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Parasitic mite and trematode abundance are associated with reduced reproductive output and physiological condition of freshwater mussels

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Abstract Although historically understudied, parasites may play an important role in freshwater invertebrate population ecology and evolution. We quantified abundance of parasitic mites and trematodes in the freshwater mussel *Pyganodon grandis*, in a southeastern Alabama stream (USA), to assess parasite impact on adult mussel physiological condition and reproductive output. We used stepwise multiple regression analyses to assess the effects of mussel size and parasites on reproduction and condition. Multiple regression analysis found no multivariate models that predicted reproductive output or physiological condition. However, univariate models revealed that increased parasite densities predict reduced mussel reproductive output and physiological condition. These findings suggest that parasites may have important negative consequences for freshwater mussels. We hypothesize that elevated parasite loads may reduce mussel fitness in impounded or nutrient-enriched streams with high densities of intermediate hosts (chironomid midges).

Keywords Glochidia · Glycogen · Parasites · Physiological condition · Reproduction · Unionoida

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Introduction

The role of parasites in the evolution, ecology, and conservation of freshwater mussels (Bivalvia: Unionoida) remains poorly understood. Historically, freshwater mussel-parasite interactions were regarded as either benign or symbiotic in nature (Mitchell, 1955; Fuller, 1974; Smith & Oliver, 1986). However, recent studies demonstrate that parasites of unionoids feed upon their host's tissues (Fisher et al., 2000), and may affect reproductive output (Taskinen & Sarrinen, 1999) and growth rates (Taskinen & Valtonen, 1995). Most recently, Gustafson et al. (2005) found decreased condition and tissue glycogen concentrations in heavily parasitized mussels.

Freshwater mussels are among the world's most imperiled groups of organisms (Ricciardi & Rasmussen, 1999; Lydeard et al., 2004). More than 35 species of freshwater mussels have become extinct in the southeastern U.S. over the last 100 years (Williams et al., 1993; Lydeard et al., 2004). Factors responsible for

these declines include but are not limited to: alteration of habitats by impoundments, industrial or mine-related water contamination, degraded water quality resulting from nonpoint sources, and introduction of exotic species (Lydeard et al., 2004; Strayer et al., 2004). We do not know the extent to which parasites may have contributed to these declines.

Parasitic mites and trematodes are widely reported from freshwater mussels (Mitchell, 1955; Hendrix & Short, 1965; Hendrix, 1968; Hendrix et al., 1985; Duobinis-Gray et al., 1991; Vidrine, 1996), yet few studies have specifically addressed their impact on hosts. Humes & Jamnback (1950) report that gills of *Pyganodon cataracta* (Say, 1817) that are parasitized by the mite *Najadicola ingens* (Koenike, 1895) are misshapen and contain a few larvae. Subsequent studies report tissue inflammation and damage resulting from mite feeding in some host mussels but do not demonstrate that high mite densities reduce host mussel condition or fitness (i.e., reproductive output, Baker, 1977; Fisher et al., 2000). Similarly, the effects of Aspidobothrean trematodes on host mussels are poorly documented (Pauley & Becker, 1968; Flook & Ubelaker, 1972). However, mussels parasitized by digenetic (host-castrating) trematodes exhibit decreased growth rates, physiological condition, and larval production (Jokela et al., 1993; Taskinen & Valtonen, 1995; Taskinen, 1998; Gustafson et al., 2005).

