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The role of fecundity and reproductive effort in defining life-history strategies of North American freshwater mussels

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ABSTRACT

Selection is expected to optimize reproductive investment resulting in characteristic trade-offs among traits such as brood size, offspring size, somatic maintenance, and lifespan; relative patterns of energy allocation to these functions are important in defining life-history strategies. Freshwater mussels are a diverse and imperiled component of aquatic ecosystems, but little is known about their life-history strategies, particularly patterns of fecundity and reproductive effort. Because mussels have an unusual life cycle in which larvae (glochidia) are obligate parasites on fishes, differences in host relationships are expected to influence patterns of reproductive output among species. I investigated fecundity and reproductive effort (RE) and their relationships to other life-history traits for a taxonomically broad cross section of North American mussel diversity. Annual fecundity of North American mussel species spans nearly four orders of magnitude, ranging from < 2000 to 10 million, but most species have considerably lower fecundity than previous generalizations, which portrayed the group as having uniformly high fecundity (e.g. > 200000). Estimates of RE also were highly variable, ranging among species from 0.06 to 25.4%. Median fecundity and RE differed among phylogenetic groups, but patterns for these two traits differed in several ways. For example, the tribe Anodontini had relatively low median fecundity but had the highest RE of any group. Within and among species, body size was a strong predictor of fecundity and explained a high percentage of variation in fecundity among species. Fecundity showed little relationship to other life-history traits including glochidial size, lifespan, brooding strategies, or host strategies. The only apparent trade-off evident among these traits was the extraordinarily high fecundity of *Leptodea*, *Margaritifera*, and *Truncilla*, which may come at a cost of greatly reduced glochidial size; there was no relationship between fecundity and glochidial size for the remaining 61 species in the dataset. In contrast to fecundity, RE showed evidence of a strong trade-off with lifespan, which was negatively related to RE. The raw number of glochidia produced may be determined primarily by physical and energetic constraints rather than selection for optimal output based on differences in host strategies or other traits. By integrating traits such as body size, glochidial size, and fecundity, RE appears more useful in defining mussel life-history strategies. Combined with trade-offs between other traits such as growth, lifespan, and age at maturity, differences in RE among species depict a broad continuum of divergent strategies ranging from strongly *r*-selected species (e.g. tribe Anodontini and some Lampsilini) to *K*-selected species (e.g. tribes Pleurobemini and Quadrulini; family Margaritiferidae). Future studies of reproductive effort in an environmental and life-history context will be useful for understanding the explosive radiation of this group of animals in North America and will aid in the development of effective conservation strategies.

Key words: life history, trade-off, fecundity, reproduction, glochidia, unionidae, margaritiferidae, unionoida.

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I. INTRODUCTION

Fecundity is an important life-history trait and is considered a measure of an organism's fitness (Charlesworth, 1994). When resources are limiting, selection is expected to optimize reproductive investment resulting in characteristic trade-offs among brood size, offspring size, and reproductive lifespan. For example, high fecundity is possible often because of reduced parental care or production of smaller offspring requiring lower energetic investment (e.g. Winemiller & Rose, 1992). High investment in reproduction may come at a cost to somatic maintenance, resulting in decreased lifespan for highly fecund organisms. However, lifetime reproductive effort is predicted to be invariant of lifespan because of the longer reproductive life of species that invest less in reproduction per unit time (White & Seymour, 2004; Charnov, Warne & Moses, 2007).

Freshwater mussels (order Unionoida) are a diverse and ecologically important group (Vaughn & Hakenkamp, 2001; Gutiérrez *et al*., 2003; Vaughn, Nichols & Spooner, 2008). Mussels have an unusual life history in which larvae (glochidia) of most species are obligate parasites on fishes. After hatching, glochidia are brooded by the female mussel, but brooding time varies among species generally corresponding to either a short-term or long-term brooding strategy. Short-term brooders brood glochidia for approximately 2–6 weeks before release usually in spring or summer. Long-term brooders brood glochidia for up to eight months, usually from late summer or autumn, until release the following spring or summer (e.g. Weaver, Pardue & Neves, 1991; Bruenderman & Neves, 1993; Garner, Haggerty & Modlin, 1999). The portion of the gills used for brooding also varies among species ranging from the use of all four gills to only a portion of the outer gills. After release from the female, glochidia must encounter a suitable host species within a few days. Host use varies among species from generalists that are able to parasitize nearly any fish species, to specialists that can use as hosts only one or a few closely related fishes (Haag, 2012). Host use of specialists encompasses a taxonomically and ecologically wide range of fishes from drift-feeding minnows to large top predators, and one species is a specialist on an aquatic salamander (*Necturus maculosus*). Accordingly, a wide array of strategies to transmit glochidia to hosts has evolved ranging from broadcast of free glochidia to complex strategies that target specific host species (Barnhart, Haag & Roston, 2008; Haag, 2012). In part because of this complex life cycle, mussels are now one of the most imperiled groups of organisms on Earth (Regnier, Fontaine & Bouchet, 2009).

As a group, freshwater mussels have been portrayed traditionally as having uniformly high annual fecundity (> 200 000) to compensate for the low chances of glochidia encountering hosts (McMahon & Bogan, 2001). However, fecundity is known for few species and relationships of fecundity to other life-history traits have received little attention. Recent studies show a much wider range in fecundity including species that produce < 10000 glochidia annually (Haag & Staton, 2003; Pilarczyk *et al*., 2005; Jones *et al*., 2010), and energetic investment in glochidia is low in some species (Bauer, 1998). Bauer (1994) showed an inverse relationship between glochidial size and fecundity as predicted by life-history theory, but his analysis included only seven species. In addition to predictions of general life-history theory, life-history traits specific to mussels also may be expected to influence fecundity. For example, if host infection strategies such as broadcasting are less efficient than other, more specialized, strategies, fecundity of broadcasters should be higher. Brooding glochidia may incur a cost to females because the presence of glochidia in the gills can reduce feeding and respiratory efficiency (Richard, Dietz & Silverman, 1991; Tankersley & Dimock 1993; Tankersley, 1996), and the duration of the brooding period and portion of the gill used for brooding are therefore expected to be inversely related to fecundity. The wide range of variation among species in fecundity, host strategies, and other traits such as growth and lifespan (Haag & Rypel, 2011) coupled with the great taxonomic diversity of this group suggests that mussels use a broad array of life-history strategies. Because of the central role of fecundity and reproductive effort in life history, patterns of variation in these traits among species and their relationships to other life-history traits are important for understanding mussel ecology and developing effective conservation strategies for these imperiled animals.

I examined fecundity and reproductive effort in North American freshwater mussels using original data and literature reports. First, I examined patterns of variation at several levels including within populations, among species, and among phylogenetic groups. Second, I report relationships of fecundity and reproductive effort with other life-history variables including body size, glochidial size, lifespan, brooding

traits, host use, and host-infection strategy. I then used multiple regression to evaluate the relative importance of these traits in explaining variation in fecundity among species and to show patterns of covariation among traits. Finally, I discuss the significance of fecundity and reproductive effort in life-history evolution of freshwater mussels.

