

## The importance of size–frequency relationships for predicting ecological impact of zebra mussel populations

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Received 20 June 1995; in revised form 20 December 1995; accepted 16 February 1996

**Key words:** introduced species, zebra mussel, size–frequency distribution

### Abstract

Although most physiological processes of bivalves are highly size-dependent in a non-linear manner, often only total densities of populations of freshwater bivalves such as the zebra mussel are reported rather than size–frequency information. This can cause serious errors when trying to predict or assess the environmental impacts of these filter feeders on planktonic communities or the role of their pseudofeces in transferring materials from the plankton to the benthos. We used a bioenergetics model to examine the effect that differing size–frequency distribution has on influencing total phytoplankton consumption and pseudofeces production. We constructed different size–frequency distributions of 1000 zebra mussels with the same mean length or same mean body mass for comparison. In addition, we used several size–frequency distributions from the published literature. The size–frequency distribution of a population had a tremendous impact on both total consumption and pseudofeces production with rates varying by more than an order of magnitude (43.5 g consumption by 1000 smaller mussels to 654 g for a population dominated by large mussels). These data emphasize the importance of knowing not only population density, but population size structure in order to accurately understand and predict the impacts of zebra mussels, or any filter feeder on pelagic and benthic communities. This work also demonstrates the usefulness of a tool such as our bioenergetics model for partitioning the relative impacts of densities and size on a variety of factors such as consumption and pseudofeces production.

### Introduction

Dreissenid mussels are among the more formidable exotic invaders of recent years due to their unusual ecological and life history characteristics, including high rates of reproduction, planktonic dispersal of larvae and attachment to hard substrata. In European lakes, dense aggregations of adult mussels occur (10,000–30,000 m<sup>-2</sup>, Stańczykowska, 1975, 1977; Kornobis, 1977; Hamburger et al., 1990) and can comprise over 80% of total living benthic biomass of heavily colonized lakes (Stańczykowska, 1964). Densities in the United States can be even higher exceeding 50,000/m<sup>2</sup>

(Dermott et al., 1993). These filter feeders may remove up to 62% of annual littoral algal production (Hamburger et al., 1990). *Dreissena polymorpha* (Pallas) may reduce planktonic herbivores through competition for phytoplankton, thus affecting the food available to planktivorous fish. Thus zebra mussels may have important ecological impacts on lake food webs as well as planktonic and benthic communities.

The predicted impacts of zebra mussel introduction are a direct result of their feeding activities and colonization of available substrata. Their impact on the aquatic ecosystem is assumed to be density-dependent (Griffiths, 1993); however, simple density compar-

isons are not sufficient to characterize populations. Biomass, filtering ability, pseudofeces production as well as population stability will depend on the size-frequency distribution of the population (Reeders et al., 1993; Deutschman, 1993). As a consequence, populations with similar densities, but different size-frequency distributions should behave very differently.

To assess the consequences of size-frequency distributions on total phytoplankton consumption and filtering by zebra mussels, we used a bioenergetics model originally developed by Kitchell et al. (1977) for fish populations. Modern versions of this model developed by Hewett & Johnson (1987, 1989) were modified by Schneider (1992) to simulate individual bivalve growth and feeding dynamics. We have improved this model so that it includes total filtration and the production of pseudofeces by mussels. This inclusion is important as zebra mussels filter many more particles from the water column than they consume, and can therefore impact more than just the consumable algae. In turbid eutrophic and shallow water bodies, over 90% of the excreted solids can be pseudofeces (Reeders et al., 1993). Pseudofeces production can relocate nutrients from the pelagic to the benthos making them available to a new community of organisms (Griffiths, 1993). Therefore, the inclusion of pseudofeces production into this bioenergetics model allows us to not only examine how environmental conditions influence zebra mussels' growth, but also allows us to examine how zebra mussels' growth and filtering will affect the environment.

Feeding studies have shown that individual filtration rates vary non-linearly with increasing body size (Sprung & Rose, 1988; Walz, 1978), water temperature (Stańczykowska, 1976) and algal density (Lewandowski, 1983; Benedens & Hinz, 1980). To assess the effects of size-frequency *per se*, we simulated feeding activity and pseudofeces production by different populations of zebra mussels representing different size or age compositions, all with identical population densities and environmental conditions.

