Sources of bias in the use of shell fragments to estimate the size of zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*)

Jeremy S. Mitchell, Robert C. Bailey, and Richard W. Knapton

Abstract: Several researchers have examined size-selective predation on dreissenid mussels by first measuring septa from crushed mussel shells found in predators' gastrointestinal tracts and then using a regression of septum length on shell length to infer the size of consumed mussels. We examine three assumptions made when using this approach: (1) that the shell length : septum length relationship is site-independent within the study area, (2) where both zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) are present, that the shell length : septum length relationship is the same for both mussel species, and (3) that the predator foraged exclusively at the site of collection. We collected mussels at 6 sites along an 8-km stretch of Lake Erie shoreline and found that the shell length : septum length relationship varied significantly both among sites and between zebra mussels and quagga mussels. We then compared the regression for quagga mussels at one of these sites with that for intact valves of mussels taken from scaup (*Aythya marila*, *Aythya affinis*) collected at the site. Although ice cover at the time of collection restricted scaup to the site while foraging within the study area, regressions were again significantly different, i.e., scaup had been foraging elsewhere. Our results indicate that for at least some study sites, the use of septa to estimate dreissenid mussel size is not appropriate. However, when intact valves are found in a predator, variation in shell morphology can help to confirm or exclude possible foraging locales.

Résumé : Plusieurs chercheurs ont étudié la prédation sélective en fonction de la taille chez les moules dreissénides en mesurant les septums des moules dans les coquilles écrasées trouvées dans le tube digestif des prédateurs et en estimant ensuite la longueur de la coquille d'après la longueur du septum pour évaluer la taille des moules consommées. Nous examinons trois suppositions inhérentes à cette approche : (1) que la relation entre la longueur de la coquille et la longueur du septum est indépendante de l'endroit dans la région étudiée; (2) que bien que deux espèces, la Moule zébrée (*Dreissena polymorpha*) et la Moule quagga (*Dreissena bugensis*), cohabitent, la relation entre la longueur du septum et la longueur de la coquille est la même chez les deux; et (3) que le prédateur a cherché sa nourriture exclusivement au site de récolte. Nous avons récolté des moules à 6 sites le long d'une portion de 8 km de la rive du lac Érié et avons constaté que la relation entre la longueur du septum et la longueur de la coquille varie significativement d'un endroit à l'autre et d'une espèce à l'autre. Nous avons ensuite comparé la régression entre la taille des Moules quagga à l'un des sites avec la taille des valves intactes de moules trouvées chez des fuligules (*Aythia marila*, *Aythia affinis*) récoltés au même endroit. Bien que la couverture de glace au moment de l'échantillonnage ait pu empêcher les fuligules de s'éloigner du site en cherchant leur nourriture dans la zone étudiée, les régressions se sont encore avérées significativement différentes, indiquant que les oiseaux s'étaient nourris aussi ailleurs. Nos résultats indiquent que, du moins à certains sites d'étude, la mesure des septums pour estimer la taille des moules n'est pas une méthode appropriée. Cependant, lorsque des valves intactes sont trouvées chez un prédateur, il est possible d'utiliser la variation dans la morphologie de la coquille pour confirmer ou nier la prise de nourriture à certains endroits.

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Introduction

In both Europe and North America, zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) have become an important prey resource for indig- enous predators, particularly fish and diving waterfowl (reviews in Stanczykowska 1977; Mackie et al. 1989; French 1993; Hamilton and Ankney 1994; among others). The impacts of fish predation on fish and mussel populations are unclear. Waterfowl predation, however, has been regularly