II. METHODS

(1) The data set

I compiled fecundity data for 72 mussel taxa (71 species plus 1 subspecies) from the literature, from original data generated by this study, and from unpublished data provided by colleagues (Table 1). These species represent a broad cross section of North American mussel diversity, containing multiple representatives of all major phylogenetic lineages (*sensu* Graf, 2002; Campbell *et al*., 2005), all recognized host-attraction strategies (Barnhart *et al*., 2008), and an array of life-history strategies (see Haag, 2012). Several species are represented by estimates from more than one population, but for most, sample sizes were too small to examine statistically differences in fecundity among populations, and no species are represented by estimates from across their geographic range.

I generated original fecundity estimates from preserved gravid female mussels following the methods of Haag & Staton (2003). I made estimates only from females whose gill marsupia appeared fully charged, in order to maximize the likelihood that estimates represented the full reproductive complement of the individual and were not biased by females having previously released a portion of their brood. For each specimen, I measured total shell length (nearest 0.1 mm) with dial calipers. For 33 species, I also measured shell volume (nearest 1.0 ml) to provide a surrogate measure of body mass. I measured shell volume by filling each shell valve with water and recording the volume of water using a graduated cylinder. I estimated fecundity by dissecting gravid gills, suspending glochidia in a known volume of water, and extrapolating total fecundity from the mean number of glochidia in three replicate aliquots. I counted only the number of developing eggs or glochidia in a sample so that fecundity estimates reflected the number of viable offspring in a brood and were not inflated by the presence of structural or other non-developing eggs (see Barnhart *et al*., 2008). Most mussel species appear to produce only a single brood per year, but multiple clutches have been reported for a few species, primarily short-term brooders. However, most of these reports are from subtropical regions south of about 31°N latitude, and the evidence for multiple brood production is equivocal in most cases (Haag, 2012). Because all of the populations sampled in this study are from temperate latitudes, I considered estimates to represent annual fecundity for an individual.

In addition to fecundity, I estimated reproductive effort (RE) for nine species (Table 2). Reproductive effort is a measure of the relative amount of energy allocated to offspring production and can be calculated as: RE = (offspring mass)/(offspring mass + adult body mass + mass of organic component of the shell) (Bauer, 1998; Gosling, 2003). This estimate assumes one brood per year and that the energetic cost of producing a mass of adult tissue is equivalent to the energetic cost of producing the same mass of offspring tissue (Charnov *et al*., 2007). All individuals in this analysis were brooding fully mature glochidia, and I flushed glochidia from gravid gills into pre-weighed pans. Glochidia, soft tissues (including flushed gills), and shells were then dried at 60°C for 48 h and weighed separately. I did not estimate directly the mass of the organic component of the shell. Shells of adult mussels typically contain about 2.3–3.8% organic matter (Cameron, Cameron & Paterson, 1979), and I used the midpoint of this range (3.1%) to estimate organic shell mass for all species. I also compiled other reported values of RE from the literature. One disadvantage of this method is that inorganic shell mass is included in estimates of glochidial mass but not in estimates of adult tissue mass, and resultant estimates of RE are likely inflated. Therefore, I also ashed adult soft tissue and glochidia at 500°C in a muffle furnace, and then subtracted ash mass from dry mass to obtain ash-free dry mass, an estimate of the organic fraction of samples. I then calculated RE using estimates of organic mass.

Measurements of tissue and shell mass necessary for calculating RE were unavailable for other species in the dataset. I used length *versus* body mass and length *versus* shell mass relationships to estimate mass (dry mass only) for an additional 10 species (13 populations) with fecundity data (Table 2). In all cases, length-mass relationships explained a high percentage of variation in body and shell mass ($r^2 = 0.85–0.98$; see also Benke *et al*., 1999) and were derived from the same population as fecundity estimates. I estimated total glochidial volume for these species as (glochidia size)^3 × fecundity (see Charnov *et al*., 2007), and converted these values to mass according to the relationship between volume and mass derived from the nine species with direct measurements of glochidial mass (log glochidial mass = 0.985(log glochidial volume) − 4.067; $r^2 = 0.817$, $P < 0.0001$). Adult length and fecundity used to predict mass were mean values for each population (see Table 1), and glochidial size was determined from sources listed subsequently. In *Fusconaia cerina* and *Pleurobema decisum*, approximately 50% of eggs typically are unfertilized and provide structure to the conglutinate (Haag & Staton, 2003; Barnhart *et al*., 2008; see Section II.2). These unfertilized eggs were not included in fecundity estimates, but because they represent an energetic cost, I multiplied estimates of glochidial mass by two for these species. I then used these estimates of adult body mass, shell mass, and glochidial mass to calculate RE for these 13 populations. I tested the accuracy of this method by estimating RE for eight of the species with direct mass measurements. For all species except *Leptodea fragilis*, direct and estimated values of RE were very similar and were strongly correlated ($r = 0.941$ without *L. fragilis*, $r = 0.712$ with *L. fragilis*; $P < 0.0001$ for both correlations; see Table 2).