### Materials and methods

Our bioenergetics model simulates growth and pseudofeces production of an individual zebra mussel as a function of temperature, mussel size and phytoplankton concentration. Therefore, in addition to physiological parameters for zebra mussels, our model requires daily temperature and algal biomass availabil-

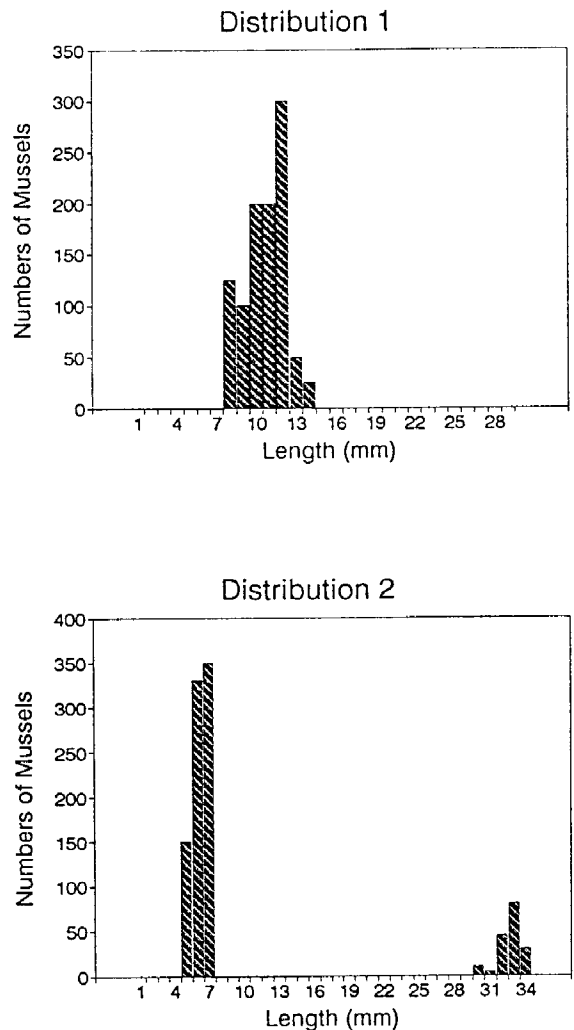


Figure 1. Size-frequency distributions of 1000 zebra mussels used in our model. Distributions 1 and 2 have the same mean shell length of 10.7 mm.

ity. In this model, algal consumption is calculated as a function of weight, temperature and food availability (see Schneider, 1992 for equations). This calculation essentially describes a linear functional response of a mussel to variable algal concentrations up to limiting concentrations (Schneider, 1992). This type of response by *D. polymorpha* to increasing algal concentrations has been reported by others (Sprung & Rose, 1988; Dorgelo & Smeenk, 1988; Walz, 1978). Pseudofeces production was calculated based on equations used by Bayne et al. (1976a) and fitted to data from Walz (1978) which incorporates dependence on weight, ingestion rate and food availability.

