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PALP TO GILL AREA RATIO OF BIVALVES: A SENSITIVE INDICATOR OF ELEVATED SUSPENDED SOLIDS

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ABSTRACT

Area measurements were made of the gills and labial palps of several freshwater bivalve species from sites with distinctly different suspended solids concentrations. Without exception, the palp to gill area ratio (PA : GA) was markedly higher for populations from sites with high versus low suspended solids concentrations. The average PA : GA (expressed as a percentage) ranged from 9·3 to 11·5 for bivalves from high suspended solids concentration sites and from 2.5 to 4.8 for bivalves from low suspended solids concentration sites. Such interpopulation differences were observed for two introduced species, *Dreissena polymorpha* and *Corbicula fluminea*, despite extremely brief residence times in an evolutionary sense. At any particular location, different species of native unionids had similar PA : GA. These results suggest that PA : GA is a sensitive biological indicator of suspended solids concentration, with interpopulation differences probably reflecting ecophenotypic rather than genetic variation.

KEY WORDS bivalves; ecophenotypic variations; freshwater bivalves; gills; palps; suspended solids; suspended solids effects

INTRODUCTION

The development and use of large floodplain rivers for waste assimilation and commercial and recreational navigation traffic typically causes increased concentrations of ambient suspended solids (Rasmussen, 1983; Wilber, 1983). Agricultural runoff, exacerbated by urban development, contributes substantial sediment loads to lotic systems. The passage of environmental legislation in the USA has directed construction agencies to monitor suspended solids associated with the construction and operation of their facilities. This requires that biologists and planners differentiate between short-term impacts, such as the passage of a commercial vessel or dredging and dredged material disposal, versus sustained increases in suspended solids due to agriculture input or poor land-use practices. Degraded water quality is often best monitored through the assessment of the biota rather than through measurement of specific physical or chemical parameters, which can exhibit considerable temporal and spatial variation (Hynes, 1966; Rosenberg and Resh, 1993).

Freshwater lamellibranch bivalves are an ecologically and economically important component of the benthos of most medium-sized to large floodplain rivers. These bivalves are highly efficient filter-feeders, stripping virtually all suspended particulate material from water that is passed, more or less continuously, through their gills (McMahon, 1991). Bivalves respond to elevated suspended solids to avoid or minimize overloading of the filtration apparatus. Typically, above an incipient limiting concentration, the clearance rate ($ml\,h^{-1}$) decreases such that the filtration rate ($mg\,h^{-1}$) remains relatively constant (e.g. Winter, 1973; Sprung and Rose, 1988).

Although such functional responses to suspended solids concentration have been extensively studied (for reviews, see Jørgensen, 1990; McMahon, 1991), far fewer studies have focused on structural adaptations. In brief overview, material filtered by the gills passes over labial palps on its way to the mouth, and the palps clear the filtration apparatus of excess material. Rejected material is bound in mucus and periodically spit

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back out the inhalant siphon as pseudofaeces. Studies of marine bivalves have indicated that individuals from habitats with high suspended solids concentrations have larger palps (Kiørboe and Møhlenberg, 1981; Theisen, 1982) and smaller gills (Theisen, 1982) than organisms from less turbid waters.

Recently we have made similar measurements of several riverine bivalve species from sites with distinctly different suspended solids concentrations (Payne *et al.*, 1995 and unpublished data). In the present report, we summarize these palp and gill measurements of riverine bivalves and discuss the utility of these measurements for assessing and monitoring biological effects of increased suspended solids in floodplain rivers.

