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Adaptive variation in palp and gill size of the zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*)

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Abstract: Significant interpopulation differences occur in palp to gill area ratios of two nonindigenous species of freshwater bivalves in North America, *Dreissena polymorpha* and *Corbicula fluminea*. Larger palps (both species) and smaller gills (*C. fluminea*) occur in individuals from habitats characterized by a relatively high suspended solids concentration. The extremely brief evolutionary history of both species in North America is strong evidence that these differences in palp to gill area ratios are ecophenotypic.

Résumé : Des différences interpopulations significatives se présentent dans les ratios de surface palpes–branchies chez deux espèces allogènes de bivalves dulçaquicoles en Amérique du Nord, *Dreissena polymorpha* et *Corbicula fluminea*. Les palpes les plus grands (chez les deux espèces) et les branchies plus petites (chez *C. fluminae*) se présentent chez des individus provenant d'habitats charactérisés par une concentration relativement élevée de solides en suspension. L'historique très bref de l'évolution de ces deux espèces en Amérique du Nord montre éloquemment que ces différences dans les ratios palpes–branchies sont écophénotypiques.

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Introduction

Lamellibranch bivalve gills are highly retentive filters that strip virtually all suspended particles from water passed through the mantle cavity. Filtration rate varies in direct proportion to the total area of the gill lamellae (Møhlenberg and Riisgård 1979; Meyerhöfer 1985). Pseudofeces (agglomerations of mucus and filtered particles that are rejected rather than ingested) are produced by the labial palps (Foster-Smith 1978). Pseudofeces production is typically initiated at a relatively low ambient suspended solids concentration and increases as the rate of particle retention on the gills increases (Foster-Smith 1975; Kiørboe et al. 1980).

Positive correlations between the concentration of mostly inorganic suspended solids and palp size of marine bivalves have been reported within closely related species or among different populations of the same species (Nelson 1960; Ansell 1961; Kiørboe and Møhlenberg 1981; Theisen 1982). Furthermore, the degree to which food and nonfood particles are sorted has been positively correlated with palp size (Kiørboe and Møhlenberg 1981). Theisen (1982) reported an inverse relationship between gill size and suspended solids concentration. It is unclear if such habitat-related differences are genetic or ecophenotypic (Theisen 1982). No such studies of freshwater bivalve populations have been conducted. Differences among populations in palp and gill size have received far less attention than functional responses of bivalves to suspended solids concentration (see Jørgensen 1990 for review). Both structural and functional adaptations allow filter-feeding bivalves to successfully exploit widely varying habitats.

We describe herein extensive interpopulation differences in palp and gill size in relation to the ambient suspended solids concentration experienced by two nonindigenous freshwater bivalves in North America, *Dreissena polymorpha* and *Corbicula fluminea*. Both species are recent introductions to North America, ecologically important due to their widespread abundance and economically important biofoulers. *Dreissena polymorpha* became established in Lake St. Clair of the Great Lakes in approximately 1986 (Hebert et al. 1989; Roberts 1990). *Corbicula fluminea* was introduced into the Pacific Northwest of the United States in approximately 1924 (McMahon 1982). The brief evolutionary history of both species in North

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America is especially relevant to an evaluation of the genetic versus ecophenotypic basis of intraspecific and interpopulation differences in palp and gill size.

Materials and methods

Dreissena polymorpha were collected from an industrial raw water intake along the lower Mississippi River (LMR) in Baton Rouge, La., and from the Black Rock Canal (BRC), a side channel of the Niagara River, in Buffalo, N.Y. *Dreissena polymorpha* has been in BRC for no more than 6 years and in LMR for no more than 2 years. The LMR at Baton Rouge drains approximately 2.9×10^6 km^2 (USGS 1988–1993*a*) and has an average discharge of 9.5×10^3 $m^3 \cdot s^{-1}$ (USACE 1977–1993). Suspended solids concentration in the LMR near Baton Rouge typically ranges from 75 to 400·$mg \cdot L^{-1}$ and averages approximately 100 $mg \cdot L^{-1}$ during sustained low discharge (USGS 1988–1993*a*). Suspended solids are largely inorganic; concentration of total organic carbon in unfiltered water samples averages only 3% of total suspended solids concentration (USGS 1988–1993*a*). The Niagara River near the Black Rock Canal site drains approximately 6.8×10^5 km^2 and has an average discharge of 5.8×10^3 $m^3 \cdot s^{-1}$ (USGS 1988–1993*c*). Suspended solids concentration is much lower in the Niagara River, usually ranging from 1 to 6 $mg \cdot L^{-1}$, although highs of approximately 30–70 $mg \cdot L^{-1}$ are occasionally measured (USGS 1988–1993*c*).