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Fig. 1. Variation in the relationship between shell length and septum length among mussels in European and North American lakes, using left valves. When right valves are used, differences among studies are similar. A, Point Pelee, western Lake Erie (Hamilton 1992); B, Lake Sniardwy (Prejs et al. 1990); C, Lake Beldamy (Olszewski 1978); D, Lake St. Clair (Hamilton 1992); E, Plas Leblanc (Draulans and Wouters 1988). The insert gives an interior view of a dreissenid mussel valve. The septum is measured as distance x–y and mussel length as distance x–z.
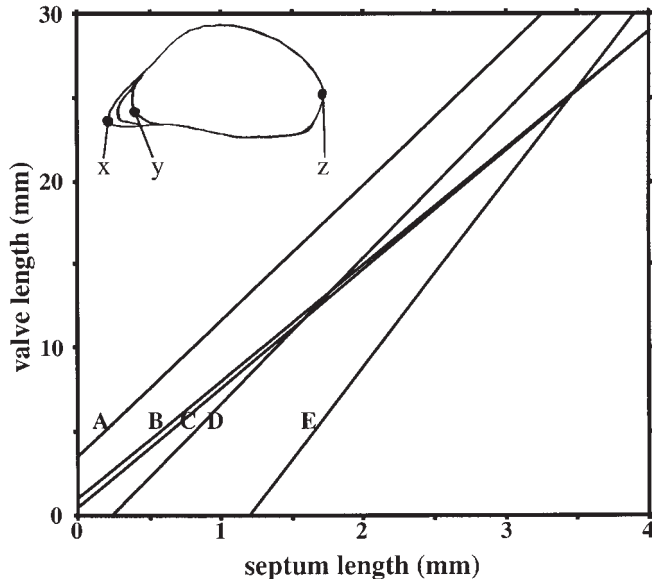
invoked as at least a seasonal structuring element of both European and North American zebra mussel populations (reviews in Stanczykowska 1977; Mackie et al. 1989; Hamilton and Ankney 1994). Further, changes in waterfowl migration patterns on both continents have been attributed to patterns of occurrence of zebra mussels (Pedroli 1981; Stanczykowska et al. 1990; Suter and Van Eerden 1992; Wormington and Leach 1992). To date, Mitchell (1995) has provided the only report of predator impacts on quagga mussel populations, but waterfowl and, potentially, fish predation may likewise affect quagga mussel density and population size structure as this species' range expands.

In many cases, fish and waterfowl predators appear to respond to size-related changes in mussel handling time and caloric value by preying preferentially on mussels of particular size classes (e.g., Draulans 1982, 1984; Draulans and Wouters 1988; Prejs et al. 1990; de Leeuw and van Eerden 1992; Hamilton and Ankney 1994; review in Mitchell 1995). Size-selective predation may be important because, where predation does have an effect on local mussel populations, predators' size preferences will influence the nature of that effect. Such preferences are also important from a predator's perspective: if predators consume only mussels of specific size classes, total mussel biomass will not be an adequate measure of resource availability.

A predator's size preferences are often inferred from comparisons of the frequency distribution of mussel sizes in the predator's gastrointestinal (GI) tract with that available where the predator was collected. This approach is not straightforward because fish predators typically crush mussel shells

using pharyngeal teeth and, while intact mussels can be found in the esophagus and crop of waterfowl, those found in gizzards are also crushed. Fortunately, the internal septa of mussel valves generally remain intact. (The septum is an internal structure at the shell umbo; see Fig. 1 insert). Therefore, beginning with Olszewski (1978), researchers have taken advantage of a strong relationship ($r^2 > 0.9$) between lengths of mussel valves and those of septa in order to infer patterns of predation from septa rather than from intact valves (Olszewski 1978; Draulans and Wouters 1988; Prejs et al. 1990; Hamilton 1992; Hamilton and Ankney 1994; Hamilton et al. 1994; French and Love 1995; Tucker et al. 1996).

This study examines three assumptions implicit in this use of a relationship between shell length and septum length to examine size-selective predation on dreissenid mussels: (1) The relationship between septum length and valve length is assumed to be site-independent within a study area. This assumption is risky because the shell length : septum length relationship does vary appreciably among study areas (Fig. 1). Roe and MacIsaac (1997) have described depth-related variation in other aspects of quagga mussel morphology. In the only study to consider the possibility of variation within a site, Hamilton (1992) found that the relationship for mussels in western Lake Erie differed from that in neighbouring Lake St. Clair. Even here, though, no attempt was made to confirm that shell morphology was consistent within either lake. (2) To date, studies in which inferences were made from mussel septa have been conducted where only zebra mussels are present, but this will become more difficult as the quagga mussel's North American range expands. The continued use of septa to estimate valve lengths in dreissenid mussels entails making the assumption that shell length : septum length relationships of the two species are the same. Our experience has been that, while intact valves of the two mussel species can be readily distinguished, their septa cannot. (3) Predators are assumed to have fed exclusively in the study area; that is, septa taken from a predator collected in the study area are assumed to have been consumed there by the predator. When this assumption is not met, two difficulties arise: (*i*) the appropriate shell length : septum length relationship is not known. (This is assumption 1 at a coarser spatial scale.) (*ii*) The size-frequency distribution of mussels at the actual foraging site, with which the size distribution of consumed mussels should be compared, is not known.