Table 1. Fecundity data for North American freshwater mussels

Species	Mean length (mm)	Mean fecundity	Fecundity range	N	Length-fecundity relationship	Site	Source
Family Margaritiferidae							
Cumberlandia monodonta	151.2	4967500	1930000–9570000	8	—	Gasconade and Meramec Rivers, MO	Baird (2000)
Margaritifera margaritifera	77.9	4421688	1030600–16851000	8	—	River Dee, UK	Young & Williams (1984)
Family Unionidae							
Tribe Amblemini							
Amblema plicata	78.5	325709	76050–681300	13	$y = 0.600x^{3.0275}$, $r^2 = 0.879$***	Little Tallahatchie River, MS	Haag & Staton (2003)
Amblema plicata	86.9	229738	40500–465300	12	$y = 0.009x^{3.825}$, $r^2 = 0.839$***	Sipsey River, AL	Haag & Staton (2003)
Tribe Anodontini							
Alasmidonta heterodon	29.0	2661	2067–2997	3	—	—	R. Mair (unpublished data)
Alasmidonta marginata	55.0	47298	42559–54391	3	—	—	R. Mair (unpublished data)
Alasmidonta viridis	35.6	6914	4432–8476	3	—	—	R. Mair (unpublished data)
Arcidens confragosus	144.0	1050750	—	1	—	St. Francis River, AR	This study
Lasmigona complanata	158.5	1449500	1048000–1930000	4	—	St. Francis River, AR	This study
Lasmigona holstonia	38.6	2883	—	5	—	—	R. Mair (unpublished data)
Pegias fabula[1]	25.0	1950	1500–2400	—	—	—	J. Layzer (unpublished data)
Pyganodon cataracta[2]	54.3†	53811	—	—	$y = 912.011x^{2.410}$, $r^2 = 0.397$**	Layton's Lake, NS	Paterson & Cameron (1985)
Pyganodon cataracta[2]	60.7†	17482	—	—	$y = 1.479x^{5.200}$, $r^2 = 0.462$**	Morice Lake, NB	Paterson & Cameron (1985)
Pyganodon grandis	107.6	412300	69300–724050	9	$y = 0.002x^{4.092}$ $r^2 = 0.8632$***	Farm pond, MS	This study
Pyganodon grandis	127.4	489600	174000–888000	10	$y = 0.220x^{2.990}$ $r^2 = 0.423$**	Farm pond, MS	This study
Pyganodon grandis	73.5	58453	20000–215000†	63	$y = 0.00006x^{4.842}$††, $r^2 = 0.880$**	Long and Narrow Lakes, AB	Hanson, Mackay & Prepas (1989)
Simpsonaias ambigua	42.3	52250	—	1	—	Wisconsin River, WI	This study
Strophitus subvexus	55.6	23214	20500–25927	2	—	Brushy Creek, AL	This study
Utterbackia imbecillis	65.7	50265	13500–85500	10	$y = 0.876x^{2.600}$, $r^2 = 0.857$***	Farm pond, MS	This study
Utterbackia imbecillis	79.5	77797	25500–146500	8	$y = 1.429x^{2.460}$, $r^2 = 0.271$**	Puskus Lake, MS	This study
Tribe Lampsilini							
Actinonaias ligamentina[3]	—	—	80616–1561224	64	—	Green River, KY	Moles & Layzer (2008)
Actinonaias ligamentina	128.2†	652843	458691–814904	17	$y = 1.080x^{2.743}$††, $r^2 = 0.580$***	Green River, KY	Moles & Layzer (2008)
Actinonaias ligamentina	118.9†	816063	310948—1170959	22	$y = 4.440x^{2.537}$††, $r^2 = 0.640$***	Green River, KY	Moles & Layzer (2008)
Cyprogenia aberti	53.0	132363	—	7	—	Verdigris River, KS	Eckert (2003)
Cyprogenia aberti	58.0	63182	—	4	—	St. Francis River, MO	Eckert (2003)

Table 1. *(Cont.)*

Species	Mean length (mm)	Mean fecundity	Fecundity range	N	Length-fecundity relationship	Site	Source
Cyprogenia aberti	44.0	69634	—	7	—	Ouachita River, AR	Eckert (2003)
Cyprogenia stegaria	41.9	43487	22393–63544	4	—	Clinch River, TN	Jones & Neves (2002)
Dromus dromas	57.4	108381.6	48267–253050	7	ns	Clinch River, TN	Jones *et al.* (2004)
Ellipsaria lineolata	56.0	97833	14000–163500	18	$y = 0.071x^{3.482}$, $r^2 = 0.810$***	Tennessee River, AL	This study
Epioblasma ahlstedti	45.7	16843	7066–31946	4	—	Duck River, TN	J. W. Jones (unpublished data)
Epioblasma capsaeformis[4]	41.4	13589	10494–16876	9	$y = 16.72x^{1.798}$, $r^2 = 0.615$*	Clinch River, TN	J. W. Jones (unpublished data)
Epioblasma triquetra	35.3	15511	13440–21000	4	—	Bourbeuse River, MO	Barnhart (2002)
Epioblasma florentina aureola	29.6	8068	5818–12558	7	ns	Clinch River, VA	J. W. Jones (unpublished data)
Epioblasma florentina walkeri	42.05	7213	1828–12822	4	—	Big South Fork Cumberland River, KY	J. W. Jones (unpublished data)
Glebula rotundata[5]	106.4	531000	—	5	—	Bayou Peyronnet, LA	Parker, Hackney & Vidrine (1984)
Hamiota australis[6]	62.0	91800	—	1	—	Natural Bridge Creek, AL	Blalock-Herod, Herod & Williams (2002)
Lampsilis ornata	74.2	281776	48625–739600	29	$y = 0.837x^{2.955}$ $r^2 = 0.620$***	Sipsey River, AL	Haag & Staton (2003)
Lampsilis ovata	136.3	717250	—	1	—	Tennessee River, AL	This study
Lampsilis rafinesqueana	113.0	1274000	1173000–1466000	4	—	Spring River, KS	Barnhart (2003)
Lampsilis siliquoidea[5]	104.8	533000	—	9	—	East Fork Little Miami River, OH	Perles, Christian & Berg (2003)
Lampsilis siliquoidea	68.3	92667	74000–125000	3	—	—	Coker *et al.* (1921)
Lampsilis straminea[7]	66.8	268464	178000–370000	7	$y = 1.034x^{2.973}$, $r^2 = 0.812$**	Sipsey River, AL	This study
Lampsilis teres	96.7	794667	605000–999000	3	—	Little Tallahatchie River, MS	This study
Lampsilis teres	129.0	4631633	1434000–8434500	6	—	St. Francis River, AR	This study
Lampsilis teres	84.4	386250	294000–478500	2	—	Sipsey River, AL	This study
All *Lampsilis teres*	112.1	2813300	—	10	$y = 0.000010x^{5.496}$ $r^2 = 0.888$***	—	This study
Lemiox rimosus	36.6	5306	4132–6479	2	—	Clinch River, TN	Jones *et al.* (2010)
Lemiox rimosus	36.6	20360	7066–58700	6	—	Duck River, TN	Jones *et al.* (2010)
Leptodea fragilis	79.9	9586987	1571250–23401500	15	$y = 5.864x^{3.217}$, $r^2 = 0.770$***	St. Francis River, AR	This study
Leptodea fragilis	99.7	10735000	10707500–10762500	2	—	Little Tallahatchie River, MS	This study
Leptodea fragilis	43.7	688250	—	1	—	Sipsey River, AL	This study
Leptodea fragilis	66.5	908000	—	1	—	Town Creek, MS	This study
Leptodea fragilis	74.0	2225000	—	1	—		Coker *et al.* (1921)
Leptodea leptodon	52.2	1077667	419000–2000000	3	—	Gasconade and Meramec Rivers, MO	Barnhart (2001, 2002, 2003)
Ligumia recta	151.6	1076833	895500–1226500	3	—	Tennessee River, AL	This study

