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COMPARISON OF GILL SURFACE MORPHOLOGY ACROSS A GUILD OF SUSPENSION-FEEDING UNIONID BIVALVES

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ABSTRACT

Freshwater mussels are found in dense, multi-species aggregations where the potential for resource partitioning should be high. One means by which mussels may be partitioning resources is through feeding on different food items. We compared gill morphology in four species of co-occurring freshwater mussels. We found differences in total gill surface area, density of latero-frontal cirri and the number of cilia per cirral plate, with one species, *Actinonaias ligamentina*, having the largest gills with densest cirral plates relative to the other three species. These differences in feeding structures might allow these species to utilize different food resources, or could be related to other functions performed by the gills, including respiration or brood storage.

INTRODUCTION

Freshwater mussels (Unionoida) are a guild of benthic, filter-feeding, burrowing bivalves that provide a number of important ecosystem functions to the rest of the aquatic community. Mussels are one of the most highly threatened freshwater groups globally (Lydeard *et al*., 2004; Strayer *et al*., 2004); populations have steadily declined due to habitat destruction, population fragmentation and introduction of non-native species (Strayer, 1999; Vaughn & Taylor, 1999). Mussels often occur in dense, patchily distributed, multi-species aggregations, known as mussel beds. In beds, mussels can dominate benthic biomass, and couple benthic and pelagic compartments by filtering materials from the water column and providing energy and nutrients to the benthos (Christian, Crump & Berg, 2008; Vaughn, Nichols & Spooner, 2008). Thus, understanding and maintaining mussel species diversity and abundance has implications for the entire stream ecosystems.

Because they all burrow and filter-feed, freshwater mussels have been assumed to belong to the same functional group. By definition, organisms of the same functional group are assumed to perform identical ecological function, such that if the biomass of one species decreases, an equivalent increase in biomass of a functionally redundant species should maintain ecosystem function (Rosenfeld, 2002). Recent work has investigated the degree to which mussels fill similar roles in ecosystems, i.e. are functionally redundant (reviewed by Vaughn *et al*., 2008). Although much of this work has shown species-specific differences in ecosystem function, we are only in the preliminary stages of understanding the mechanisms behind these differences. One way that mussels could differentially influence the environment is by feeding on different food resources. Mussels can feed on a variety of food particles, including algae, bacteria, zooplankton, rotifers and detritus (Vaughn *et al*., 2008), which can vary greatly in size and quality.

Mussels use the cilia on their gills to pump water through the inhalant siphon into the mantle cavity where ciliary action along the gills draws the water over these filter-feeding organs (Gardiner, Silverman & Dietz, 1991; McMahon & Bogan, 2001). Cilia are arranged in pairs of fused plates known as latero-frontal cirri (or cirral plates), which are used to capture food particles like a sieve. Frontal cilia then send captured particles to the food groove on the medial gills, where food becomes incorporated in a strand of mucus (Way *et al*., 1989; Silverman, Lynn & Dietz, 1996a). This mucus strand is then directed to the labial palps, where food particles are further sorted and ingested (Tankersley, 1996). Researchers have hypothesized that differences in the number and spacing of cilia on the gills might allow different mussel species to specialize on different particle types or sizes (Silverman *et al*., 1997). Here we asked whether gill area and the organization of latero-frontal cirri on the gills differed among four co-occurring species of mussels.

MATERIAL AND METHODS

Mussels were collected from the Kiamichi River in the Ouachita Uplands of southeastern Oklahoma. This relatively undisturbed medium-sized river (basin area 4,800 km^2) contains a diverse, healthy mussel fauna. Over 30 mussel species are known from the river, and historical (1990s) mussel beds averaged 13 species and densities of 23 individuals m^{-2} (Galbraith, Spooner & Vaughn, 2008). We examined four species of mussels collected from one site: *Actinonaias ligamentina* (Lamarck, 1819), *Amblema plicata* (Say, 1817), *Fusconaia flava* (Rafinesque, 1820) and *Obliquaria reflexa* (Rafinesque, 1820). These four species are widely distributed throughout the USA and Canada and are common in the Kiamichi River; together, they make up an average of 84 ($\pm$18)% of the relative abundance of species within mussel beds and represent a substantial portion of the biomass of mussels within the river (Vaughn, Spooner & Galbraith, 2007). In addition, they cover a range of body sizes and phylogeny, and thus should encompass variation in life history, behaviour, morphology and feeding attributes within this guild (Table 1; Campbell *et al*., 2005).

