linearly related to total body length. In order to apply the size-frequency method I converted antennal scale length size classes into total body length size classes using a relation derived from Grossnickle & Beeton (1979):

Total body length (mm) $= 6.18$ [antennal scale length (mm)] $+ 0.50$.

Reynolds & DeGraeve's 1970–71 data

Reynolds & DeGraeve (1972) presented density and size class data obtained on 10 dates during 1970–1971 at station depths of 9–73 m. The data used here were restricted to collections from 45 to 73 m depths as little size-frequency information was available from shallower stations.

Watson's 1971 data

Dr. N. H. F. Watson provided unpublished size category data from the study of *Mysis relicta* in Lake Huron reported by Carpenter *et al.* (1974). Approximately 33 stations were sampled on eight synoptic cruises between April and December 1971. Stations were visited on a predetermined path and samples collected day or night. Production estimates were derived only from stations >90 m in depth as little size-frequency data were available from shallower stations. Furthermore, data from station depths of 90–130 m were used only if sampling was conducted at night. For station depths >130 m, data were used regardless of sampling time. The few deep stations sampled at night during April provided inadequate size-frequency information so only data from the other seven cruises were used in production calculations.

Morgan's 1975–76 data

Morgan (1976) presents data collected between August 1975 and July 1976 at a 115 m station northeast of Milwaukee in Lake Michigan. Dr. M. D. Morgan provided unpublished size category data derived from approximately 100 mysids from each sampling date. Morgan pooled replicate samples and measured a subsample of animals to the nearest 0.5 mm from the tip of the rostrum to the apical cleft of the telson. Since this body length measure differs from that used in other studies, Morgan's (1976) lengths were converted into weight using Morgan's (1976) relationship:

Dry weight (mg) = 0.00016 (Length in mm) $^{3.94}$.

Grossnickle's 1975–76 data

Dr. N. E. Grossnickle and the Center for Great Lakes Studies of the University of Wisconsin-Milwaukee allowed the examination of an extensive series of samples collected with vertical net hauls of a 0.75-m diam., 0.570-mm plankton net. Three to five replicate samples were taken at a 50-m station off Milwaukee on 17 sampling dates between June 1975 and May 1976. Total mysid density estimates from 15 of these dates were reported by Grossnickle & Morgan (1979), but no size measurements were made. I measured total body length to the nearest millimeter for all specimens in at least two samples from each date.

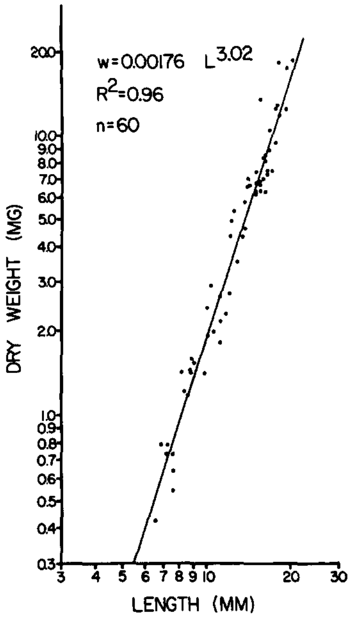

Fig. 2. Logarithm of dry weight (in mg) versus logarithm of total body length (in mm) for 60 Lake Michigan *Mysis relicta* specimens. The least squares regression line and equation are indicated.

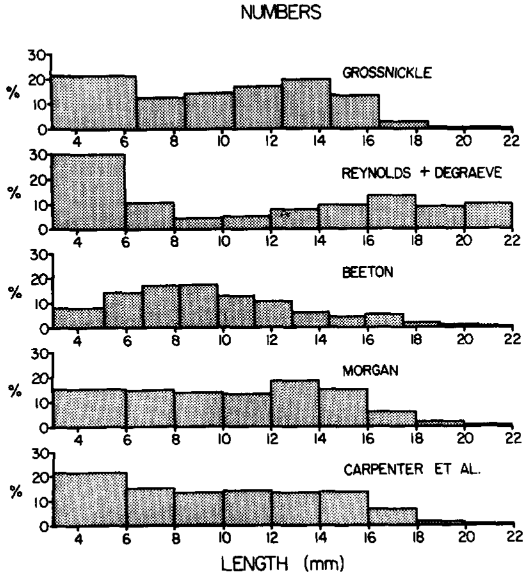

Fig. 3. Size-frequency plots of the total numbers of *Mysis relicta* estimated to grow into total body length (in mm) size categories for five Great Lakes studies. Note that the smallest size class spans a wider range of sizes than others and size categories differ between studies. Reynolds & DeGraeve's (1972) data for animals >22 mm lengths are included in the 20–22 mm size category for the purpose of presentation.