Corbicula fluminea were collected from the Tensas River (TEN) in northeast Louisiana and the Tangipahoa River (TAN) in southwest Mississippi. *Corbicula fluminea* probably has been in TEN and TAN for less than 35 years (McMahon 1982). The TEN is a muddy river. At the site sampled, the TEN drains approximately 8.0×10^2 km^2 of mostly cotton and soybean fields and has average discharge of 9.9 $m^3 \cdot s^{-1}$ (USGS 1988–1993*a*). Suspended solids, comprised mostly of clay (microscopic inspection), range in concentration from 30 to 500 $mg \cdot L^{-1}$, with values of 50–100 $mg \cdot L^{-1}$ typifying low discharge periods (USGS 1988–1993*a*). At the site sampled, the TAN is a headwater stream with a sand and gravel bed. Drainage area is approximately 2.0×10^2 km^2 of mostly forest and livestock rangeland, and discharge averages less than 2 $m^3 \cdot s^{-1}$ (USGS 1988–1993*b*). Suspended solids at this TAN site average less than 5 $mg \cdot L^{-1}$ (Way et al. 1990).

Shell length (SL), width (SW), and height (SH) were measured to the nearest 0.01 mm using digital calipers. Analyses of covariance did not reveal any significant interpopulation variation in shell morphometries (linear regressions of SW and SH on SL and of SW on SH) of either species. Thus, interpopulation comparisons of palp (PA) and gill area (GA) were based on covariance of these areas with SL. Palp area estimates included both ciliated medial surfaces of the right and left palps; gill area estimates were for both ascending and descending lamellae of all four demibranchs. Area measurements were made to the nearest 0.1 mm^2 from magnified images of excised organs using a high-resolution video camera and associated image analysis software. Both PA and GA were estimated in units of square millimeters; ratios of PA/GA were multiplied by 100 to express PA as a percentage of GA.

Results

Average PA/GA was 3.6 times higher in *D. polymorpha* from LMR (high suspended solids) than BRC (low suspended solids) ($t = 17.5$; $p < 0.001$) (Fig. 1). The average SL, PA, and GA of *D. polymorpha* from LMR equaled 14.6 ± 3.3 mm, 13.4 ± 8.0 mm^2, and 139 ± 76 mm^2 (mean ± SD), respectively. Individual SLs ranged from 10.6 to 20.8 mm. *Dreissena polymorpha* from BRC had average SL, PA, and GA of 22.7 ± 7.0 mm, 9.4 ± 5.3 mm^2, and 363 ± 191 mm^2, respectively. Individual SLs ranged from 11.4 to 33.6 mm.

Analyses of covariance revealed that *D. polymorpha* interpopulation differences in regressions of PA on GA and of PA on SL were highly significant, but that regressions of GA on SL were not significantly different (Table 1). Based on regressions summarized in Table 1, predicted PA of a 20-mm-long individual from LMR and BRC equaled 26.2 and 7.5 mm^2, respectively. Predicted GA of a 20-mm-long individual from LMR and BRC differed only slightly and equaled 262 and 291 mm^2, respectively.