Members of the mite family Unionicolidae (phylum Arthropoda, class Arachinida, subclass Acari, order Actinedida) are well-known parasites of freshwater mussels. Unionicolid life cycles are complex and although some species complete their entire life cycle exclusively in mussels, the vast majority briefly parasitize chironomid (Diptera) larvae or other aquatic invertebrates (Mitchell, 1955; Jones, 1965; Smith & Oliver, 1986; Pennak, 1989; Edwards & Dimock, 1995). Adult mites move about within the mantle cavity and some species consume host mucus and gill tissue (Fisher et al., 2000). Mite eggs are typically deposited in mussel gill tissues, and larval mites also may occur encysted in mussel gill or mantle tissues prior to nymphal transformation (Mitchell, 1955; Gordon et al., 1979; Fisher et al., 2000). Gills of freshwater mussels serve both as respiratory/excretory organs and as marsupia for developing larvae (glochidia, Pennak, 1989). Thus, it is possible that parasitic mites interfere not only with mussel gas exchange and nitrogenous waste removal, but also glochidial development or retention, even if glochidia are not directly consumed.

Aspidobothrean trematodes (phylum Platyhelmenthes, class Trematoda, subclass Aspidobothrea, family Aspidogastridae) are common parasites of freshwater mussels. The life cycle for *Cotylaspis insignis* (Leidy, 1857) is poorly known. Adults are commonly reported from freshwater mollusks as well as from the intestinal tracts of vertebrates (Osborn, 1903; Noble & Noble, 1976; Huehner & Etges, 1977; Kearn, 1998). Adult *C. insignis* can be found in the mantle cavity, oral groove and within the pericardial chambers of unionids (Flook & Ubelaker, 1972; Kearn, 1998). As *C. insignis* has not been associated with tissue pathology or castration in unionids, we hypothesized that their effects were likely to be more subtle than those associated with mites.

Here, we present results of a study designed to examine relationships between parasite (mite and trematode) abundance and the size, physiological condition, and reproductive output of their freshwater mussel host, *Pyganodon grandis* (Say, 1829).

Methods

Study site

We studied mites and trematodes in a population of *P. grandis* in Opintlocco Creek, a tributary of Uphapee Creek and the Tallapoosa River, at the northern edge of the Gulf Coastal Plain, eastern Alabama (32.3704°N, 85.4447°W). The stream channel is low gradient (<1%), with poorly defined runs and riffles, and abundant submerged and emergent vegetation. Predominant stream substrate is sand and silt (particle sizes $\leq$2 mm diameter) mixed with coarse and fine particulate organic material. Mean current velocity and depth were low (<0.1 m s^{-1} and <1 m, respectively).

Mussel parasitism and physiological and reproductive conditions

We collected 29 *P. grandis* adults from the study site in early February 2000, prior to release of larvae by adults. Subsequent observations revealed that the population in Opintlocco Creek released glochidia

from March through August 2000 (MMG, personal observation). We placed mussels in individual Whirl-pack© bags, held them in a cooler of stream water, and then transported them to the laboratory. There, we cut the hinge ligament, opened the shell, and clipped a small portion of the mantle from each mussel for glycogen assays, using a 5-mm^2 corer to remove 3 samples of mantle tissue per animal. We took tissue samples from within 1.5 cm of the mantle margin to reduce effects of variation in glycogen storage reported for different mantle regions (Naimo & Monroe, 1999). We snap-froze tissue samples in Eppendorf microcentrifuge tubes in liquid N and then stored them at −95°C for later analysis. We thawed tissue, weighed it to the nearest 0.1 mg, quantified glycogen level using amyloglucosidase to digest glycogen to its glycosyl subunits (Keppler & Decker, 1974), and then quantified subunits using a Sigma 16–50 hexokinase enzymatic-based assay.

Using calipers, we measured shell length, height, and width of collected mussels and estimated age by counting external annuli. External annuli were used despite their tendency to underestimate ages of older mussels (e.g., Neves & Moyer, 1988) because shells were generally uneroded and external annuli were readily distinguishable. We sacrificed all mussels, flushed parasites (mites and trematodes) from the mantle cavity with tap water, concentrated them on using a 120-μm sieve, and then preserved them in 70% ethanol. We dissected soft parts of adult mussels from the shell and preserved them in 70% ethanol, and used a dissecting microscope (30–60×) to screen the visceral mass, oral groove, labial palps, and gill tissues for parasites. We identified mites to family (Unionicolidae) and trematodes to species (*C. insignis*) using keys in Krantz (1978) and Schell (1970), respectively.