Results

A least-squares fit to logarithmically transformed length-weight data is shown in Fig. 2. The fitted exponent has a value close to 3.

Size-frequency plots for the estimated numbers of animals growing into size categories (N_j) are shown in Fig. 3 for all five Great Lakes investigations. In contrast to the other studies, estimates from Reynolds & DeGraeve's (1972) study indicate a large fraction of animals observed were in >16 mm size categories. The size-frequency plot for Beeton's data peaked in the 8.2–9.8 mm size category despite the wider range in lengths spanned by the smallest size class. This suggests that numbers of animals growing into the two smallest size categories may have been underestimated either in the original sampling or as a result of growth rate assumptions in the calulations.

Histograms of average annual standing crop for body length size categories are shown in Fig. 4. Highest fractions of average biomass occurred in size classes >14 mm for all five studies. In contrast to the other studies, average biomass was highest in the 20–22 mm size category for Reynolds & Degraeve's (1972) data. Total standing crop versus month of sampling is shown in Fig. 5. Of the three studies having nearly year-round sampling, standing crop reached lowest values during November-February. However, the large date-to-date variations in biomass estimates prevents more detailed conclusions. The ratios of maximum to minimum biomass values within a year were 15, 519, 9, 17 and 3 for the data of Grossnickle, Reynolds and DeGraeve, Beeton, Morgan and Carpenter *et al.*, respectively.

Annual secondary production, average annual biomass ($\bar{B}$), mean annual density ($\bar{D}$), and P : $\bar{B}$ ratio estimates are given in Table 2. P, $\bar{B}$ and P : $\bar{B}$ estimates in Table 2 were calculated for the size categories, which span approximately 2.0 mm length classes, shown in Figs. 3 and 4. These estimates are altered by <2% if size categories are based on the original measurement classes, which generally spanned 0.5 or 1.0 mm length ranges. Lowest values of P, $\bar{B}$ and D were obtained for Reynolds & DeGraeve's (1972) study and highest values were calculated from Grossnickle's data. Although these estimates differ by an order of magnitude, P : $\bar{B}$ ratios differed by less than 50%.

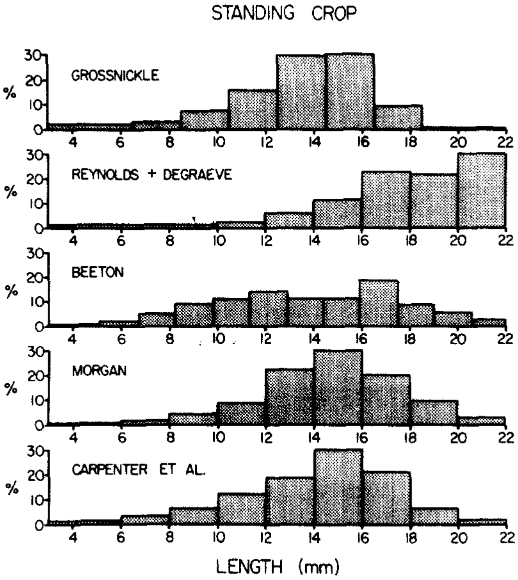

Fig. 4. Size-frequency plots of the average annual biomass present in total body length (in mm) size classes for *Mysis relicta* populations described in five Great Lakes studies. Note that the smallest size class spans a wider range of sizes than others and size categories differ between studies. Reynolds & DeGraeve's (1972) data for animals > 22 mm lengths are included in the 20–22 mm size category for the purpose of presentation.

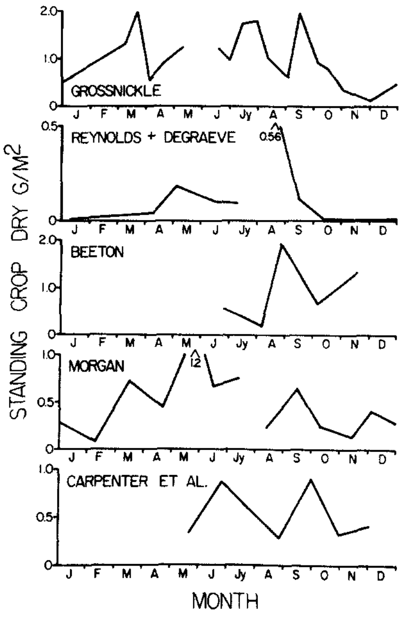

Fig. 5. Standing crop (in dry g/ m^2) versus month of sampling for five Great Lakes studies. Biomass estimates are derived from length-weight regressions and length data. Note the different vertical scales used.

Table 2. Estimates of secondary production (P), average annual biomass ($\bar{B}$), mean annual density ($\bar{D}$) and P : $\bar{B}$ ratios for five Great Lakes studies of *Mysis relicta* populations.