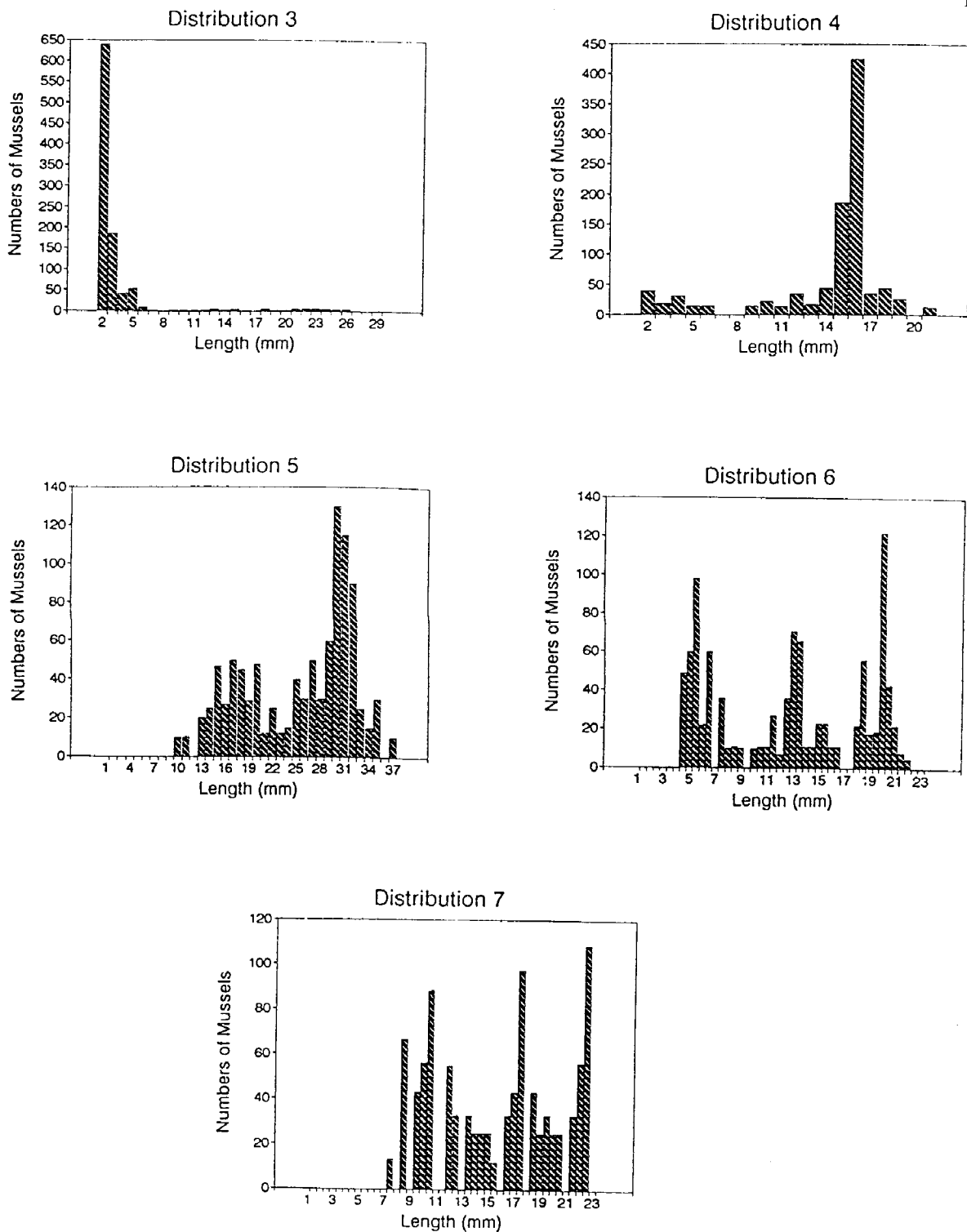


Figure 2. Distributions 3 and 4 are size-frequency data for Lake Erie from Griffiths (1991). Distribution 3: Little Chicken Island Shoal, October, 1989. Mean shell length is 3.53 mm. Distribution 4: Power Plant, Monroe, Michigan, February, 1989. Mean shell length is 14.04 mm. Distribution 5 is based on Lake Vechten, The Netherlands (Dorgelo, 1993). Mean shell length is 25.4 mm. Distributions 6 and 7 represent data from Lake St. Clair in July 1989 (Mackie, 1993). Mean shell length is 12.69 mm for Distribution 6 and 15.69 mm for Distribution 7.

We used the bioenergetics model to predict total algal consumption (g wet weight) and total pseudofeces production (g) for each of nine different size–frequency distributions of zebra mussels (Figures 1–3). All populations were comprised of 1000 individuals. Distributions 1–2 (Figure 1) were constructed to represent two pairs of populations with the same mean shell length within each pair. Distributions 3–4 represent actual data for *D. polymorpha* populations from two sites in Lake Erie as reported by Griffiths (1991) (Figure 2). Distribution 5 is a population of larger mussels in Europe and is based on data from Dorgelo (1993) for Lake Vechten (Figure 2). Distributions 6 and 7 represent actual size–frequency distributions for Lake St. Clair in 1989 as provided by Mackie (1993) (Figure 2). Distributions 8 and 9 represent two populations with the same mean biomass distributed differently across size classes (Figure 3).

Growth and pseudofeces production were evaluated for a 30-day period; in this case we chose the month of July which is the middle of the summer growth period. For our environmental conditions, we used daily water temperature and food availability for Western Lake Erie. Water temperature ranged from 19.73° C to 23.36° C during this month. The proportion of maximum consumption realized by zebra mussels was estimated as 0.79–0.96 of total consumption for this period. Algal caloric value was estimated at 1000 cal/g. This model has been adjusted for growth typical in Lake Erie (Leach, unpub. growth data for Lake Erie) and Madenjian (1995) has demonstrated its predictive power for zebra mussel growth in Lake Erie. In our simulations, all populations experienced identical environmental conditions and parameters. Zebra mussel shell length to body mass conversions were based on a growth curve by Kryger and Riisgård (1988).