To estimate gill surface area, we dissected one lateral and one medial gill from 10 individuals of each species and photographed the gills on gridded transparent paper. We then used ImageJ digital analysis software (Abramhoff, Magelhaes & Ram, 2004) to determine the surface area of these two gills.

To examine gill morphology, we used five individuals of each species and fixed a *c*. 3 × 3 mm piece of the outer demibranch of each individual in a 3:1 mixture of osmium tetroxide and

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Table 1. Mussels used in study and their gill characteristics. All species are members of the family Unionidae and subfamily Ableminae

Species	Tribe	Length (mm)	Shell-free dry mass (g)	Live gill surface area (cm^2)	Number of cirri/cm
Actinonaias ligamentina	Lampsilini	108.47 (1.80)	5.60 (0.37)	29.11 (1.40)[a]	5287 (383)[a]
Amblema plicata	Amblemini	84.17 (1.80)	1.90 (0.16)	18.88 (6.09)[b]	5890 (220)[a,b]
Fusconaia flava	Pleurobemini	60.91 (2.42)	1.16 (0.16)	11.48 (4.08)[c]	5014 (634)[a]
Obliquaria reflexa	Lampsilini	53.33 (0.96)	0.77 (0.06)	10.78 (4.71)[c]	4779 (441)[a,c]

Data are means ± SE (in parentheses) and superscripts indicate differences among species. Surface area estimates are for a single lateral and single medial gill combined and are not dry mass-corrected means.