We did not attempt to determine the sex of mussels using gonadal structures because these features are seldom informative unless viewed microscopically. Further, *P. grandis* may exhibit hermaphroditism, so we determined reproductive condition based on presence of glochidia (Heard, 1975), and thus considered 23 of 29 glochidia-bearing mussels as "reproductive" rather than "female". We quantified glochidial production of individual mussels by counting the number of longitudinal gill chambers (marsupia) containing larvae, and estimated the % of the total gill used to brood glochidia (i.e., gill fullness) by averaging the number of marsupia containing glochidia in the left and right gills (Saarinen & Taskinen, 2005). We determined dry mass of mussel soft tissues (including glochidia) by drying tissues for ~24 h at 50°C, and then measured them to the nearest 0.01 g on a microbalance.

We used percentage of the gill containing glochidia as a measure of reproductive output because the total number of brooded glochidia is positively correlated with mussel size (Haag & Staton, 2003). As individual gill tubes in larger mussels can ostensibly support more glochidia than those in smaller mussels, simply counting numbers of glochidia does not provide a size-independent measure of individual reproductive output. By simply measuring the percentage of gill containing glochidia, we can provide a measure of reproductive output that is independent of body size.

Statistical analyses

We conducted all statistical analyses using SPSS software (Version 11.0.1, SPSS Inc., Chicago, IL). In order to correct for the influence of variable host gill surface area on parasite abundance for dissimilar-sized mussels we expressed parasite abundance per unit dry mass of mussel tissue. In order to attain normality, data were transformed ($\log_{10}$ for arithmetic data, logit for proportional data) prior to statistical analyses (Sokal & Rohlf, 1995). We used Principal Components Analysis (PCA) to reduce dimensionality of mussel size data (shell length, height, width, dry mass) into a single derived variable (Sokal & Rohlf, 1995), and we examined relationships between parasite abundance, and mussel size, age, glycogen level, and glochidial output data using stepwise multiple regression.

Results

Twenty-three of the 29 mussels examined contained glochidia (76%), and all were parasitized by both unionicolid mites and aspidogastrid trematodes. The mean number of mites per mussel was 136.5 and the mean number of trematodes per mussel was 41.3 (Table 1). Mean mussel shell length was 11.96 cm and mean mussel age was 11.9 years (Table 1). PCA revealed that only one principal component (PC_1)

Table 1 Summary statistics for mussel shell length, width, age, tissue mass, mite, and trematode parasite abundance, reproductive output (% of gill demibranchs with glochidia), and glycogen level of *Pyganodon grandis* from Opintlocco Creek, February 2000

Variable	*N*	Mean (SE)	Range
Shell length (cm)	29	11.96 (2.4)	8.35–13.66
Shell width (cm)	29	4.87 (1.14)	3.27–5.79
Mussel age (years)	29	11.91 (1.82)	6–18
Tissue mass (g)	29	5.46 (0.35)	1.37–9.2
Number of mites per mussel	29	136.45 (15.42)	18–324
Number of trematodes per mussel	29	41.28 (3.9)	6–86
% demibranchs with glochidia	29[a]	26.76 (4.6)	0–100
Tissue glycogen (mg/g)	28	31.53 (3.81)	8.77–85.39

[a] Glochidia were found in only 23 of 29 mussels examined. In mussels with glochidia the mean percentage of demibranchs with glochidia was 33.74% (SE = 4.9, Range 0.5–99%)

was necessary to describe almost all of the observed variation in mussel size (89.5%, eigenvalue = 3.58). In order to simplify model clarity, we used PC_1 as a surrogate variable for mussel size.