MATERIALS AND METHODS

Dreissena polymorpha were collected from the lower Mississippi River in Baton Rouge, Louisiana and the Niagara River in Buffalo, New York. The lower Mississippi River is characterized by high suspended solids concentrations, typically ranging from 77 to 400 $mg\,l^{-1}$, with sustained lows of approximately 100 $mg\,l^{-1}$. The Niagara River has suspended solids concentrations usually ranging from 1 to 6 $mg\,l^{-1}$, although April highs of approximately 30 $mg\,l^{-1}$ are measured. *Corbicula fluminea* were collected from the Tensas River in north-east Louisiana and the Tangipahoa River in south-west Mississippi. In addition, six species of unionids were collected for analysis from the Tensas site: *Amblema plicata*, *Megalonaias nervosa*, *Plectomerus dombeyanus*, *Quadrula apiculata*, *Q. pustulosa* and *Q. quadrula*. This site is characterized by suspended solids concentrations ranging from 50 to 300 $mg\,l^{-1}$, with 50–100 $mg\,l^{-1}$ being typical of low discharge periods. In contrast, the Tangipahoa site has suspended solids concentrations less than 5 $mg\,l^{-1}$ during all but the high discharge conditions. These estimates are based on water year reports of the United States Geological Survey, supplemented by our own measurements at the Tangipahoa site. A more detailed account of sites and methods can be found in Payne *et al.* (in press).

Unionids were also collected from the Sunflower River in west Mississippi and the Duck River in central Tennessee. Species analysed from the Sunflower River were *A. plicata*, *Plectomerus dombeyanus*, *Glebula rotundata*, *Lampsilis teres* and *Q. pustulosa*. Species analysed from the Duck River were *Cyclonaias tuberculata*, *A. plicata*, *Truncilla truncata*, *Q. pustulosa*, *Ptychobranchus fasciolaris* and *Lasmigona costata*. The Sunflower site is extremely turbid with a soft, muddy bottom; suspended solids concentrations of at least 50–100 $mg\,l^{-1}$ are typical during sustained low discharge (unpublished data, US Army Corps of Engineers, Vicksburg District). The Duck site has relatively clear water running over bedrock, cobble and gravel; suspended solids concentrations at this site are less than 10 $mg\,l^{-1}$ during low discharge conditions (unpublished data compiled by Dr Ralph Brinkhurst and associates, Aquatic Resources Center, Franklin, TN, USA).

Gill and palp area measurements were made to the nearest 0.1 mm^2 by digitizing the outline of magnified images of excised organs of live mussels using a high resolution video camera and associated image analysis software (Payne *et al.*, in press). Both the left and right palps were excised. Each palp was laid flat with the ciliated surfaces directed upward and, within 60 seconds of excision, a magnified video image was recorded. Thus palp area (PA) refers to a two-dimensional representation of total medial palp surface area per individual mussel. Magnified images of both the inner and outer demibranchs of each gill were recorded within a minute of excision. The total area of both ascending and descending lamellae of each demibranch was estimated by measuring the area of the ascending lamella and multiplying by two. Thus gill area (GA) corresponds to a two-dimensional representation of the inhalent side of all gill lamellae per individual. The shell length (SL) of each individual was measured to the nearest 0.01 mm using dial calipers.

Relationships of PA to GA and of both PA and GA to SL^2 were analysed using reduced major axis regression, a model II procedure (Sokal and Rohlf, 1981). These model II regressions were used due to measurement errors associated with all area and length measurements.

RESULTS

Linear regressions of PA on GA were distinctly different for *D. polymorpha* collected from the turbid lower Mississippi River versus the relatively non-turbid Niagara River, with no overlap occurring between the two

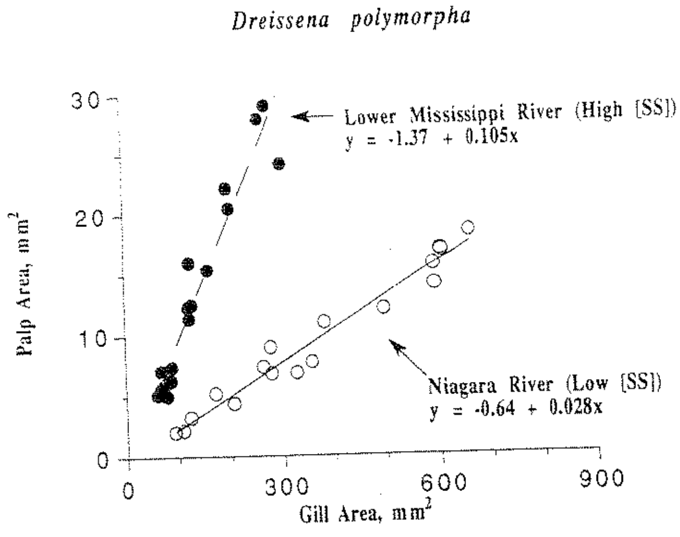


Figure 1. Palp area as a linear function of gill area of *Dreissena polymorpha* from the Niagara River at Buffalo, NY and the Mississippi River at Baton Rouge, LA