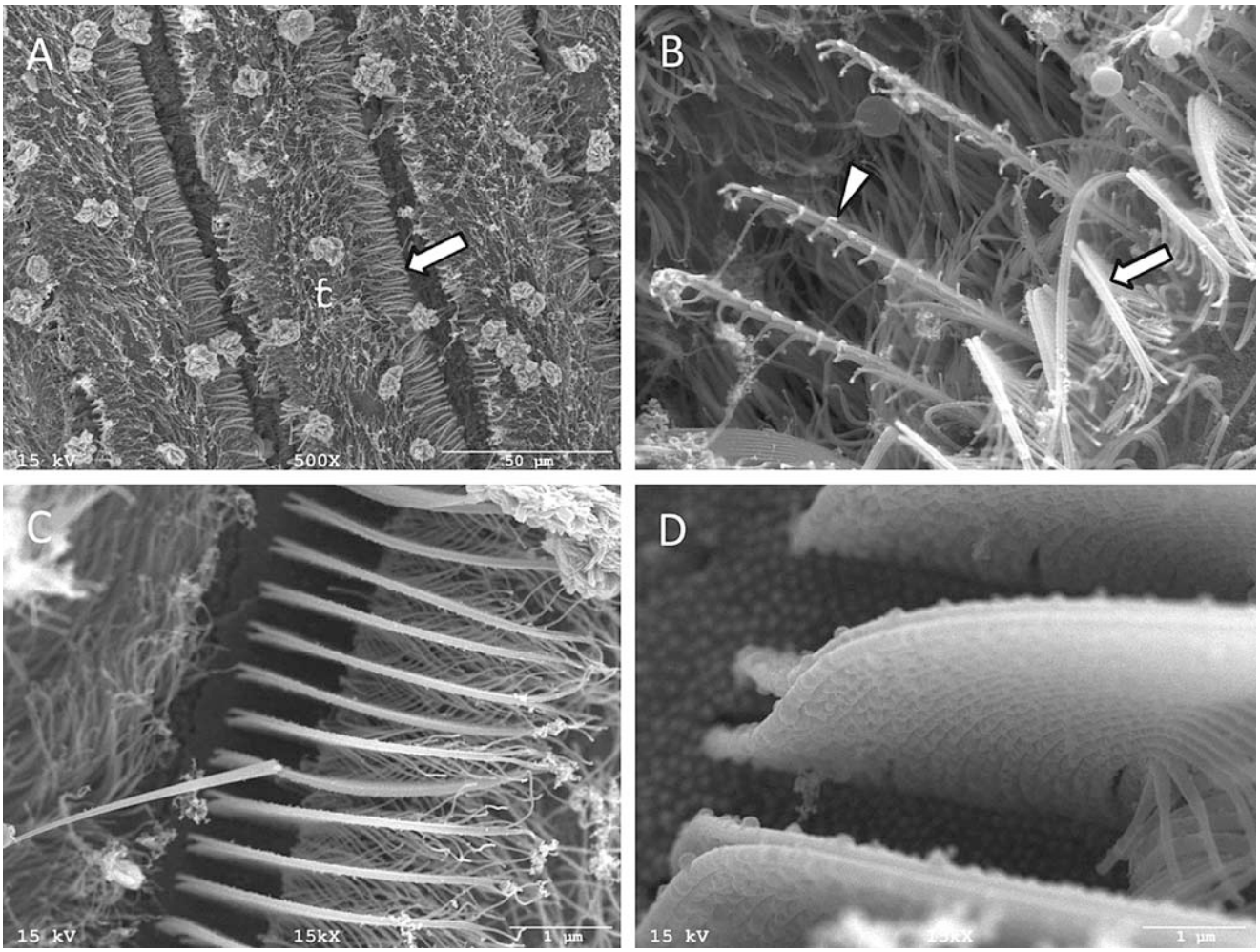

Figure 1. Scanning electron micrographs of *Actinonaias ligamentina* gills. **A**. Configuration of frontal cilia (fc) and laterofrontal cirri (arrow) along the surface of the gill. **B**. Illustration of the relaxed (arrow) and extended (triangle) nature of cirri. **C**. Typical photograph of the rows of cirral plates used to estimate the number of cirri per centimetre in our study. **D**. Close-up of the cilia on a cirrus.

saturated mercuric chloride for *c*. 2 h (Parducz, 1967; Small & Marszalek, 1969). The gills were then washed with distilled water and dehydrated in an ethanol series. The gill pieces were critical-point dried and sputter coated with 60% gold/40% palladium, mounted and viewed with a JEOL JSM-880 high-resolution scanning electron microscope. We counted the number of cilia per latero-frontal cirrus and used ImageJ to determine the number of latero-frontal cirri per linear centimetre of gill filament to measure cirral plate abundance (Fig. 1).

All data were transformed using natural logarithms to satisfy the assumptions of ANOVA. We used ANCOVA to test for differences between species in total gill surface area with mussel dry tissue weight as a covariate. We used ANOVA to determine the differences in cirral plate abundance. We used Tukey's *post-hoc* comparisons to test for species-specific differences when ANCOVA or ANOVA results were significant.

The number of cilia per cirrus is often difficult to quantify, given that the cirral plates tend to split during fixation and that the dense packing of the plates tends to obscure their bases for easy counting (Fig. 1; Silverman *et al*., 1997). We attempted to find cirral plates that were clearly exposed to estimate the number of cilia per cirrus. The number of exposed plates varied greatly from individual to individual; we were able to find several exposed plates in some individuals and none in others. Therefore, rather than analysing these data with parametric statistics, we averaged the total number of cilia per cirrus within a species and graphically compared differences among species.

RESULTS

We found a significant difference in gill surface area among species ($F_{(3,34)} = 17.81$, $P < 0.001$) with mussel dry weight as a significant covariate ($F_{(1,34)} = 13.47$, $P = 0.001$). All species were significantly different from one another with the exception of *Fusconaia flava* and *Obliquaria reflexa* (Table 1). We found a marginally significant difference in the density of cirral plates among species ($F_{(3,15)} = 2.73$, $P = 0.08$). In particular, *Amblema plicata* had more cirri per centimetre than *O. reflexa* (Table 1).