Stepwise multiple regression analysis failed to construct any statistically significant multivariate models. However, univariate regressions indicated significant negative relationships between mussel size (as PC_1) and both mite and trematode abundance (Fig. 1). Further, univariate regressions revealed a significant negative relationship between mite abundance and the percentage of mussel gill marsupia containing glochidia (Fig. 2a). Finally, regressions indicated a significant negative relationship between trematode abundance and mussel tissue glycogen declined with increasing trematode abundance (Fig. 2b).

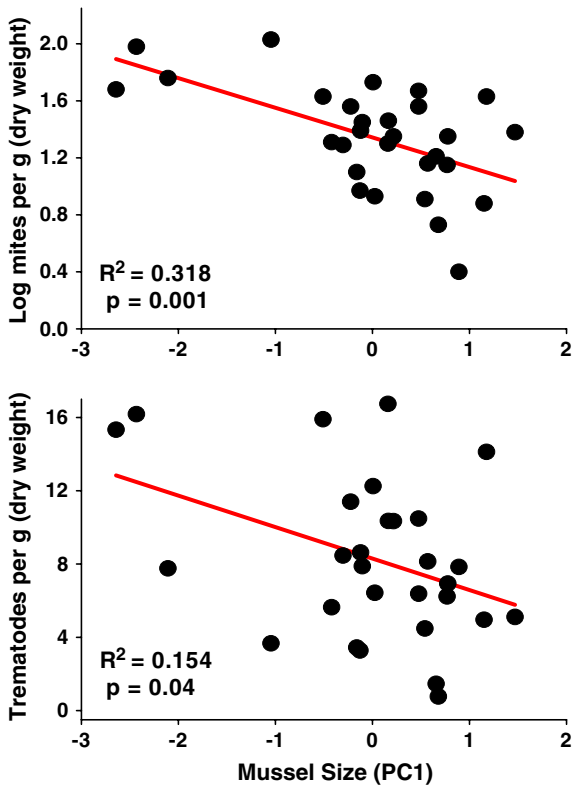

Fig. 1 Relationships between *P. grandis* size (as PC_1 score) and abundance of parasitic mites (Top—log numbers per g host tissue) and trematodes (Bottom—numbers per g host tissue)

Discussion

Results of regression analysis suggest that parasites have strong negative associations with both physiological condition and reproductive output of *P. grandis*. Our findings are in direct contrast to earlier studies characterizing mites and trematodes as benign commensal inhabitants of freshwater mussels (e.g., Mitchell, 1955) and they suggest that parasites can have important fitness consequences for host mussel populations.

At the present time, the mechanisms by which parasites affect host mussel condition and reproduction are unclear. It is possible that mites directly consume glochidia or gill tissue, although there are few empirical studies of mite feeding behavior that substantiate or even address this hypothesis (but see Fisher et al. 2000). Mites may dislodge immature glochidia from the demibranchs prematurely during the extended brooding season of *P. grandis*. The most likely scenario is that mites interfere with glochidial