We tested these assumptions using mussels collected near the Nanticoke Generating Station in eastern Lake Erie. Both quagga and zebra mussels occur at Nanticoke, where they are preyed on by staging and overwintering diving ducks, particularly greater and lesser scaup (*Aythya marila*, *Aythya affinis*) and bufflehead (*Bucephala albeola*), and by at least one fish species, freshwater drum (*Aplodinotus grunniens*) (Mitchell 1995). Waterfowl are attracted to warm water discharged from the generating station's condenser cooling system. A plume of warm water runs east from the discharge canal mouth and creates an ice-free hole during winter (McCullough 1984). We tested assumptions 1 and 2 by measuring shell and septum lengths of quagga and zebra mussels taken from 6 sites along an 8-km stretch of shoreline encompassing the generating station. Assumption 3 was addressed by comparing the shell length : septum length relationship of

Fig. 2. Location of the study area, Nanticoke, along the northeastern shoreline of Lake Erie, and of specific sample collection sites at Nanticoke. For each site, depth and water temperature at that depth (at the time of collection) are given. Collection-site names are taken from Mitchell et al. (1996).
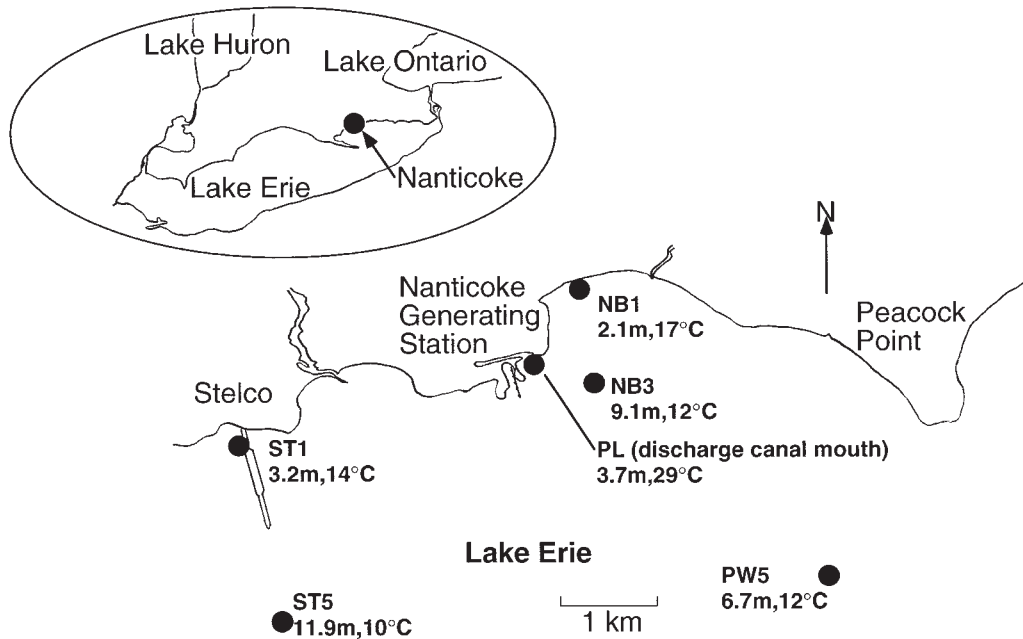
intact mussels from scaup esophagi with that of mussels from the site of scaup collection. If ducks foraged exclusively at the study site, the regression of shell length on septum length from mussels consumed by ducks should match that of mussels taken from the collection site. This is a conservative test of assumption 3 because intact valves will have been consumed more recently than the septa of mussels already crushed.