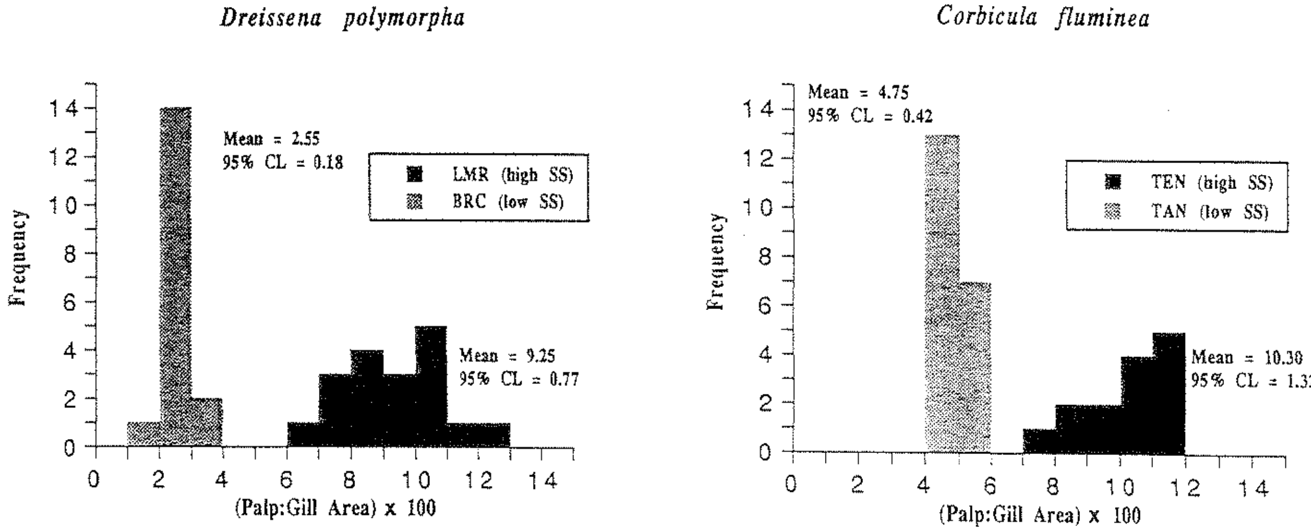
Similar to *D. polymorpha*, average PA/GA was 2.2 times higher in *C. fluminea* from TEN (high suspended solids) than TAN (low suspended solids) ($t = 10.7$; $p < 0.001$) (Fig. 1). Average SL, PA, and GA of *C. fluminea* from TAN equaled 23.5 ± 8.7 mm, 50.3 ± 28.2 mm^2, and 465 ± 246 mm^2, respectively. Individual SLs ranged from 9.3 to 32.4 mm. Average SL, PA, and GA of *C. fluminea* from TEN equaled 21.1 ± 6.8 mm, 25.3 ± 14.5 mm^2, and 516 ± 273 mm^2, respectively. Individual SLs ranged from 8.7 to 38.3 mm.

Unlike *D. polymorpha*, interpopulation differences in PA/GA of *C. fluminea* were the result of significant differences in both palp and gill size. Analyses of covariance revealed significant interpopulation differences in regressions of PA on GA, PA on SL, and GA on SL (Table 1). Based on regressions summarized in Table 1, predicted PA of 20-mm-long *C. fluminea* from TEN and TAN equaled 39.0 and 23.2 mm^2, respectively. Predicted GA of a 20-mm-long *C. fluminea* from TEN and TAN equaled 367 and 475 mm^2, respectively.

Discussion

Palp and gill size of marine and freshwater lamellibranch bivalves varies between and within populations. Such variation appears to be adaptively related to variation in suspended solids conditions. Kiørboe and Møhlenberg (1981) and Theisen (1982) observed larger palps in *Mytilus edulis* from sites characterized by high versus low concentrations of mostly inorganic solids. Similar adaptive variation in palp size of other marine bivalves has been reported (Nelson 1960; Ansell 1961). In addition to palp size variation, Theisen (1982) showed that *M. edulis* had smaller gills at a turbid than nonturbid site. Franz (1993), sampling from a single population, measured larger gills in another mytilid mussel, *Geukensia demissa*, from the high versus low intertidal zone. He attributed this difference to briefer submersion, and, thus, reduced time for feeding by high intertidal mussels. In the present study of freshwater bivalves, distinct interpopulation differences were measured

Fig. 1. Palp to gill area ratios of *Dreissena polymorpha* and *Corbicula fluminea* from sites characterized by a high versus low suspended solids (SS) concentration (CL, confidence limits).



in both palp and gill area of *C. fluminea* and palp area of *D. polymorpha*. As with marine bivalves, these differences were associated with intersite differences in suspended solids concentration.

Some basic aspects of gill and palp function must be discussed to support speculation on the adaptive value of palp and gill size variation (see Jørgensen 1990 for a detailed review of the functional morphology of palps and gills). Møhlenberg and Riisgård (1979) as well as Meyerhöfer (1985) demonstrated strict proportionality of clearance rate to gill area of several species of filter-feeding bivalves. Under conditions of limited food availability, involving very low suspended solids concentrations, increased gill area may enhance filtration potential.