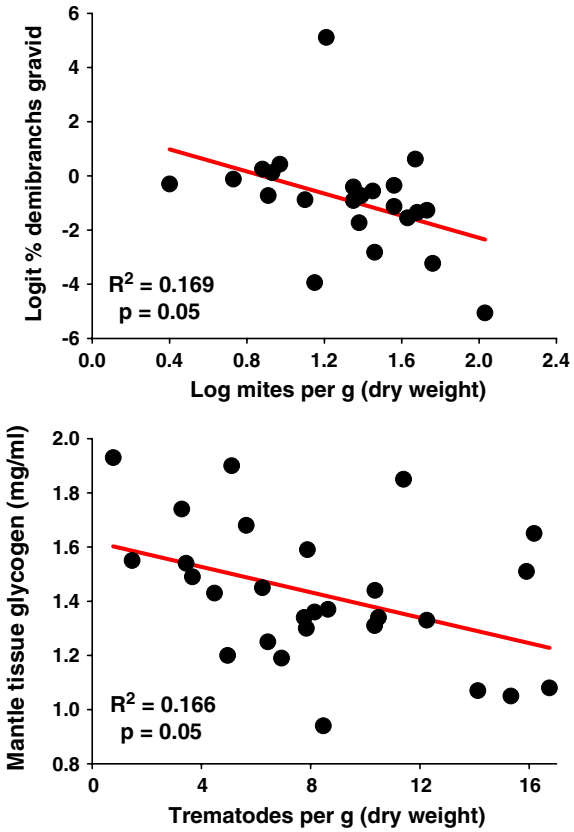

Fig. 2 Relationship between parasite abundance (as log-transformed number of individuals per g mussel tissue dry mass) and (Top) mussel reproductive output (% of gill chambers containing glochidia) and (Bottom) physiological condition (log-transformed mg/ml glycogen, $N = 28$)

development and retention by damaging gill tissues while feeding on mucus. This possibility is supported by earlier reports of damage to gill tissues and papillae (i.e., tubular extensions of gill tissue resulting from mite feeding) formation in heavily parasitized mussels (Humes & Jamnback, 1950, 1951) and by our unpublished observations of damage to the gill tissues of other mussels (MMG, unpublished data).

Feeding and behavior of the trematode *C. insignis* are more poorly understood. It is possible that larval *C. insignis* affect mussel physiological condition during their development within the mussel but developmental biology is largely undescribed. For example, Kearn (1998), citing Osborn's (1903) observations, characterizes *C. insignis* as an ectoparasite; no individuals were found during dissections of the bivalve host's visceral mass. Osborn (1903) describes *C. insignis* feeding in the bivalve mantle cavity but does not identify food items. Most authors agree that the distal, sucker-like holdfast organ plays some role in feeding but specific details are lacking (Osborn, 1903; Huehner & Etges, 1977; Kearn, 1998).

Our data suggest that mussels with high mite abundance also typically exhibited high trematode abundance. Although it is possible that infestation with one type of parasite may render mussels more susceptible to other parasites, stepwise multiple regressions never included both mite and trematode abundance in predictive models. This suggests that if physiologically compromised mussels are indeed more susceptible to parasitism, other factors are likely responsible for decreased mussel condition.

We found that mite and trematode abundance (as numbers per unit host dry mass) were greater in smaller mussels. Humes & Jamnback (1950) also report increased mite abundance in smaller-bodied mussels. Similarly, Taskinen (1998) found a negative effect of trematodes on mussel growth rate. Ultimately, our data may be insufficient to adequately address this question. We targeted reproductive mussels and did not sample all size classes of this population. Thus, it is unclear whether this relationship is due to decreased immune capabilities of smaller mussels, or perhaps simple physical differences (e.g., decreased aperture flow velocity allows for increased colonization by mites) between small and large mussels.

Earlier studies noted that parasitism rates tend to be greatest in mussels from lentic habitats and nutrient-enriched streams (Humes & Jamnback, 1950; Fuller 1974). Many unionicolid mites also must parasitize larval dipterans (primarily Chironomidae) during their final developmental stage (Smith & Oliver, 1986; Edwards & Dimock, 1995). As chronomids are more abundant in lentic habitats and nutrient-enriched streams, increased host abundance in these systems may regulate mussel populations. To date, no studies have addressed links among environmental conditions, parasite abundance, and mussel reproductive output or condition.

Parasitic interactions remain a relatively unexplored aspect of unionid ecology. Our study provides evidence from the field that parasites may impart substantial reproductive and physiological costs on their freshwater mussel hosts. It is important to note that we did not demonstrate experimentally that

parasite infections caused mussel physiological and/or reproductive impairment. However, regression models suggest that parasites were more important predictors of mussel reproductive effort and physiological condition than mussel size or age. Alternatively, mussels in poor condition may simply be more susceptible to parasites. Well-designed experiments will greatly enhance our understanding of the magnitude of parasite impacts on mussel populations and would help illuminate mechanisms that drive global mussel declines.

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