Methods

Nanticoke is on the northeast shore of Lake Erie, at the northeastern tip of Long Point's outer bay. Mussels were collected here in June 1993 from a subset of sites used in a more extensive survey of nearshore mussel densities at Nanticoke (Mitchell et al. 1996) (Fig. 2). Sites were selected to reflect the range of environments present within the study area. From mussel collections made at each site, shell and septum lengths of approximately 30 quagga and 30 zebra mussels were measured. We tried to ensure the use of an even distribution of mussel sizes across the range present. Large mussels were rare, and so tended to be underrepresented, and mussels less than 4–5 mm long were excluded because handling, measurement, and species identification became difficult. Beyond these constraints, no formal protocol was followed in selecting mussels.

Scaup were collected at site PL in February 1994. Throughout February, Lake Erie was frozen over nearshore, so that birds overwintering at the site were confined to the ice-free hole at the mouth of the generating station's discharge canal. Nineteen greater scaup were shot early in the month. Later the same month, a further 18 greater and lesser scaup were found dead in the outflow canal, having apparently starved after depleting the local mussel population below the density needed for subsistence (Mitchell 1995). The upper GI tract of each bird was removed and the contents were examined for the presence of intact mussels and mussel shell fragments.

Mussel shell length was measured under low power ($6.4\times$) and septum length, under medium power ($16\times$) of a dissecting micro-

scope using a camera lucida and Digitize software (Version 1.3, R. Hopcroft, Zoology Department, University of Guelph).

Differences in the relationship between septum length and valve length were assessed using analysis of covariance (ANCOVA) in SYSTAT (Wilkinson 1989) to estimate the effects of site and mussel species on valve length, with septum length as a covariate. The shell length : septum length relationship is known to differ between the left and right valves, so we analyzed data for the two valves separately. Analyses were initially run with all interaction terms included. Nonsignificant interactions were then sequentially removed. Using this approach, a significant effect can appear as an interaction with the covariate (a difference in regression slopes) or as direct effect of mussel species or source after that interaction term has been removed (a difference in regression intercepts). We used separate ANCOVAs to compare the shell length : septum length regression for intact valves taken from waterfowl GI tracts with that for mussels collected at site PL. In testing this third assumption, we initially ran separate analyses of left and right valves, but also used all valves in a single ANCOVA (see below).

Results

Zebra mussels were less abundant than quagga mussels at Nanticoke. At site NB3 we obtained only 14 zebra mussels, and at site PL only 2. Site PL was therefore excluded from some analyses. The relationship between shell length and septum length was strong for all combinations of species and site using left or right valves ($r^2 > 0.9$ in all but two cases and >0.95 in most) (Table 1). Using left valves, the three-way interaction between site, species, and septum length was not significant (ANCOVA, $F_{[5,296]} = 0.7$, $p = 0.6$), but when that term was removed, the two-way interaction between site and species was significant (ANCOVA, $F_{[5,302]} = 2.4$, $p = 0.04$). Using right valves, the three-way interaction term was suggestive (ANCOVA, $F_{[5,296]} = 2.1$, $p = 0.07$) and, when removed, also left a significant two-way interaction

Table 1. Variation in the relationship between septum length and valve length for left and right valves of quagga and zebra mussels at the six sites sampled.