Table 1. *(Cont.)*

Species	Mean length (mm)	Mean fecundity	Fecundity range	N	Length-fecundity relationship	Site	Source
Ligumia recta	119.6	604269	283500–1096964	9	$y = 0.006x^{3.833}$, $r^2 = 0.727$**	St. Croix River, MN	This study
Ligumia subrostrata	60.0	74821	35500–137500	7	$y = 11.377x^{2.133}$ $r^2 = 0.844$**	Farm pond, MS	This study
Medionidus acutissimus	21.7	16258	1450–35375	15	$y = 0.003x^{4.937}$ $r^2 = 0.900$***	Sipsey River, AL	This study
Medionidus conradicus[8]	33.2	16400	11400–21400	7	$y = 6.919x^{2.215}$, $r^2 = 0.779$**	Clinch River, TN	This study
Obliquaria reflexa	48.8	40975	447–135750	21	$\mathrm{sqrt}(y) = 5.238x - 53.191$, $r^2 = 0.679$***	Little Tallahatchie River, MS	Haag & Staton (2003)
Obliquaria reflexa	40.8	25767	3250–82500	12	$\mathrm{sqrt}(y) = 5.238x - 53.191$, $r^2 = 0.679$***	Sipsey River, AL	Haag & Staton (2003)
Obovaria unicolor[9]	32.5	56390	24200–105925	31	$y = 572.160x^{1.310}$ $r^2 = 0.408$***	Sipsey River, AL	This study
Potamilus ohiensis	68.7	1062768	—	1	—	St. Francis River, AR	This study
Potamilus purpuratus	104.5	417407	75000–688750	10	$y = 0.002x^{4.134}$ $r^2 = 0.891$***	St. Francis River, AR	This study
Potamilus purpuratus	113.3	425500	271000–580000	2	—	Little Tallahatchie River, MS	This study
Ptychobranchus subtentum[5]	76.1	247000	43300–502000	29	—	Clinch River, TN	V. Mengel & J. Layzer (unpublished data)
Toxolasma texasensis	27.6	20089	8214–31964	2	—	Quarterliah Creek, MS	This study
Toxolasma texasensis	35.4	33500	18250–48750	2	—	St. Francis River, AR	This study
Truncilla donaciformis	20.8	351900	—	1	—	St. Francis River, AR	This study
Truncilla truncata	45.3	883889	286000–1851000	5	—	St. Croix River, MN	This study
Venustaconcha ellipsiformis	62.4	138700	123500–161500	5	—	Pomme de Terre River, MO	This study
Venustaconcha pleasii	37.3	46947	—	1	—	James River, MO	Barnhart (2001)
Villosa iris	41.7	57667	48500–67750	3	—	Little River, TN	This study
Villosa lienosa	63.5	525500	—	1	—	Catalpa Creek, MS	This study
Villosa lienosa	43.5	73025	32600–107100	4	—	Sipsey River, AL	This study
Villosa nebulosa	46.5	140000	39750–240250	2	—	Holly Creek, GA	This study
Villosa vanuxemensis	42.7	58667	45400–68000	3	—	Holly Creek, GA	This study
Villosa vanuxemensis	39.2	26275	17875–33750	3	—	Spring Creek, TN	This study
all *Villosa*	—	—	—	—	$y = 0.010x^{4.169}$ $r^2 = 0.794$***	—	This study
Tribe Pleurobemini							
Elliptio arca	69.9	136227	19300–206875	35	$y = -100.930x^2 + 17093x - 565429$, $r^2 = 0.645$***	Sipsey River, AL	Haag & Staton (2003)
Elliptio complanata[2]	58.0†	16668	1878–68655	23	$y = 12.618x^{4.088}$††, $r^2 = 0.563$***	Morice Lake, NB	Paterson (1985)
Elliptio crassidens	114.7	651250	—	1	—	Sipsey River, AL	This study
Elliptio dilatata	84.1	81089	48393–112589	5	—	St. Croix River, MN	This study

Table 1. *(Cont.)*

Species	Mean length (mm)	Mean fecundity	Fecundity range	N	Length-fecundity relationship	Site	Source
Fusconaia burkei	44.1	6058	3880–10395	4	—	Eightmile Creek, FL	Pilarczyk *et al*. (2005)
Fusconaia cerina	46.0	23890	8750–55422	36	$y = 3.973x^{2.273}$ $r^2 = 0.476$*	Sipsey River, AL	Haag & Staton (2003)
Fusconaia cuneolus[5]	63.0	113000	—	1	—	Clinch River, VA	Bruenderman & Neves (1993)
Fusconaia ozarkensis	68.9	15840	8582–29470	8	ns	Spring River, MO	M. C. Barnhart (unpublished data)
Pleurobema decisum	46.7	29433	6721–73581	16	$y = 0.653x^{2.788}$, $r^2 = 0.7654$***	Sipsey River, AL	Haag & Staton (2003)
Pleurobema decisum	47.9	40887	27860–69553	10	$y = 30.313x^{1.863}$, $r^2 = 0.429$*	Sipsey River, AL	Haag & Staton (2003)
Pleurobema collina	49.9	12423	—	8	—	Johns and Dicks Creeks, VA	Hove & Neves (1994)
Pleurobema strodeanum[10]	43.1	18413	10320–39733	9	ns	Eightmile Creek, FL	Pilarczyk *et al*. (2005)
Tribe Quadrulini							
Megalonaias nervosa	117.1	607455	361000–815250	11	$y = 156.170x^{1.732}$ $r^2 = 0.799$ ***	Tennessee River, AL	This study
Quadrula asperata	40.4	9647	250–28250	74	sqrt $(y) = 3.796x - 55.040$, $r^2 = 0.646$***	Sipsey River, AL	Haag & Staton (2003)
Quadrula cylindrica	91.5	115000	—	5	—	Clinch River, VA	Yeager & Neves (1986)
Quadrula pustulosa	53.0	28369	49–50625	30	sqrt $(y) = -0.099x^2 + 13.758x - 281.810$ $r^2 = 0.646$***	Little Tallahatchie River, MS	Haag & Staton (2003)
Quadrula pustulosa	59.9	36875	—	1	—	St. Croix River, MN	This study
Quadrula rumphiana[11]	50.7	30750	2500–68250	10	$y = (8 \times 10^{-16})x^{11.371}$, $r^2 = 0.857$**	Sipsey River, AL	This study
Uniomerus tetralasmus	55.5	8606	5420–10725	4	—	Thompson Creek, MS	This study
Unionidae, *incertae sedis*							
Plectomerus dombeyanus	100.4	553500	163500–943500	2	—	Leaf River, MS	This study

Fecundity refers here to a single clutch and includes fertile eggs only; for some species, reported estimates have been adjusted to account for the characteristic presence of a large number of unfertilized eggs (e.g. *Fusconaia* spp., *Pleurobema* spp.; see Haag & Staton, 2003). Multiple values for a species represent different populations. For length (x) *versus* fecundity (y) relationships, length is in mm unless noted otherwise. — = not reported or not available. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns = not significant. †Values estimated from graphical presentation of data. ††Equation given originally in linear form using log-transformed data.

[1]Length not available; stated length is a typical value for the species; [2]length-fecundity relationship based on length in centimeters; [3]range across three populations; [4]excludes one outlier: 7780 (42.0 mm); [5]mean length not given, value is midpoint of reported length range; [6]fecundity reported as an estimated range (61200–122400), value is midpoint of range; [7]excludes one outlier: 203000 (73.3 mm); [8]estimates exclude one outlier: 6200 (34.6 mm); [9]estimates exclude two outliers: 197000 (39.9 mm length) and 175000 (32.3 mm); [10]excludes two outliers: 860 (41.1 mm length) and 330 (46.2 mm); [11]excludes two outliers: 6000 (53.2 mm) and 10750 (60.0 mm).