	Grossnickle	Reynolds & DeGraeve	Beeton	Morgan	Carpenter *et al.*
P (dry g m^{-2} yr^{-1})	3.2.	0.25	2.5	1.7	1.5
$\bar{B}$ (dry g m^{-2})	1.11	0.11	0.85	0.52	0.53
$\bar{D}$ (No. m^{-2})	434	25	349	171	204
P : $\bar{B}$ (yr^{-1})	2.9	2.2	2.9	3.3	2.8

Discussion

Despite the original intent of the size-frequency method's proponents, Waters (1977) cites only one instance in which the size-frequency method has been used to calculate production of an aggregate of species. Apparently, few investigators have chosen to work with species aggregates because many assumptions are necessary. When the size-frequency model is applied to a single species the assumptions are less severe: 1) animals spend a known amount of time in each size class; 2) sampling times are equally spaced throughout a year; 3) all sizes of animals are sampled quantitatively. Hamilton (1969) and Cushman *et al.* (1978) have used simulations to examine the robustness of the method to departures from the first two assumptions.

Assuming overall life span is accurately defined, both studies conclude that errors due to violations of assumptions 1 and 2 are minor compared to sampling errors associated with density estimates. In their analysis of approximate confidence intervals for size-frequency production estimates, Krueger & Martin (1980) identify the number of sampling dates as having an important influence on the variability of the production estimator. Waters & Crawford (1973) and Cushman *et al.* (1978) have compared the size-frequency method to other methods under circumstances in which cohorts can be followed and conclude that size-frequency production estimates are quite accurate when applied to single species.

Differences in the estimates of *Mysis relicta* standing stocks may be largely attributed to differences in sampling location, particularly station depth, as well as differences in sampling gear and year-to-year variations in abundance. Robertson *et al.* (1968) observed that mysid abundance increased with depth for six Lake Michigan stations ranging in depth from 17 to 262 m. Reynolds & Degraeve (1972) reported increasing mysid densities (numbers/m^2) with depth to 150 m in lake Michigan. Carpenter *et al.* (1974) found that mysid densities increased with depth up to depths of 200 m in Lakes Huron, Ontario, and Superior. McWilliam (1970) reported that over a four year period densities determined from vertical hauls were more than three times greater at a 270 m station in Lake Michigan than at a 150 m station. Because of the direct relationship of mysid abundance to depth demonstrated by these studies, it is expected that mysid production would also show a strong relationship to depth. This expectation is not substantiated by the calculations presented here, apparently because of differences in sampling techniques between studies. However, production estimates (McWilliam & Sell, unpublished) drawn from density data reported by McWilliam (1970) indicate secondary production by *Mysis relicta* at a 270-m station in Lake Michigan exceeds the maximum value reported here by a factor of 2.

Grossnickle & Morgan (1979) compared sampling methods for collecting *M. relicta* and concluded that daytime vertical net hauls severely underestimated mysid densities. They also found that late instar mysids made up a significantly larger percentage of sled catches than catches from vertical tows at a 115-m station in Lake Michigan. Although Beeton's samples were taken at night, the bottom 30 m of the water column was not sampled. Thus, larger mysids, which tend not to migrate as high into the water column as small mysids (Beeton 1960), may not have been well represented in Beeton's samples. Nevertheless, density and biomass estimates from Beeton's collections are almost as high as values from Grossnickle's samples. Two of the chief problems in using sleds are that the bottom area sampled can not be accurately measured (McWilliam 1970; Reynolds & DeGraeve 1972; Morgan 1976) and that mysids may reside above bottom in deep waters even during the day (Robertson *et al.* 1968; Malley & Reynolds 1979). The low estimates of P, $\bar{B}$, and $\bar{D}$ derived from Reynolds & DeGraeve's (1972) study may represent a systematic bias resulting from sled sampling. The problem of quantifying sled data also may have contributed to the dramatic annual variation in biomass observed by Reynolds & DeGraeve (1972).

Although a linear growth model was used in production calculations here, Clutter & Theilacker's (1971) study suggests that an asymptotic growth curve is a reasonable characterization of growth under laboratory conditions for another mysid, *Metamysidopsis elongata.* Under natural conditions of varying temperature, pressure, and food availability, neither a simple asymptotic curve nor a linear relationship would be expected to apply strictly. McWilliam (1970) presents evidence that growth is slower in deep areas of Lake Michigan than in shallower regions. Reynolds & Degraeve (1972) suggest that average growth of mysids in Lake Michigan is greater during January-April than during the rest of the year. Studies from other lakes (Lasenby & Langford 1972; Hakala 1978; Morgan 1981) indicate that mysid populations may have seasonal changes in growth rate in which growth during winter is slower than in warmer seasons. In the absence of better information on growth rates of *Mysis relicta* in the Great Lakes, a simple linear growth model, such as the one used for calculating production estimates in the present study, is an appropriate approximation. Indeed, a linear growth curve would not appear to be distinguishable from the slightly S-shaped curve that Morgan & Beeton (1978) fit by eye to Lake Michigan data. Furthermore, Hamilton (1969) and Cushman *et al.* (1978) concluded that size-frequency production estimates are affected relatively little by the use of linear versus curvilinear growth models. The overall rate of growth, and hence whether all D_j estimates are systematically biased, deserves further study.