	Quagga mussels				Zebra mussels				Between species
Site	Slope	Intercept	r^2	n	Slope	Intercept	r^2	n	
Left septa									
NB1	7.94±0.26	0.16±0.29	0.97	29	6.69±0.72	1.04±1.04	0.78	26	Slope: $F_{[1,51]} = 3.3, p = 0.08$; Intercept: $F_{[1,52]} = 6.5, p = 0.01$
NB3	8.67±0.31	−0.25±0.34	0.96	30	8.44±0.36	−0.23±0.39	0.98	14	Slope: $F_{[1,40]} = 0.2, p = 0.66$; Intercept: $F_{[1,41]} = 0.6, p = 0.45$
PL	8.06±0.31	0.18±0.38	0.96	30	—	—	—	—	—
PW5	7.67±0.29	0.17±0.27	0.96	34	7.33±0.45	0.40±0.55	0.90	31	Slope: $F_{[1,61]} = 0.4, p = 0.5$; Intercept: $F_{[1,62]} = 0.5, p = 0.5$
ST1	8.16±0.26	−0.08±0.29	0.97	34	7.34±0.43	0.70±0.48	0.91	30	Slope: $F_{[1,60]} = 2.8, p = 0.1$; Intercept: $F_{[1,61]} = 0.2, p = 0.6$
ST5	8.75±0.28	0.01±0.33	0.97	31	7.91±0.16	−0.04±0.20	0.99	30	Slope: $F_{[1,57]} = 6.2, p = 0.02$
Among sites	Slope: $F_{[5,176]} = 2.2, p = 0.06$; Intercept: $F_{[5,181]} = 4.7, p < 0.001$				Slope: $F_{[4,121]} = 2.2, p = 0.07$; Intercept: $F_{[4,125]} = 3.2, p = 0.015$				
Right septa									
NB1	8.78±0.30	−0.10±0.31	0.97	29	7.50±0.55	0.18±0.77	0.88	26	Slope: $F_{[1,51]} = 4.4, p = 0.04$
NB3	9.23±0.35	−0.40±0.37	0.96	29	8.17±0.40	0±0.43	0.97	14	Slope: $F_{[1,39]} = 3.55, p = 0.07$; Intercept: $F_{[1,40]} = 4.18, p = 0.048$
PL	8.27±0.24	0.07±0.29	0.98	30	—	—	—	—	—
PW5	8.04±0.32	0.07±0.29	0.95	34	7.66±0.39	0.06±0.47	0.93	31	Slope: $F_{[1,61]} = 0.6, p = 0.5$; Intercept: $F_{[1,62]} = 5.1, p = 0.03$
ST1	9.18±0.24	−0.65±0.25	0.98	34	7.11±0.43	0.87±0.48	0.91	30	Slope: $F_{[1,60]} = 19.1, p < 0.001$
ST5	9.42±0.24	−0.41±0.27	0.98	31	7.77±0.22	0.12±0.26	0.98	30	Slope: $F_{[1,57]} = 25.7, p < 0.001$
Among sites	Slope: $F_{[5,175]} = 4.0, p = 0.002$				Slope: $F_{[4,121]} = 1.1, p = 0.37$; Intercept: $F_{[4,125]} = 1.4, p = 0.24$				

Note: Slopes and intercepts, along with standard errors, are from ordinary least squares regressions. Only two zebra mussels were found at site PL. Also given are the results of ANCOVAs testing for among-site and between-species differences in these regressions. In each case the result of a test of common slope (an interaction between septum length and either site or mussel species) is presented first, and then, where differences in regression slopes are not evident, the results of tests of intercept differences with a common slope assumed.

Table 2. Results of ANCOVAs comparing the shell length : septum length relationship for quagga mussels collected at site PL with that for mussels from GI tracts of ducks collected at site PL.

	Effect	F	df	p
Left valve	Septa × source	2.3	1,123	0.13
	Source	3.6	1,124	0.06
Right valve	Septa × source	3.4	1,126	0.07
	Source	2.1	1,127	0.15
Both valves	Septa × source × left/right	0.01	1,249	0.94
	Septa × left/right	0.77	1,250	0.38
	Septa × source	5.6	1,250	0.02
	Source × left/right	0.22	1,250	0.64

Note: "Source" refers to duck GI tract or site, "septa" to septum length, and "left/right" to the left or right septum. First, the data for the left and right septum were analyzed separately. From each, the result of a test for common slope (the effect of the septa × source interaction) in the saturated model is given, and then the result of a test for an intercept difference (source) with the interaction term removed. Then the data for the left and right valves were combined and the left/right septum was treated as a third variable in a single ANCOVA. From this analysis, the results of the F test for the three-way interaction (septa × source × left/right) in the saturated model are given, and then the results of tests for effects of the three two-way interactions when the model was rerun without the three-way interaction term.

between site and species (ANCOVA, $F_{[5,301]} = 3.29$, $p = 0.007$). Since, for both left and right valves, differences among levels of one factor varied with the value of the other, we split the data by species in both cases to evaluate site differences (assumption 1), and by sites to evaluate species differences (assumption 2).

Test of assumption 1

For quagga mussels, the relationship between shell length and septum length varied significantly among sites for both left ($p < 0.001$) and right ($p = 0.002$) valves. Site differences were clearly present when zebra mussel left valves were used ($p = 0.015$) but not with right valves ($p = 0.24$) (Table 1).