## Results

Although all populations contained the same number of individuals, the size–frequency distributions of populations of zebra mussels used in our model ranged from normally distributed around a mean size (Distribution 1, Figure 1; Distribution 8, Figure 3) to bimodal distributions (Distribution 2, Figure 1; Distribution 9, Figure 3) to both positively skewed (Distribution 3, Figure 2) and negatively skewed (Distributions 4–7, Figure 2).

Populations with the same mean shell length varied in their total algal consumption with the normally

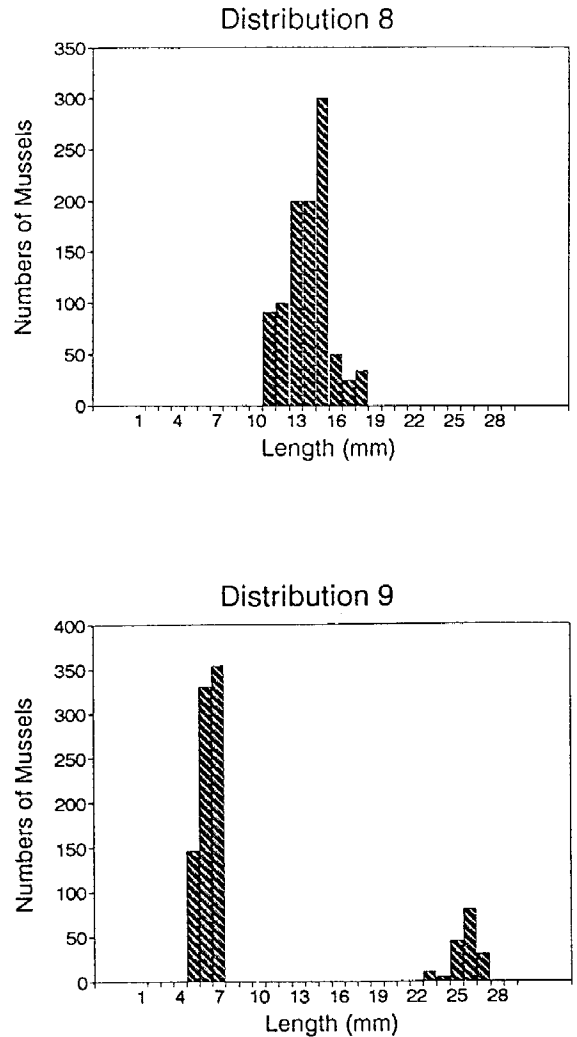


Figure 3. Distributions 8 and 9 representing two populations with different size–frequencies but the same average mussel mass (0.10 g).

distributed population consuming 72% of the amount consumed by the bimodal distribution (Distributions 1 and 2, mean length = 10.7 mm, 163 g versus 225 g, Table 1). Variation in pseudofeces production between populations with the same mean shell length was negligible (Table 1, 1 vs 2, 6 vs 8).

Predicted algal consumption rates based on data from natural populations ranged from 44 g for a population dominated by small mussels with mean shell length of 3.5 mm to 654 g for a population composed of larger individuals with mean shell length of 25.4 mm (Table 1; Figure 2). Pseudofeces production generally increased with the larger mean shell sizes (ranging