The length-weight relationship used here is similar to ones presented for *Mysis relicta* in Lake Tahoe (Morgan 1979) and in Stony Lake (Lasenby & Langford 1972). However, more extensive examination of length-weight relationships for the smallest and largest size category animals would strengthen production calculations. Also, regression techniques other than least-squares may prove useful (Ricker 1973).

Another minor improvement is suggested by the work of Martien & Benke (1977). Although Hamilton (1969) cautioned that negative production values for individual size categories must be included to avoid biasing the total production sum, Martien & Benke (1977) argue that negative production values obtained from small size groups less susceptible to sampling gear should be ignored. This amounts to recognition that the assumption of no gear selectivity among size classes does not hold. This adjustment would increase the production estimate from Beeton's data by only 3.3.%. Underestimates of densities of large mysids would be expected to have a more pronounced effect on production estimates because of their greater weight.

The only previous estimate of annual production by *M. relicta* in the Great Lakes is Morgan's (1976) estimate of 0.95 g m^{-2} yr^{-1} (and $P : \bar{B} = 2.0$). This is a production value approximately half that calculated from Morgan's data using the size-frequency method. To obtain his estimate, Morgan used density estimates of newly released young in each of three spurts of reproduction occurring within a year and extrapolated a linear decline in numbers of each cohort up to an age of 16 months. Because his estimates of the peak density of young in a cohort were based on individual sampling times, Morgan cautioned that his annual production estimate might be low. Also, Morgan's production value should be considered an underestimate because reproduction occurring between the three major cohorts was ignored. The size-frequency estimates presented here have the advantage of utilizing density data for all sizes of animals on all sampling dates.

Annual production has been estimated using cohort discrimination methods for *Mysis relicta* in two lakes (Table 3). Although the standing stocks of *M. relicta* in Lake Pääjärvi are low compared to estimates for Lake Michigan, $P : \bar{B}$ ratios are comparable. The very low production in the main basin of Lake Tahoe is partially a result of a steady decline in the mysid population between 1975 and 1979 (Morgan 1979, 1980). However, low $P : \bar{B}$ ratios for main basin and Emerald Bay populations indicate the production dynamics of *Mysis* in Lake Tahoe differ considerably from those of populations in the Great Lakes and Lake Pääjärvi. *Ponto-*

Table 3. Estimates of secondary production (P), average annual biomass ($\bar{B}$) and P : B ratios derived using cohort discrimination techniques for studies of *Mysis relicta* and *Pontoporeia hoyi* populations.

	Mysis relicta		
	Hakala (1978)	Morgan (1979)	
	Lake Pääjärvi	Lake Tahoe	Emerald Bay
P (dry g m^{-2} yr^{-1})	0.17-0.28	0.06-0.20	0.99-1.24
$\bar{B}$ (dry g m^{-2})	0.05-0.09	0.12-0.30	0.60-0.65
P : $\bar{B}$ (yr^{-1})	3.0 -3.8	0.47-0.66	1.6 -1.9

	Pontoporeia hoyi	
	Lubner (1974)	Lubner (1979)
	Lake Michigan (140 m)	Lake Michigan (65-115 m)
P (dry g m^{-2} yr^{-1}	0.8-1.3	2.9-6.0
$\bar{B}$ (dry g m^{-2})	1.95	2.56-5.24
P : $\bar{B}$ (yr^{-1})	0.41-0.67	1.09-1.14

poreia hoyi is the only large and abundant crustacean in the Great Lakes for which production is comparable to that of *Mysis* (Table 3). Lubner's (1974, 1979) examinations of *P. hoyi* populations substantiate Cook & Johnson's (1974) suggestion that production by benthic communities may range as high as 5.0 g m^{-2} yr^{-1} in offshore regions of Lake Michigan.

In conclusion, Grossnickle's data represent the most complete information available for *Mysis relicta* populations at a single location in the Great Lakes due to the high sampling frequency and the collection efficiency of night-time vertical hauls. Although the production estimates derived from Grossnickle's data set are the best presently available for the Great Lakes, these estimates should be considered conservative for populations at depths greater than 50 m. Beyond problems in the frequency and bias of sampling, future refinements of production estimates for Great Lakes mysid populations will require more precise information on growth rates.

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