populations (Figure 1). The slope of PA on GA was approximately four times greater for lower Mississippi than Niagara River mussels. Average PA : GA was approximately four times greater in *D. polymorpha* from the lower Mississippi versus Niagara River, and equalled ($\pm$SD) $9{\cdot}3 \pm 1{\cdot}5$ and $2{\cdot}5 \pm 0{\cdot}4$ in the two sites ($t = 17{\cdot}5$; $p < 0{\cdot}001$).

Both PA and GA increased as a linear function of SL^2 (Table I). Based on the regressions summarized in Table I, larger palps are responsible for the higher PA : GA of lower Mississippi River *D. polymorpha*. The predicted PA values for 20 mm long individuals from the lower Mississippi and Niagara rivers are 27 and 7 mm^2, respectively. The predicted GA values for 20 mm long individuals are 267 and 264 mm^2. The average SL values for individuals from the lower Mississippi and Niagara rivers are $14{\cdot}6 \pm 3{\cdot}3$ and $22{\cdot}7 \pm 7{\cdot}0$ mm, respectively.

Table I. Regression statistics of palp area (PA) and gill area (GA) on shell length squared (SL^2) of *Dreissena polymorpha* from the lower Mississippi and the Niagara rivers and of *Corbicula fluminea* from the Tensas and Tangipahoa rivers. All variables are expressed in mm^2.

Regression	River	Regression statistics $Y = a + bX$			
		a	b	SD_b	n
Dreissena polymorpha					
PA on SL^2	Mississippi	−3·69	0·0761	0·00395	18
PA on SL^2	Niagara	0·0522	0·0166	0·000735	17
GA on SL^2	Mississippi	−21·9	0·723	0·00337	18
GA on SL^2	Niagara	24·8	0·599	0·00338	17
Corbicula fluminea					
PA on SL^2	Tangipahoa	0·825	0·0501	0·00235	20
PA on SL^2	Tensas	5·30	0·0714	0·00389	14
GA on SL^2	Tangipahoa	54·2	0·943	0·0441	20
GA on SL^2	Tensas	72·2	0·624	0·0323	14

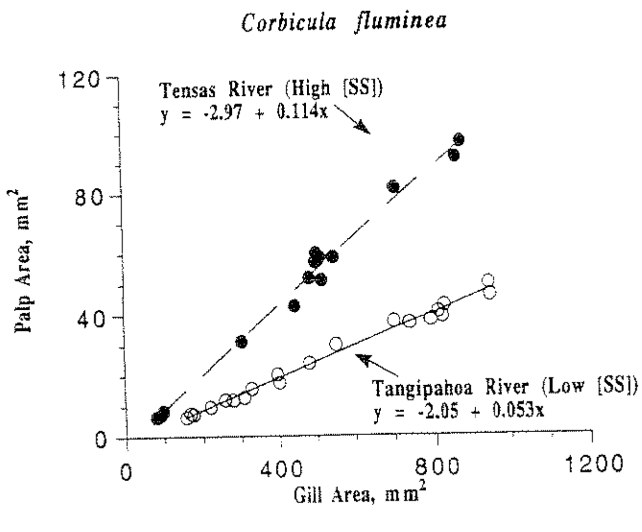


Figure 2. Palp area as a linear function of gill area of *Corbicula fluminea* from the Tensas River, LA and Tangipahoa River, MS

Interpopulation differences in *C. fluminea* were similar to those observed in *D. polymorpha*, with individuals from the turbid Tensas River having distinctly greater PA relative to GA values than individuals from the non-turbid Tangipahoa River (Figure 2). In *C. fluminea*, PA : GA was approximately two times greater in individuals from the site characterized by high suspended solids concentrations, as indicated by the twice higher slope of PA on GA in Tensas River mussels. Average PA : GA values were 10·3 ± 2·3 and 4·8 ± 0·4 in the Tensas and Tangipahoa populations, respectively ($t = 10{\cdot}7$; $0 < 0{\cdot}001$).