Test of assumption 2

Using left septa, differences between the species were apparent at sites NB1 and ST5 ($p = 0.013$, $p = 0.016$) but not at site NB3, PW5, or ST1 ($p > 0.4$) (Table 1). For right valves, between-species differences were significant at all five sites ($p < 0.05$) (Table 1). Site PL is not included in this analysis.

Test of assumption 3

Six of the scaup contained a total of 217 intact valves. Of these, 197 (97 left, 100 right) were from quagga mussels. When left and right quagga mussel valves were analyzed separately, differences between regression slopes (left valves) or intercepts (right valves) approached significance ($p = 0.06$, $p = 0.07$) (Table 2). We then combined data from the two valves and ran a single ANCOVA in which left/right valve was a third factor. The three-way interaction was not significant ($p = 0.94$). When this term was removed, the two-way interaction between septum length and mussel source (duck GI tract or site PL) was significant (Table 2). That is, after controlling for whether septa were from left or right valves,

we found that septa from the consumed quagga mussels were too long relative to valve length for those mussels to have been consumed at site PL (Fig. 3). Zebra mussels' rarity at site PL precluded any comparison using that species' valves.

Discussion

None of the three assumptions tested was validated. Shell length : left septum length regressions for both species varied among sites. Right valve regressions for quagga mussels varied among sites but those for zebra mussels did not. At most sites, regressions differed between species. Finally, waterfowl had apparently not been foraging exclusively at the site where they were collected.

Among-site differences would lead to increasingly biased estimates of shell length with larger mussels. Excluding site NB1, the only site at which the correlation coefficient was not consistently greater than 0.9, the most extreme difference was found between quagga mussel right valves at sites PW5 and ST5. From a 4-mm septum one would infer a 32.2-mm quagga mussel at PW5 but a 37.2-mm mussel at ST5. Site ST5 is west of the discharge canal mouth, and is unaffected by it. Site PW5, 4 km east of the canal mouth, is the least affected of the eastern sites. Thus, differences in quagga mussel morphology between sites ST5 and PW5 are unlikely to be caused by the warm-water plume.

For zebra mussel right valves, among-site variation was not significant, a result that could be interpreted as supporting the use of right valves at sites where only this species is present. In our opinion, though, it would be risky to assume that such consistency in the shell length : right septum length relationship is widespread. The evidence of among-site variation in quagga mussels and in zebra mussel left valves argues for a similar potential for variation in zebra mussel right valves.

Interspecies differences were also found at several sites. For a given valve length, quagga mussels tended to have smaller septa than zebra mussels. This difference was significant at all sites when right valves were used and at 2 of 5 sites when left valves were used. Again the error magnitude was potentially large: at site ST1, a 4-mm right septum would be used to infer a 37.2-mm quagga mussel but a 29.3-mm zebra mussel. Depending on the nature of the shell fragment containing the septum, it may be possible to determine the species from which that septum came, but in other cases we suspect that identification errors would be frequent.

Most startling were the results of our examination of mussels consumed by scaup. The shell length : septum length relationship for these mussels differed significantly from that of mussels at site PL, where the ducks had been collected. At the time, PL was the only ice-free site within the study area, so we conclude that the scaup had been foraging elsewhere. The abundance of zebra mussels in duck GI tracts supports this conclusion: 9% of intact valves in scaup were from zebra mussels, but we found only 2 zebra mussels among the dreissenids collected at site PL. In October 1993, zebra mussels accounted for less than 1% of total dreissenid abundance at PL (J.S. Mitchell, R.C. Bailey, and R.W. Knapton, unpublished data). Even using intact valves, presumably from