The number of cilia per cirrus was variable both within and among species (Fig. 2). The number of cilia per cirrus ranged from 13 to 23 in *Actinonaias ligamentina*, 6 to 16 in *A. plicata*, 21 to 26 in *O. reflexa* and 15 to 21 in *F. flava*. On average, *O. reflexa* had the highest number of cilia per cirrus and *A. plicata* had the lowest (Fig. 2). Gill pieces shrunk an average of 11.6% after fixation, but there were no significant differences in shrinkage among species. Therefore, the data presented in Table 1 and Figure 1 have not been adjusted for gill shrinkage.

DISCUSSION

We found differences in gill size and morphology among the four species. Species varied in gill surface area, even after accounting for size differences among species. Mussel clearance rates can vary in proportion to gill surface area (Meyhofer, 1985; Lei, Payne & Wang, 1996; Silverman *et al*., 1997). When this occurs, gill size should predict the amount of food a mussel can potentially filter out of the water column. In this study, *Actinonaias ligamentina* had the largest gill surface area, and thus would be predicted to have the highest clearance rates. However, our laboratory measurements have found that *A. ligamentina* clearance rates are not higher than other mussel species after correcting for body size (Vaughn, Gido & Spooner, 2004; Spooner & Vaughn, 2008). This probably reflects a trade off between filtration rate and body size. *Actinonaias ligamentina* is larger than other mussel species we have studied, and per capita metabolic rates and consequently filtration rates generally decrease with increasing body size in bivalves (Gosling, 2003). Further comparisons between similarly sized mussel species will be needed to draw conclusions about the clearance rate capabilities of *A. ligamentina*.

We found differences in cirral plate abundance and variation in the number of cilia comprising a cirrus within and among species. Mussels may be able to use these differences in gill morphology to utilize different types and sizes of food resources, a phenomenon that has been documented in marine mussels. Wright *et al*. (1982) attributed differences in marine bivalve clearance rates to differences in latero-frontal cirral structure, while Dunphy *et al*. (2006) found that the inability of oysters to clear small plankton particles was related to their gill morphology. These studies suggest that size-selective feeding in freshwater mussels also may be due to differences in gill morphology. Recent work by Beck & Neves (2003) showed that unionids are capable of size-selective feeding even as juveniles, while the works by Lei *et al*. (1996) and Pires *et al*. (2004) have shown the same in the invasive zebra mussel, *Dreissena polymorpha*. Although mussels typically have been assumed to feed primarily on phytoplankton, recent evidence indicates that mussels also consume alternate food sources such as bacteria, zooplankton, rotifers and detritus (Vaughn *et al*., 2008).

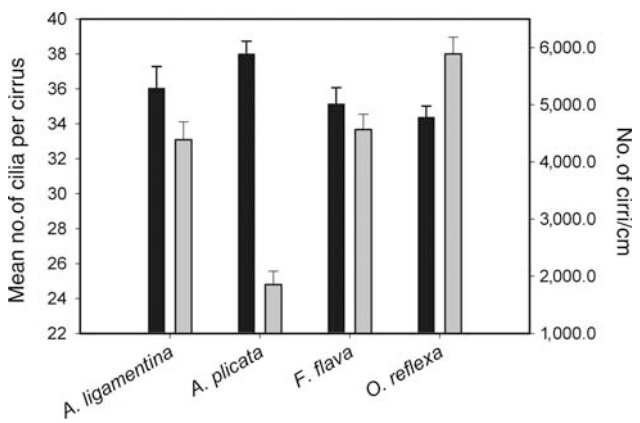

Figure 2. Inverse relationship between mean (±SE) number of cirri per centimetre (black bars) and the mean (±SE) number of cilia per cirrus (grey bars).