Table 2. Reproductive effort (RE) in freshwater mussels

Species	Site	*N*	Observed RE (%) dry mass	Estimated RE (%) dry mass	Observed RE (%) ash-free	Ash (%) adult (w/o shell)	Ash (%) glochidia (w/shell)
Family Margaritiferidae							
Margaritifera margaritifera[1]	Central Europe	—	0.8–5.3	—	—	—	—
Family Unionidae							
Tribe Amblemini							
Amblema plicata	Little Tallahatchie River, MS	—	—	3.8	—	—	—
Amblema plicata	Sipsey River, AL	—	—	1.6	—	—	—
Tribe Anodontini							
Anodonta anatina[2]	Sweden	—	15–45	—	—	—	—
Pyganodon cataracta[3]	Morice Lake, NB	—	—	10.8	—	—	—
Pyganodon cataracta[3]	Layton's Lake, NB	—	—	19.9	—	—	—
Pyganodon grandis	Hatchery pond, AL	35	25.4 (1.8)	—	—	—	—
Utterbackia imbecillis	Puskus Lake, MS	8	14.3 (1.6)	12.0	—	—	—
Tribe Lampsilini							
Lampsilis ornata	Sipsey River, AL	4	7.3 (1.0)	6.4	—	—	—
Lampsilis straminea	Sipsey River, AL	6	8.5 (0.5)	8.2	3.4 (0.6)	20.0 (1.2)	66.5 (6.4)
Lampsilis teres	Sipsey River, AL	2	8.9 (0.7)	8.7	5.1 (0.6)	17.5 (1.3)	53.1 (1.7)
Leptodea fragilis	Sipsey River, AL	2	25.4 (8.7)	8.5	—	—	—
Medionidus acutissimus	Sipsey River, AL	7	15.6 (0.9)	17.6	8.0 (0.6)	18.4 (1.4)	58.9 (4.1)
Obliquaria reflexa	Little Tallahatchie River, MS	—	—	1.7	—	—	—
Obliquaria reflexa	Sipsey River, AL	—	—	1.8	—	—	—
Obovaria unicolor	Sipsey River, AL	24	5.5 (0.3)	5.0	2.0 (0.2)	22.7 (1.0)	67.7 (3.2)
Truncilla donaciformis	Little Tallahatchie River, MS	—	—	7.5	—	—	—
Villosa lienosa	Sipsey River, AL	4	9.3 (0.3)	10.8	3.8 (1.0)	32.7 (14.8)	63.2 (9.1)
Tribe Pleurobemini							
Elliptio arca	Sipsey River, AL	—	—	6.2	—	—	—
Fusconaia cerina	Sipsey River, AL	—	—	0.9	—	—	—
Pleurobema decisum	Sipsey River, AL	—	—	3.4	—	—	—
Tribe Quadrulini							
Quadrula asperata	Sipsey River, AL	—	—	1.0	—	—	—
Quadrula pustulosa	Little Tallahatchie River, MS	—	—	1.1	—	—	—
Quadrula rumphiana	Sipsey River, AL	—	—	0.1	—	—	—

Observed values of RE are from this study except where otherwise noted. Sample sizes in this analysis differ from those in Table 1 because mass was not determined for all individuals with fecundity estimates. Estimated RE was based on length *versus* dry mass relationships (W. R. Haag, unpublished data, except where otherwise noted) using estimates of mean adult length and fecundity for each population (Table 1; see text). Values in parentheses are standard errors. — denotes that values either were not determined, not reported in the source, or are not applicable because estimated RE is based on mean values of mass and fecundity for the population. Other sources: [1]Bauer (1998); [2]Haukioja & Hakala (1978), cited in Bauer (1998); [3]Cameron *et al*. (1979; length–dry mass relationships).

(2) Life-history variables

I examined variation in fecundity among mussel species with regard to seven life-history variables: body size, offspring (glochidia) size, lifespan, brooding period, area of the gill used for brooding, host-infection strategy, and host use. When possible, I used estimates of these variables specific to the same population from which fecundity estimates were made, but estimates from other populations were used in some cases. Sources and methods for determining life-history variables are described below.

Body size: determined as the mean shell length (mm) of individuals from which fecundity estimates were made as reported in Table 1. I also used shell volume when available as a surrogate measure of body mass.

Glochidia size: defined as the mean of glochidial shell length and height (mm) following Barnhart *et al*. (2008). Data on glochidia size were obtained from Hoggarth (1999), Kennedy & Haag (2005), and Barnhart *et al*. (2008), and were available for 67 species in the dataset.

Lifespan: determined as the maximum age (years) reported for a species. Information was obtained primarily from Haag & Rypel (2011), but also van der Schalie & van der Schalie (1963), Harmon & Joy (1990), Barnhart (2001), Rogers, Watson & Neves (2001), Fobian (2007), Jones *et al*. (2010) and Jones & Neves (2011). If estimates of lifespan were available for more than one population of a species, I used the maximum reported value. Estimates of lifespan were available for 51 species in the dataset.

Brooding period: classified as short-term or long-term brooders according to information summarized in Williams, Bogan & Garner (2008). Brooding period was available for all species.

Gill brooding area: determined as the proportion of the gills used for brooding glochidia. For example, species that brood glochidia throughout the length of all four gills were assigned a value of 1.00, and species that brood only in the posterior half of the outer gills were assigned a value of 0.25. *Cyprogenia* spp. and *Obliquaria reflexa* brood only in a few water tubes in the outer gills and were assigned a value of 0.17. Brooding area was determined mostly from information summarized in Williams *et al*. (2008) and was available for all species. Because gill area had only four values (0.17, 0.25, 0.50, and 1.00), I treated this as a nominal variable in data analysis.

Host infection strategy: determined as one of five strategies used by mussels to transmit glochidia to hosts, including broadcasting, mucus webs, mantle lures, conglutinates, and mantle magazines (see Barnhart *et al*., 2008). Broadcasting includes species that release free glochidia, which encounter hosts apparently by chance. Release of glochidia in mucus webs is similar to broadcasting, but glochidia are bound in a mucus matrix that entangles potential host fishes. Mantle lures are modified portions of the female mantle that attract potential fish hosts to the mussel by mimicking prey items of fishes; glochidia are released when attacking fishes rupture the gravid gill which is also displayed as part of the lure. Conglutinates are discrete packets of glochidia that mimic prey items of fishes; after release from the female mussel, conglutinates are ingested by fishes facilitating transmittal of glochidia. The mantle magazine strategy involves short-term storage of glochidia within a chamber associated with the excurrent aperture; glochidia are discharged rapidly from the chamber apparently upon tactile, photosensory, or chemosensory stimulation by a host fish. Host infection strategies were determined for 58 species based on Barnhart *et al*. (2008). Host infection strategies are well-described for most species in the data set except for a few species classified as broadcasters by default because of the apparent absence of other adaptations for host infection (e.g. *Leptodea*, *Potamilus*, *Truncilla*; see Section IV).