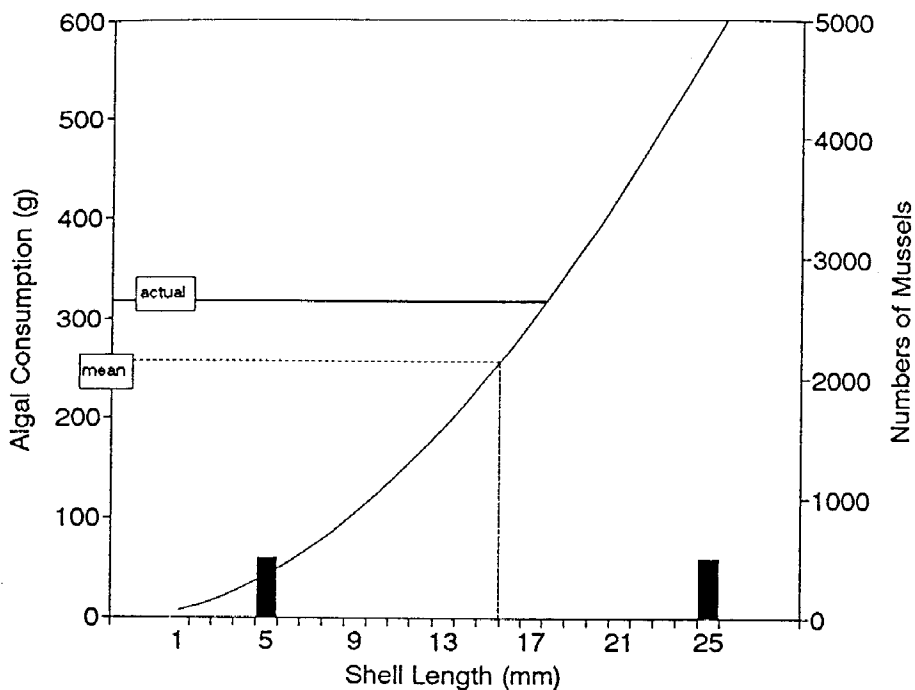


Figure 4. Curve represents total algal consumption for 1000 individuals at each shell length. The bars represent a frequency distribution of 500 individuals at 5 and 25 mm. The total consumption of this population is represented by the actual consumption. The dashed line indicates the consumption of 1000 individuals of the average shell length for this distribution.

from 67–765 g); however, this increase was not linear (Table 1).

Figure 3 illustrates populations with similar mean biomass, but differing distributions of individual biomass (mean shell lengths are 12.9 mm and 8.6 mm respectively). These populations differed in both their algal consumption (217 g vs 152 g) and their pseudofeces production (361 g vs 220 g), with the more skewed population consuming 70% of the total for the normally distributed population (Table 1) and producing 60% of the pseudofeces of that population.

The relationship between the total consumption of a bimodal population versus the average of its subpopulations is illustrated in Figure 4. Consumption by 1000 15 mm mussels is predicted to be less than the consumption by 500 in each of 5 mm and 25 mm size classes.

## Discussion

Most zebra mussel distributional and abundance data are currently presented as densities rather than as size or age distributions. Density data are easy to obtain

from enumeration of shells of both living and dead bivalves. These data may be useful in determining relative coverage rates by zebra mussels, but densities have little predictive power when considering filtering impacts on plankton abundance. In addition to algal consumption, bivalves influence community structure by increasing organic content of sediments via deposition of feces and pseudofeces (Griffiths, 1993). Both of these physiological processes are known to be strongly size-dependent (Reeders et al., 1993). Knowing the size structure of a population is also necessary to accurately predict future reproductive potential for a population (Neumann et al., 1993) and consequently the future impact on the aquatic ecosystem.

Predicted impacts of zebra mussels due to feeding activities include improved water clarity, reduced algal availability, alterations in macroinvertebrate and macrophyte communities and potentially dwindling zooplankton and fish populations (Reeders et al., 1993). Our bioenergetics model incorporates water temperature and food availability for a given water body to forecast zebra mussel growth, algal consumption and pseudofeces production. Table 1 demonstrates that differences in algal consumption and pseudofeces

*Table 1.* Total algal consumption and pseudofeces production for nine size–frequency distributions subjected to food and temperature regimes comparable to Lake Erie for a 30-day period using July conditions for the western basin of Lake Erie. Mean shell length, biomass, skewness and kurtosis are given for each distribution. Distributions 1, 2, 8 and 9 were simulated populations. The references for other data used are given in the table.

Distribution	Mean shell length (mm), standard deviation, skewness and kurtosis	Mean Biomass (g) and standard deviation	Total Algal Consumption (g wet weight)	Total pseudofeces production (g)	Reference
1	mean = 10.7 s.d. = 1.54 skewness = -0.24 kurtosis = -0.71	mean = 0.06 s.d. = 0.02	162.6	279.9	Same Avg. Length as 2
2	mean = 10.7 s.d. = 9.97 skewness = 1.75 kurtosis = 1.10	mean = 0.22 s.d. = 0.46	224.5	276.0	Same Avg. Length as 1
3	mean = 3.53 s.d. = 4.36 skewness = 3.98 kurtosis = 15.52	mean = 0.02 s.d. = 0.09	43.5	67.6	Griffiths, 1991 Little Chicken Island Shoal, Lake Erie
4	mean = 14.04 s.d. = 4.28 skewness = -1.69 kurtosis = 1.96	mean = 0.13 s.d. = 0.12	229.4	372.4	Griffiths, 1991 Monroe, February 1989, Lake Erie
5	mean = 25.38 s.d. = 6.75 skewness = -0.5 kurtosis = -1.03	mean = 0.71 s.d. = 0.42	653.8	765.4	Dorgelo, 1993 Lake Vechten, The Netherlands
6	mean = 12.69 s.d. = 5.78 skewness = -0.01 kurtosis = -1.46	mean = 0.13 s.d. = 0.12	212.6	331.2	Mackie, 1993, Lake St. Clair
7	mean = 15.69 s.d. = 4.75 skewness = -0.05 kurtosis = -1.35	mean = 0.20 s.d. = 0.14	284.8	434.9	Mackie, 1993, Lake St. Clair
8	mean = 12.94 s.d. = 1.64 skewness = 0.14 kurtosis = -0.07	mean = 0.10 s.d. = 0.03	216.5	360.9	Avg. Biomass same as distribution 9
9	mean = 8.6 s.d. = 7.34 skewness = 1.74 kurtosis = 1.10	mean = 0.10 s.d. = 0.21	152.0	219.6	Avg. Biomass same as distribution 8