Both PA and GA were linear functions of SL^2 (Table I). The slopes of these regressions indicated that intersite differences in PA : GA were a consequence of a combination of larger palps and smaller gills in

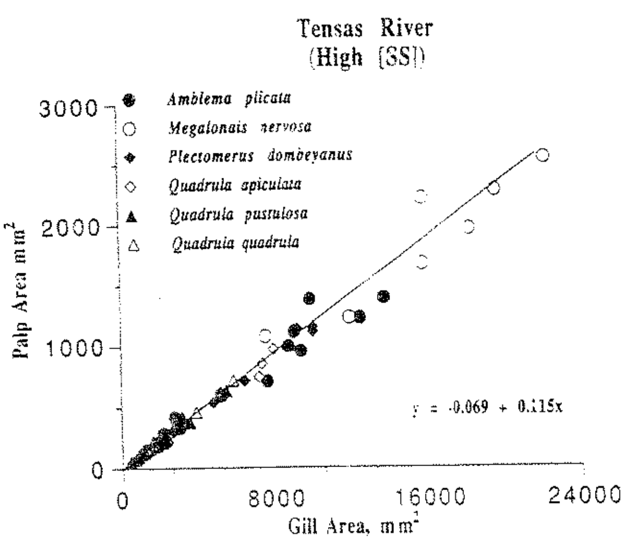
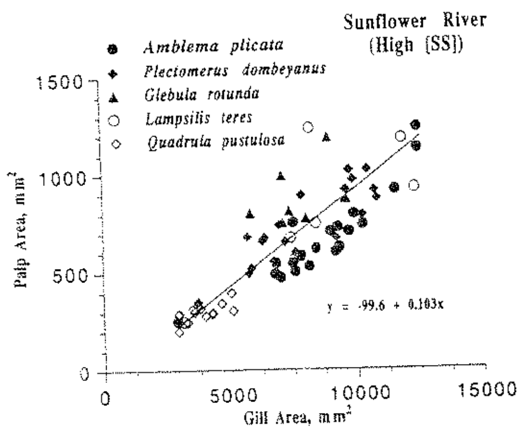


Figure 3. Palp area as a linear function of gill area of several unionid species from the Tensas River, LA

Table II. Regression statistics of palp area (PA) and gill area (GA) on shell length squared (SL^2) of unionids from the Tensas River. All variables are expressed in mm^2

Regression	Species	Regression statistics $Y = a + bX$			
		a	b	SD_b	n
PA on SL^2	*Amblema plicata*	−60·0	0·115	0·00842	10
	Megalonaias nervosa	37.0	0·0928	0·00785	10
	Plectomerus dombeyanus	−33·5	0·0811	0·00651	10
	Quadrula apiculata	−44·4	0·125	0·00768	10
	Quadrula pustulosa	38·1	0·103	0·0136	12
	Quadrula quadrula	18·9	0·103	0·00296	11
GA on SL^2	*Amblema plicata*	−1191	1·11	0·120	10
	Megalonaias nervosa	402	0·794	0·0418	10
	Plectomerus dombeyanus	−409	0·714	0·0479	10
	Quadrula apiculata	−149	1·05	0·0399	10
	Quadrula pustulosa	349	0·884	0·131	12
	Quadrula quadrula	141	0·863	0·0210	12



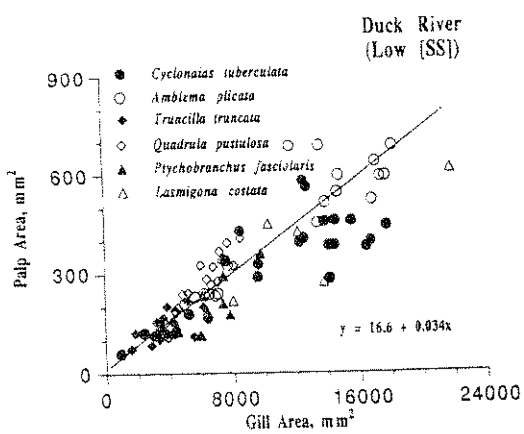


Figure 4. Palp area as a linear function of gill area of several unionid species from the Sunflower River, MS and the Duck River, TN