Host use: determined as the primary hosts for a mussel species (see Haag & Warren, 1997; O'Brien & Williams, 2002). To facilitate broad comparisons in host use, I categorized host use into guilds according to the highest taxonomic level that encompassed the range of fishes or amphibians used by a particular mussel species. Host guilds included freshwater drum (*Aplodinotus grunniens*), black basses (*Micropterus* spp.), sunfishes (*Lepomis* spp.), darters (Percidae), sculpins (*Cottus* spp.), catfishes (Ictaluridae), minnows (Cyprinidae), salmonids (Salmonidae), gar (Lepisosteidae), skipjack herring (*Alosa chrysochloris*), mudpuppy (*Necturus maculosus*), sauger and walleye (*Sander* spp.), and generalists that do not specialize on a particular host group. I obtained host information from a large number of studies summarized in the Mussel/host database, The Ohio State University Museum of Biological Diversity, Division of Mollusks, http://www.biosci.ohio-state.edu/~molluscs/OSUM2/index.htm.

(3) Data analysis

For original data and datasets provided by colleagues, I tested for length-fecundity relationships for populations with sample sizes exceeding seven individuals. When sample sizes were sufficient, I generated separate length-fecundity relationships for species represented in the dataset by more than one population. Because mussel fecundity typically is related to length by a power function (e.g. Paterson, 1985; Haag & Staton 2003; Moles & Layzer, 2008), I fitted power functions for all species, but also evaluated alternative models by examining residuals and coefficients of determination. I omitted a small number of outlier observations for some species if these values deviated widely from length–fecundity relationships. In most cases, outliers were exceptionally small numbers suggesting that these females had already released a portion of their brood; all omitted outliers are reported in the footnotes to Table 1. For species with shell volume data and sufficient sample sizes, I also tested for relationships between fecundity and volume. Although the dataset included two or more populations for some species, small sample sizes did not allow me to test for differences in length-specific fecundity among any populations.

I examined bivariate relationships between fecundity and life-history variables using linear regression and analysis of variance with all continuous variables $\log_{10}$-transformed. For these analyses, I used mean fecundity, shell length, and shell volume for species represented in the dataset by more

than one estimate. Because shell length was strongly related to fecundity, I accounted for the influence of length on relationships with other life-history variables either by using length-standardized fecundity (obtained as the residuals of fecundity regressed on length) or with analysis of covariance. I also examined relationships between reproductive effort (RE) and life-history variables (shell length, glochidial size, lifespan, brooding period, and fecundity). For these analyses, life-history variables were specific to the population for which RE was estimated except for *M. margaritifera*; for this species, I used data from other central European populations (see Table 2). I did not examine relationships between RE and host strategies because of the smaller number of species with estimates of RE. In addition to estimates of annual fecundity presented in Table 1, I was interested in how lifetime fecundity was related to life-history variables, especially lifespan. In organisms with indeterminate growth, lifetime fecundity can be calculated by summing mean fecundity of each age class. However, because age-fecundity relationships were available for few species in the dataset, I estimated lifetime fecundity as the product of mean fecundity and lifespan, assuming one brood per year. I evaluated the accuracy of this approach in three species for which complete age-specific fecundity information was available (Haag & Staton, 2003). Estimates were similar for both methods for all three species (*Elliptio arca*: summed age-specific fecundity = 4077374, mean fecundity x lifespan = 4086810; *Lampsilis ornata*: 6220106, 5071968; *Quadrula pustulosa*: 1433387, 1361712).

I examined the relationship between annual fecundity and suites of life-history variables simultaneously using multiple regression. I used this approach to provide a simple comparison of the relative amount of variation in fecundity explained by various factors and not to develop a predictive model for estimating fecundity. Further, to avoid problems with stepwise procedures, I analyzed only the full models including all effects (e.g. Whittingham *et al*., 2006). In this analysis, I used as independent variables shell length, glochidial size, lifespan, brooding period, and host-infection strategy. I did not include host use in this analysis because it is highly associated with host-infection strategy; host-attraction strategies typically target specific fish feeding or behavioural guilds (Barnhart *et al*., 2008; Haag, 2012). The categorical variables brooding period and host-infection strategy also covary to a considerable extent. For example, all species with mantle lures are long-term brooders, but long-term brooders are also present among other infection strategies. In addition, brooding was weakly correlated with glochidial size ($r = 0.306$, $P < 0.0121$; on average, larger glochidia in long-term brooders) and lifespan ($r = 0.654$, $P < 0.0001$; on average, shorter lifespan in long-term brooders), but not with shell length; despite these correlations, glochidial size and lifespan overlapped widely among brooding periods. There was a weak relationship between shell length and lifespan ($r = 0.281$, $P < 0.0464$), but the other continuous independent variables were not correlated with each other.

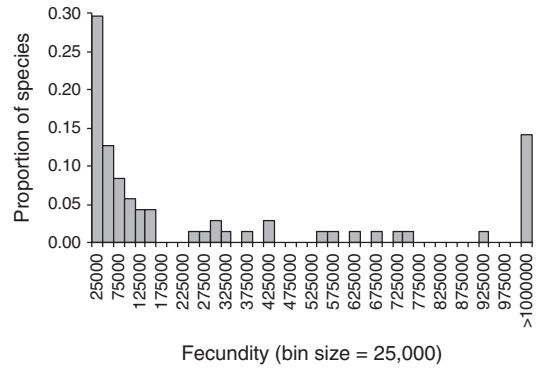

Fig. 1. Distribution of average fecundity values for North American freshwater mussel species ($N = 71$ species plus one subspecies).

III. RESULTS

(1) Overall patterns of fecundity

Fecundity varied widely among mussel species and spanned nearly 4 orders of magnitude (Table 1). Mean population-level species fecundities ranged from 1950 (*Pegias fabula*) to 10735000 (*Leptodea fragilis*). Fecundity was even more variable among individuals and ranged from 49 for a small specimen of *Quadrula pustulosa* to 23401500 for a large adult *Leptodea fragilis*. Fecundity values showed an apparently multimodal distribution (Fig. 1). Species with relatively low fecundity (< 25000) composed the largest percentage (30%), and 65% of species had fecundity < 150000; 14% of species had very high fecundity (> 1000000), and about 20% had fecundity between 250000–950000.

Among populations of a species, mean fecundity was generally similar and well within the same order of magnitude. In many cases where populations appeared to vary more widely, these differences were due to samples containing individuals that differed widely in length (e.g. *Lampsilis teres*, *Ligumia recta*, *Leptodea fragilis*). For example, mean fecundity of *Pyganodon grandis* from two Mississippi populations was more than seven times higher than a population from Alberta, but mean length of these populations also differed widely, and the predicted fecundity of a 90 mm individual was similar in all three populations (Mississippi, 198514, 153323; Alberta, 174018; see Hanson *et al*., 1989). However, some populations did appear to show substantial differences in length-specific fecundity. Predicted fecundity of a 55 mm *Pyganodon cataracta* from Layton's Lake, Nova Scotia (55498), was more than five times higher than a similarly sized individual from nearby Morice Lake, New Brunswick (10468), and the slopes of these relationships also differed widely (Table 1; see Paterson & Cameron, 1985). Slopes of length-fecundity relationships were similar between two populations of *Actinonaias ligamentina* in the Green River, Kentucky, but length-specific fecundity was over 1.5 times higher in one population (see Moles & Layzer, 2008).