Recent work that allows tracking of nutrient assimilation, such as stable isotope and fatty acid studies, suggests that bacteria can be a predominant food item for some freshwater mussels (Nichols & Garling, 2000; Vaughn *et al*., 2008). This phenomenon appears to be related to habitat type, which governs the abundance and availability of bacteria, and gill morphology, which determines if mussels can successfully capture bacteria. In large, primarily lentic habitats such as lakes and large rivers, mussels feed primarily on phytoplankton (Thorp *et al*., 1998; Vander Zanden & Rasmussen, 1999). However, in many small-to-medium temperate streams, mussels are omnivores that feed heavily on both bacteria and algae (Nichols & Garling, 2000; Raikow & Hamilton, 2001; Christian *et al*., 2004). In general, all particles identified as major food items for unionids are <20 μm (Vaughn *et al*., 2008), but bacteria typically are much smaller, ranging from 1 to 4 μm (Silverman *et al*., 1996b), and are thought to require more cirri and denser cirral spacing, i.e. more cirri per centimetre of gill (Silverman *et al*., 1995).

Silverman *et al*. (1997) found differences in gill morphology and clearance rates of bacteria between mussel species living in lentic and lotic habitats. In particular, they found that species from lentic habitats had smaller cirri, fewer cilia per cirrus, smaller cirral surface area per milligram of dry tissue, and slower bacterial clearance rates than mussels from lotic systems. In addition, Silverman *et al*. (1997) found that mussels with large gill surface area, many cilia per cirrus and dense cirral surface area could clear more bacteria and at a faster rate. On the basis of this argument, of our four species, *A. ligamentina* should be most efficient at clearing bacteria from the water column based on its large gill area, dense cirral plates and high numbers of cilia per plate (Table 1, Fig. 2). Interestingly, *A. ligamentina* was the only one of the four mussel species found to have this unique combination of large gills coupled with a large cirral surface area; in the other three mussel species, cirral plate density varied inversely with the number of cilia per plate (Fig. 2). This implies that *A. ligamentina* may be a size generalist (i.e. can feed on both large and small particles), while the other three species might be large-particle specialists, unable to take advantage of smaller food items such as bacteria. Of course, this is likely complicated by the fact that some bacteria can be found bound to larger suspended particles (particle aggregates), which could still make them available for consumption by large-particle specialists (Kirchman & Mitchell, 1982; Kirchman, 1983).

The average number of cilia per cirrus varied among and within species, and fell in the range of those observed in lentic unionids by Silverman *et al*. (1997) (between 11 and 16). This is particularly evident in *Amblema plicata* with the number of cilia per cirrus ranging between 6 and 16. In contrast, the maximum number of cilia per cirrus found in the other three species (21–26) approaches the number found in other lotic

species by Silverman *et al.* (1997), but never reaches the maxima found in their study (30–42). The lotic habitats studied by Silverman *et al.* (1997) were actually second-order, fast-flowing streams in Louisiana where primary production is very low and bacteria is believed to be the primary food source (Silverman *et al.*, 1997). In contrast, our mussels came from the Kiamichi River, a fifth-order river with high primary production that also carries large suspended sediment loads; thus, the Kiamichi River is actually more similar in habitat characteristics to the lentic habitats studied by Silverman *et al.* (1997).

We do not know the ultimate or proximate causes underlying differences in gill size and morphology within this functional group of filter feeders. Potential reasons include differences in microhabitat use (e.g. riffle *vs* pool habitats), feeding modes (e.g. suspension feeding from the water column *vs* utilizing benthic food items) or morphological adaptations in response to historical competition for food resources. For example, seasonal variation in phytoplankton quantity and quality may force certain mussel species to rely on alternative feeding strategies for coping with decreased food availability (Kreeger *et al.*, 1997).

Alternatively, differences in gill structure may not be related to feeding, but may be adaptations for other gill functions, such as respiration or larval brooding, or may reflect an historical phylogenetic constraint. There is some debate concerning the precise feeding mechanisms in bivalves (Riisgard & Larsen, 2000); for example, some marine oysters and mussels (Ward, 1996; Ward *et al.*, 1998) can filter without using the cirri and most bivalves also pre-sort food particles using the labial palps. Studies of freshwater species relating particle types and sizes ingested by mussels to gill morphology will help address this question. The four species we studied represent different phylogenetic histories and life history strategies. Observed differences in gill structure could reflect these factors rather than feeding strategies. Resolving this issue will require examination of a broader range of species from different phylogenetic groups and with contrasting life-history strategies.

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