Table III. Regression statistics of palp area (PA) and gill area (GA) on shell length squared (SL^2) of unionids from the Sunflower and Duck rivers. All variables are expressed in mm^2

Regression	Species	Regression statistics $Y = a + bX$			
		a	b	SD_b	n
Sunflower River					
PA on SL^2	*Amblema plicata*	−329	0·120	0·0160	20
	Plectomerus dombeyanus	−111	0·0913	0·0129	20
	Glebula rotundata	−374	0·176	0·0585	8
	Lampsilis teres	122	0·0773	0·0346	7
	Quadrula pustulosa	102	0·0667	0·0128	14
GA on SL^2	*Amblema plicata*	−1059	1·16	0·0992	20
	Plectomerus dombeyanus	−1305	0·993	0·102	20
	Glebula rotundata	−2123	1·38	0·234	8
	Lampsilis teres	2477	0·682	0·305	7
	Quadrula pustulosa	617	1·09	0·187	14
Duck River					
PA on SL^2	*Cyclonaias tuberculata*	44·7	0·0360	0·00455	21
	Amblema plicata	−17·1	0·0441	0·00312	18
	Truncilla truncata	−6·14	0·0508	0·00765	20
	Quadrula pustulosa	−30·8	0·0649	0·00758	18
	P. fasciolaris	−118	0·0427	0·00756	10
	Lasmigona costata	−247	0·0469	0·0142	6
GA on SL^2	*Cyclonaias tuberculata*	516	1·24	0·0702	21
	Amblema plicata	−428	1·15	0·100	18
	Truncilla truncata	329	1·08	0·109	20
	Quadrula pustulosa	639	1·16	0·0741	18
	P. fasciolaris	−528	0·936	0·146	10
	Lasmigona costata	−8467	1·58	0·167	6

Tensas River versus Tangipahoa River individuals. Base on the regressions summarized in Table I, the predicted PA values for 20 mm long individuals from the Tensas and Tangipahoa rivers are 34 and 21 mm^2, respectively. The predicted GA values for 20 mm long individuals are 322 and 431 mm^2 in the Tensas and Tangipahoa rivers, respectively. The average SL value for individuals from the Tensas River is 21·1 ± 6·8 mm; the average value for individuals from the Tangipahoa River is 23·5 ± 8·7 mm.

A single linear regression adequately described the PA to GA relationships of several unionid species collected from the Tensas River (Figure 3). Thus regardless of species, PA : GA values converged on a single value. Furthermore, the average PA : GA of unionids (11·5 ± 1·3) was similar to the ratio observed in *C. fluminea* (10·3 ± 2·3) from the same site. Table II provides regression statistics, per species, for both PA and GA as linear functions of SL^2: the slopes of PA were approximately an order of magnitude less than the slopes of GA on SL^2.

Similar interspecific convergence of PA : GA characterized unionids from both the Sunflower and Duck rivers (Figure 4). As with *D. polymorpha* and *C. fluminea*, interhabitat differences were clear. The slope of the linear regression of PA on GA for Sunflower River mussels (exposed to high suspended solids concentrations) was three times greater than the slope of PA on GA for Duck River mussels (exposed to low suspended solids concentrations). The average PA : GA values of Sunflower and Duck River unionids were 8·85 ± 1·87 and 3·78 ± 0·95, respectively.

Species-specific relationships of PA and GA on SL^2 are summarized in Table III. Both *A. plicata* and *Q. pustulosa* were obtained from both sites. *Amblema plicata* had comparably sized gills from both locations, but palps were markedly larger in mussels from the relatively turbid Sunflower River than in those from the relatively non-turbid Duck River. In contrast, *Q. pustulosa* showed remarkably similar relationships of PA and GA on SL^2 at both locations, indicating that the characteristic intersite difference in PA : GA did not apply to all species.