Within a population, fecundity varied among individuals by 0–2 orders of magnitude and this variation was strongly

related to female size (Table 1). Shell length was a significant predictor of fecundity for all populations with datasets of seven or more individuals with the exception of *Epioblasma florentina aureola* ($P < 0.4373$, $N = 7$), *Fusconaia ozarkensis* ($P < 0.4468$, $N = 8$), and *Pleurobema strodeanum* ($P < 0.0532$, $N = 9$). Length explained a high percentage of variation in fecundity in most populations, even those with small sample sizes ($r^2 = 0.40–0.90$; Table 1). Length-fecundity relationships for most species were best described by power functions. Values of the allometric constant b ranged from 1.3 to 5.5 and averaged 3.2 (median value 3.0). The value of b for *Quadrula rumphiana* departed widely from this range (11.4). Length-fecundity relationships for five species were best described by equations of other forms including second-order polynomials (*Elliptio arca*) and square-root functions (*Obliquaria reflexa, Quadrula asperata*, and *Q. pustulosa*) (see Haag & Staton, 2003). The length-fecundity relationship for *Obovaria unicolor* was described equally well by a power function ($r^2 = 0.408$, see Table 1) and a linear function ($r^2 = 0.441$, $P < 0.001$; fecundity = 2491.6[length] − 24031); however, the 95% confidence interval for b in the power function contained 1, providing little support for a curvilinear relationship in this species.

Shell volume and body mass were generally equivalent predictors of fecundity compared with length (Table 3). For 8 of 11 populations, volume explained less variation in fecundity than length, but r^2 values were similar. For nine populations, volume-fecundity relationships were best described by power functions, which explained more variation in fecundity than linear functions. However, in most cases, the 95% confidence interval for b contained 1, providing little support for a curvilinear relationship between volume and fecundity. Female body mass also was a nearly equivalent predictor of fecundity compared with length. The relationship between mass and fecundity was best described by a linear function for two species and by a power function for two others; however, in the latter cases, 95% confidence intervals for b contained 1.

Fecundity differed among phylogenetic groups, but was highly variable within most groups (Fig. 2). The Margaritiferidae had by far the greatest median fecundity of any group, and the two species in the dataset had similarly high fecundity (*Cumberlandia monodonta* and *Margaritifera margaritifera*). The Amblemini and Lampsilini had moderately high median fecundity, but fecundity of the Lampsilini spanned an enormous range. The Lampsilini included the highest observed fecundity of any species (*Leptodea fragilis*) and several other species with fecundity > 500000 (*Actinonaias ligamentina, Glebula rotundata, Lampsilis* spp., *Leptodea leptodon, Ligumia recta, Potamilus ohiensis*, and *Truncilla truncata*), as well as species with fecundities < 20000 (*Epioblasma* spp., *Lemiox rimosus*, and *Medionidus* spp.). The Anodontini, Pleurobemini, and Quadrulini all had similar, low median fecundities, but each group had conspicuous outliers with high fecundity (Anodontini: *Arcidens confragosus, Lasmigona complanata, Pyganodon grandis*; Pleurobemini: *Elliptio crassidens*; Quadrulini: *Megalonaias nervosa*). Species with very low fecundity (< 10000) occurred in all phylogenetic groups except the Margaritiferidae and Amblemini (Anodontini: *Pegias fabula, Alasmidonta heterodon, A. viridis, Lasmigona holstonia*; Lampsilini: *Epioblasma florentina aureola, E. florentina walkeri*; Pleurobemini: *Fusconaia burkei*, Quadrulini: *Uniomerus tetralasmus, Quadrula asperata*).

Fecundity standardized by length showed a similar pattern among phylogenetic groups (Fig. 2). Length-standardized fecundity was highest on average for the Margaritiferidae, intermediate for the Amblemini and Lampsilini, and lowest for the Anodontini, Pleurobemini, and Quadrulini. However, length-specific fecundity was less variable than total fecundity in the Anodontini, Pleurobemini, and Quadrulini and was uniformly low compared to other groups (studentized residuals for most species < 0). Similar to total fecundity, length-specific fecundity was highly variable within the Lampsilini and included the highest values for any species (*Truncilla* spp., *Leptodea* spp.), as well as other species with high values despite their low-to-moderate total fecundity (e.g. *Lampsilis* spp., *Medionidus acutissimus*, *Obovaria unicolor*, *Villosa* spp.).

(2) Overall patterns of reproductive effort

Direct estimates of reproductive effort (RE) based on dry mass ranged among nine species from 5.5 to 25.4% (Table 2). Estimates of RE based on ash-free dry mass were roughly half of those based on dry mass. This was due to a much higher percentage of inorganic material (ash) in glochidia compared with adult soft tissues. Only three species had sufficient sample sizes to test relationships between size and RE within a population. For *Obovaria unicolor*, dry mass RE was negatively related to length but explained little of the variation in RE ($r^2 = 0.328$, $P < 0.004$; log length = −19.482[arcsine(RE/100)] + 42.438). Ash-free RE of *O. unicolor* and dry mass RE of *Pyganodon grandis* and *Utterbackia imbecillis* were not related to length ($P < 0.210$). Estimated RE ranged from 0.06 to 19.9%. Estimates of RE differed substantially between populations of *Amblema plicata* and *Pyganodon cataracta* but were similar between populations of *Obliquaria reflexa*.

Patterns of variation in RE among phylogenetic groups departed in several ways from those for fecundity (Fig. 2). Despite their high fecundity, RE of *Margaritifera margaritifera* (Margaritiferidae) and Amblemini was low. Conversely, although median fecundity of Anodontini was relatively low, their reproductive effort was the highest of any group. Similar to fecundity, median RE of Lampsilini was moderately high but was highly variable among species, and RE was uniformly low for the Pleurobemini and Quadrulini.