production may occur between populations with identical numbers of individuals even when two populations of zebra mussels have the same mean shell length or biomass (Distributions 1–2, 8–9). Consumption rates for an ‘average’ mussel can also underestimate the total for a population (Figure 4). With populations of mussels in excess of 20,000/m<sup>2</sup> across a large body

of water, the magnitude of these differences becomes substantial. Populations can be normally distributed around a mean shell length as a result of stable recruitment and mortality rates. Bimodal distributions can represent cohorts of recruits or size-selective mortality patterns in a habitat (Griffiths & Griffiths, 1987). Normally distributed and bimodally distributed popu-

lations perform differently because the latter typically has greater numbers of larger mussels. In our simulations, a bimodally distributed population with a mean shell length of 10.7 mm had a higher consumption rate than a population with a mean shell length of 12.7 mm (Table 1).

Pseudofeces production by zebra mussels can impact nutrient availability to plankton. Although the nutrients may not be utilized by the bivalves, they are removed from the plankton and deposited in the benthos. Nutrients are then available to macrophytes and other benthic organisms potentially changing the composition of the aquatic community (Griffiths, 1993). Our model predicts that variation in pseudofeces production can occur between two populations of the same mean biomass (Table 1), thus different bivalve size distributions are likely to vary in their nutrient translocation rates throughout the water column.

These data emphasize the need for incorporating size-frequency information before predicting the impact of an introduced species like zebra mussels both in the initial phases of establishment and in long-term interactions. Sudden or large increases in density are the result of extensive recruitment and are often characteristic of invading species. Size-frequency distributions are not likely to be similar throughout a body of water. The initial phases of colonization will be affected by spatial and temporal variation in larvae. Age structure may be skewed depending on the time of invasion resulting in a mosaic of subpopulations with similarly aged mussels. Differences in size-frequency distributions with depth have been observed, perhaps influenced by changes in numbers of veligers in different locations due to weather conditions, currents and lake morphology (Stańczykowska, 1975, 1976; Stańczykowska and Lewandowski, 1993). Environmental variables which influence veliger settling may also explain extreme variations of density and age structure in different bodies of water with similar characteristics (Stańczykowska, 1975, 1976; Stańczykowska & Lewandowski, 1993). Stańczykowska also suggests that differential dynamics of recovery of zebra mussel populations may result in different age structure between lakes, even if lakes are interconnected (Stańczykowska 1964, 1976; Stańczykowska & Lewandowski, 1993). Additionally, gregarious larval settlement can lead to notable differences in age and size structure of different populations. Thus, the effects of feeding and pseudofeces production by zebra mussels may be spatially variable reflecting the patchiness

of density and age/size distributions. Models like ours can be used to estimate the extent of potential impact of zebra mussels given patches of variable size-structure.

The calculated differences from model populations with different size-frequency distributions are not surprising because it is widely accepted that the majority of bivalve physiological changes in oxygen consumption or filtering ability with change in size (Bayne et al., 1976a, 1976b; Bayne & Newell, 1983). Deutschman (1993) has reported that population age (and size) structure influences population size fluctuations and that density estimates alone are insufficient as predictors of population stability, or achievement of a stable size/age distribution within a population. Although size-frequency or biomass data are more difficult to collect for populations, they are necessary in order to make accurate predictions regarding the introduction of zebra mussels.

### Acknowledgments

This research was supported by a grant from NOAA, National Sea Grant to DKP. DWS was supported by a grant from the U.S. EPA. Comments by anonymous reviewers were greatly appreciated.

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