DISCUSSION

Many workers have investigated the effects of elevated suspended solids on bivalves (Moore, 1977; Bayne *et al.*, 1979; 1981; Widdows *et al.*, 1979; Bricelj *et al.*, 1984; Robinson *et al.*, 1984; Aldridge *et al.*, 1987). The possible negative effects of elevated suspended solids on freshwater bivalves have been discussed in taxonomic and distributional papers on bivalves (Parmalee, 1967; Stansbery, 1965; 1970; Starrett, 1971; Williams *et al.*, 1993). However, structural adaptations of bivalves to altered suspended sediment concentrations should not be ignored. Our studies of freshwater species (Payne *et al.*, in press, and data reported herein), combined with related studies of marine species (Theisen, 1982; Kiørboe and Møhlenberg, 1981; Franz, 1993), show that filter-feeding bivalves have larger palps or smaller gills, or both, at sites characterized by high versus low suspended solids concentrations.

Theisen (1982) speculated that such structural differences among marine populations of *Mytilus edulis* probably reflected genetic differences. However, the brief evolutionary history of the introduced populations of *D. polymorpha* and *C. fluminea* we studied strongly suggests that interpopulation differences in PA : GA are ecophenotypic. *Dreissena polymorpha* populations studied herein were probably established between 1988 and 1992, and *C. fluminea* were probably introduced in approximately 1960 to the sites we sampled (Payne *et al.*, in press and references cited therein). Thus there has been little time for natural selection to act on these populations. Furthermore, the PA : GA value of *C. fluminea* in the Tensas River was similar to the PA : GA value of native unionids from the same site. In addition, the close similarity of PA : GA among unionid species suggests ecophenotypic variation.

These structural responses are possibly triggered during extreme changes in feeding structures that occur early in development. In marine species and *D. polymorpha*, the transition from a planktonic larval to a benthic juvenile stage involves the loss of the velum (the ciliated larval feeding and locomotory organ), the development of palp and gill primordia and subsequent growth of the palps and gills (Meisenheimer, 1901; Allen, 1961; Bayne, 1965). Although the planktonic veliger larval stage is replaced by the parasitic glochidium larval stage in freshwater unionids, palps and gills still must be formed and grow enormously during the early stages of post-larval benthic life. *Corbicula fluminea* retains fertilized eggs and broods developing juveniles in a gill marsupium. Nonetheless, upon release, tiny benthic juveniles still must undergo enormous development of palps and gills. Detailed experimental studies, including intersite reciprocal transfers, are needed to determine how the capacity for palp and gill size adjustment varies with bivalve age and size.

The great range of life-span among species (from less than one to greater than 25 years), the ubiquitous distribution of many species and an essentially sessile benthic lifestyle make freshwater bivalves particularly useful in environmental assessment and monitoring. As filter-feeders, bivalves are potentially very sensitive to elevated suspended solids. Evidence presented herein indicates that the palp to gill ratios of freshwater bivalves are sensitive biological indicators of ambient suspended solids concentrations, and have potential utility in environmental assessment and monitoring. For example, comparative assessments could be made of mussels at different distances from navigation channels to determine if varying levels of exposure to turbulence and elevated suspended solids concentrations associated with commercial navigation traffic are correlated with spatial variations in PA : GA. It is noteworthy that we observed interspecific differences both in the sensitivity of PA : GA and the relative contribution of palp and gill size variation to intersite differences in PA : GA.

Successful application of these ratios as environmental indicators will be strengthened by additional data on the relative sizes of gills and palps of several species from a variety of habitat types where the annual mean suspended solids concentrations have been established for various hydrological conditions. In addition, quantification is need of the potential relationships of PA : GA and physiological conditions. For example, it is important to know whether populations characterized by extremely high PA : GA values show reduced condition. Nevertheless, the repeated pattern of site-related PA : GA differences summarized herein suggests a potentially useful and relatively easy method for assessing the effects of elevated suspended solids concentrations on an ecologically and economically important faunal group in large floodplain rivers.

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