Fig. 3. Relationship between shell length and septum length for intact valves taken from scaup GI tracts and for valves from mussels collected at site PL (the site at which scaup were collected).
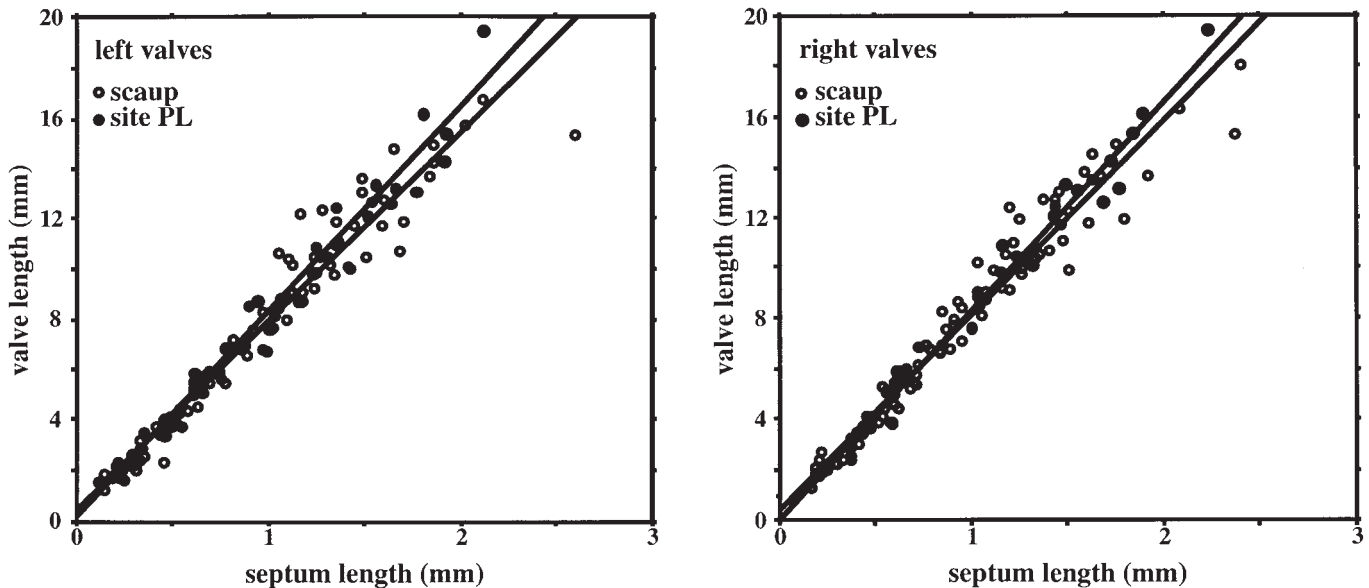
recently consumed mussels, and with a restricted local foraging area, size-selective predation cannot be adequately quantified by comparing the mussel size distribution at the collection site with that in a predator's GI tract. Using septa from mussels consumed earlier would compound this problem. If predators forage outside the study area, the appropriate shell length : septum length regression and the size-frequency distribution of the relevant mussel population are both unknown.

Using a broader collection area to obtain mussels for shell length : septum length regressions does not solve these problems. Unless site weighting in the regression corresponds to site utilization by the predator, estimates will be biased. Moreover, as the predator cannot be assumed to have selected sites randomly within the study area, the degree of bias introduced cannot be measured. At best, if a broad collection area is used, the maximum bias can be estimated through a comparison of site-specific regressions and, in some cases, one may then conclude that the bias is acceptable, particularly if predation is on smaller mussels. The approach still assumes that the predator is known to have foraged exclusively within the study area.

Where among-site variation in shell morphology results in an unacceptable bias, two alternatives to the use of septa exist. The use of predator-exclosure cages is one. Hamilton et al. (1994), Mitchell (1995), and Boles and Lipcius (1997) have successfully used exclosures to restrict predator access to dreissenid mussels. Size selectivity can then be inferred from differences beneath and adjacent to cages following predation. This method is sound but labour-intensive. Alternatively, the upper GI tract of waterfowl predators frequently contains intact valves, which may allow an accurate estimate of size selectivity if the bird's recent history is known. For example, waterfowl caught accidentally in fishing nets may be assumed to have foraged near where the net was deployed. In such cases, comparison of the shell length : septum length relationship at the collection site with that

from intact valves in the predator's GI tract may prove a useful supplementary means of confirming that the predator was foraging at the site. In this study, such a comparison indicated that valves, although still intact, were from mussels consumed outside the study area, an observation that emphasizes the need for more direct knowledge of the predator's recent history.

While we have focused on dreissenid mussels, our conclusions may also be applicable to other systems in which similar assumptions are made. For example, in his initial description of reconstructing mussels from septa, Olszewski (1978) outlined a similar technique for estimating gastropod size from operculum size. Stein et al. (1975) also used this approach. Inferring gastropod size from operculum size entails the same assumptions and may generate the same problems as we have demonstrated for dreissenid mussels.

Acknowledgments

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