Pseudofeces production by the palps varies with both the quality and quantity of material filtered. Kiørboe and Møhlenberg (1981) showed that palp size was positively correlated with the ability of *M. edulis* and nine other marine lamellibranchs to sort nonfood from food particles. However, even pure algal suspensions elicit production of copious quantities of pseudofeces if filtration is of a high concentration suspension (e.g., Loosanoff and Engle 1947; Ballantine and Morton 1956). Variation in palp size probably reflects both qualititative and quantitative characteristics of suspended solids.

Both the LMR and TEN sites, where *D. polymorpha* and *C. fluminea*, respectively, had enlarged palps, are characterized by a high suspended solids concentration with a high inorganic component. Indeed, the organic component of suspended solids is typically low when suspended solids concentration is high in natural aquatic habitats (e.g., Reid 1961; Hynes 1970; Widdows et al. 1979; Jørgensen 1990). A high concentration of mainly inorganic particles favors enlarged palps, both to sort food from nonfood particles and to clear excess filtered material regardless of its quality. It is especially noteworthy that gill area of *D. polymorpha* did not significantly differ between populations, suggesting that high filtration rate potential characterizes mussels from sites with either high or low suspended solids concentration. Conversely, *C. fluminea* from TAN had larger gills than individuals from TEN. This difference may reflect trophic limitation at TAN, which has both a low suspended solids concentration and is a headwater stream.

Theisen (1982) speculated that interpopulation differences in palp and gill area of *Mytilus edulis* were genetically based. However, the intrapopulation differences in gill area of *M. edulis* subsequently reported by Franz (1993) almost certainly reflect developmental plasticity that may also apply to interpopulation differences. The present study of freshwater lamellibranchs involved populations that are extremely young in an evolutionary sense, greatly reducing the likelihood of genetic differentiation among populations. Furthermore, *C. fluminea* in North America shows very little genetic variability, appearing to have gone through a severe genetic bottleneck during its introduction (Smith et al. 1979). In contrast, the founding population of *D. polymorpha* in Lake St. Clair showed considerable genetic variability (Hebert et al. 1989), and slight differences in allozyme frequencies have been reported among different Great Lakes populations that have subsequently established (May and Marsden 1992). However, there has been very little time for selection to markedly differentiate North American populations of this species. Thus, developmental plasticity similar to that observed for *M. edulis* gills by Franz (1993) is likely to also characterize gills of *C. fluminea* and palps of both *C. fluminea* and *D. polymorpha*.

Extensive changes in feeding structures occur during early development of lamellibranchs, involving loss of the velum, development of palp and gill primordia, and subsequent enlargement and structural organization of the palps and gills (Meisenheimer 1901; Allen 1961; Bayne 1965). Adaptive structural differences between populations in individual palp and gill size appear to reflect developmental plasticity that is channeled by ambient suspended

Table 1. Regression and analysis of covariance statistics for palp and gill comparisons of *Dreissena polymorpha* from the lower Mississippi River (LMR) and Black Rock Canal (BRC) of the Niagara River and of *Corbicula fluminea* from the Tensas (TEN) and Tangipahoa (TAN) rivers.

Regression	Site	Regression statistics ($Y = a + bX$) a	b	r^2	F	p
		Dreissena polymorpha				
Palp area on gill area	LMR	−0.855	0.102	0.931	156	<0.0001
	BRC	−0.444	0.0272	0.962		
Palp area on shell length	LMR	−21.4	2.38	0.970	236	<0.0001
	BRC	−7.25	0.735	0.954		
Gill area on shell length	LMR	−188	22.5	0.961	2.11	>0.10
	BRC	−237	26.4	0.947		
		Corbicula fluminea				
Palp area on gill area	TEN	−2.66	0.114	0.988	352	<0.0001
	TAN	−1.92	0.0529	0.990		
Palp area on shell length	TEN	−25.0	3.20	0.985	53.4	<0.001
	TAN	−18.2	2.07	0.955		
Gill area on shell length	TEN	−193	28.0	0.986	22.9	<0.001
	TAN	−305	39.0	0.955		

Note: F values of covariance analyses are for intraspecific, interpopulation comparisons of b. Palp and gill area are expressed in mm^2 and shell length in mm.

solids concentration. This structural adaptability of lamellibranchs to spatially variable conditions, combined with more thoroughly studied functional responses to temporally variable conditions (see Jørgensen 1990), allows these filter feeders to successfully exploit a wide range of habitat conditions.

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