(3) Relationships of fecundity and life-history variables

Across species, shell length was a strong, significant predictor of fecundity and explained just over half of the variation among species [log fecundity = 2.808(log length) 0.055; $P < 0.0001$, $r^2 = 0.513$]. This relationship was influenced by five outliers representing species with very high fecundity (*Leptodea fragilis, L. leptodon, Margaritifera margaritifera, Truncilla*

Table 3. Comparison of shell length, volume, and body mass for explaining variation in fecundity among individuals in freshwater mussel populations

Species	Population	Variable	r^2	a	b	N
Amblema plicata	Little Tallahatchie River, MS	Length	0.828	0.006	3.921	10
		Volume	0.805	1770	1.246†	10
A. plicata	Sipsey River, AL	Length	0.879	0.600	3.027	13
		Volume	0.669	9323	0.921†	13
Ellipsaria lineolata	Tennessee River, AL	Length	0.810	0.071	3.482	18
		Volume	0.762	3385	1.170†	18
Lampsilis straminea	Sipsey River, AL	Length	0.825	0.268	3.300	6
		Volume*	0.701	87802	6132	6
		Mass*	0.752	49614	720841	6
Leptodea fragilis	St. Frances River, AR	Length	0.770	5.864	3.217	15
		Volume	0.698	212253	0.984†	15
Medionidus acutissimus	Sipsey River, AL	Length	0.939	0.037	4.095	8
		Volume	0.866	19201	0.892†	8
		Mass	0.947	473265	1.125†	8
Megalonaias nervosa	Tennessee River, AL	Length	0.799	156.170	1.732	11
		Volume	0.731	9181	0.888†	11
Obovaria unicolor	Sipsey River, AL	Length	0.408	572.160	1.310†	24
		Volume*	0.469	28409	6326	24
		Mass*	0.3873	28470	73026	24
Pyganodon grandis	Farm pond, MS	Length	0.423	0.220	2.990	10
		Volume	0.433	3109	0.952†	10
Potamilus purpuratus	St. Francis River, AR	Length	0.891	0.002	4.134	10
		Volume	0.874	441	1.460	10
Utterbackia imbecillis	Puskus Lake, MS	Length	0.271	1.429	2.460	8
		Volume	0.382	4190	0.824†	7
		Mass	0.247	69744	0.944†	8

a and b are fitted constants of the allometric equation: fecundity $= a$(length, volume, or mass)^b, except for relationships denoted by *, which are linear: (fecundity $= a + b$(length, volume, or mass). All relationships are significant at $P < 0.001$ except for *P. grandis*, volume ($P < 0.03$). In some cases, constants for length relationships differ from those presented in Table 1 because mass and shell volume was not determined for all individuals with fecundity estimates. † denotes the 95% confidence interval for the constant contains 1.

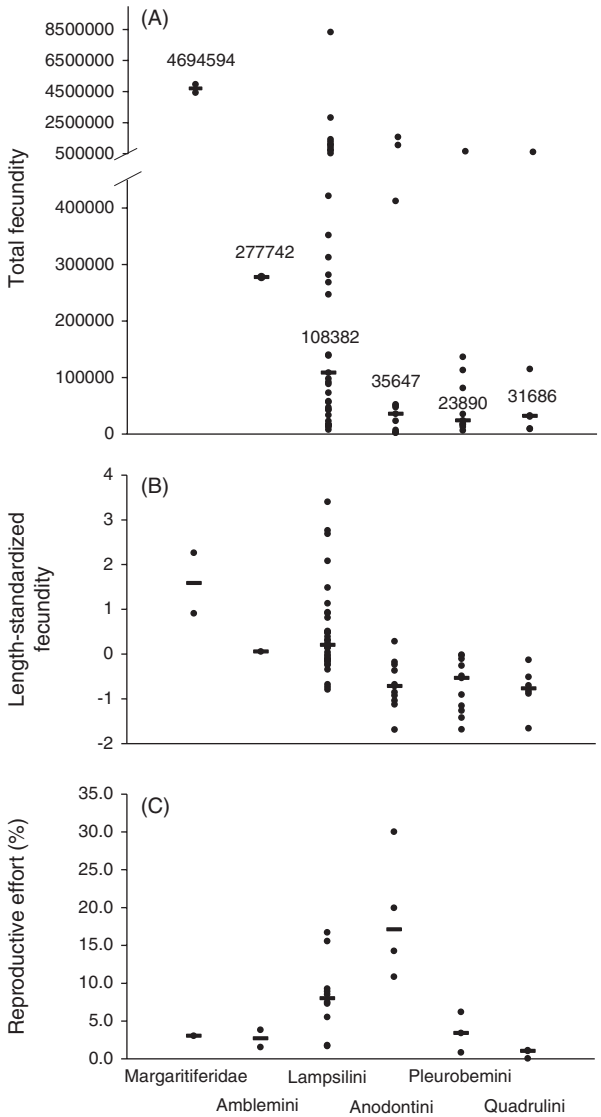

Fig. 2. Phylogenetic patterns of fecundity and reproductive effort for North American freshwater mussel species. (A) Total annual fecundity ($N = 70$ species plus 1 subspecies, excluding *Plectomerus dombeyanus*, which is of uncertain phylogenetic affinity, see Campbell *et al*., 2005). Numbers and horizontal bars are median fecundity for each group; note change in scale between 400000 and 500000. (B) Length-standardized fecundity obtained as the residuals of fecundity regressed on length (both variables log-transformed). Horizontal bars are median residuals for each group. (C) Reproductive effort for 20 species. Horizontal bars are median values.

donaciformis, and *T. truncata*; studentized residuals ≥ 2.0). After omitting these species from the analysis, the proportion of variation in fecundity explained by length increased dramatically (Fig. 3). Other species with high length-specific fecundities but not identified as significant outliers were *Cumberlandia monodonta*, *Lampsilis teres*, *Medionidus acutissimus*, *Obovaria unicolor*, *Potamilus ohiensis*, and *Villosa nebulosa*. Shell volume was nearly equivalent to length for predicting fecundity. For 33 species with volume data (excluding

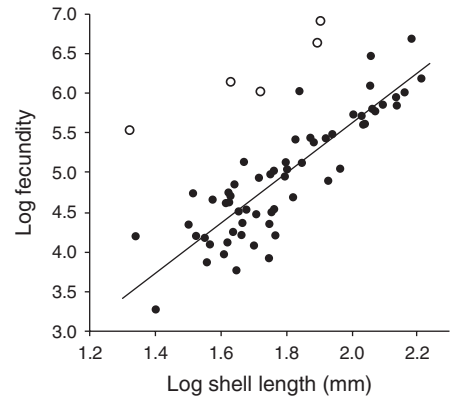

Fig. 3. Relationship between fecundity and shell length for North American freshwater mussels ($N = 71$ species plus one subspecies). Open circles were identified as significant outliers based on very high length-specific fecundity (see text). The plotted regression line is for the dataset excluding these outliers [log fecundity $= 3.146$(log length) $- 0.672$; $P < 0.0001$, $r^2 = 0.751$].

the outliers *L. fragilis* and *Truncilla* spp.), length explained 69.8% of the variation in fecundity [log fecundity $= 2.739$(log shell volume) $+ 0.109$; $P < 0.0001$], and volume explained 68.1% [log fecundity $= 0.958$(log shell volume) $+ 3.766$; $P < 0.0001$]. Among species, shell volume was closely related to length [log shell volume $= 2.716$(log shell length) $- 3.551$; $r^2 = 0.940$, $P < 0.0001$].

Glochidial size was significantly and negatively related to fecundity, but glochidial size explained little of the variation in fecundity among species [Fig. 4; log fecundity $= -1.6984$(log glochidial size) $+ 8.9575$; $P < 0.0008$, $r^2 = 0.163$, $N = 67$]. This relationship was driven by a group of six species with small glochidia and very high fecundity; this group included the five high-fecundity species identified previously as outliers and also *Cumberlandia monodonta*. Another species with small glochidia, *Quadrula rumphiana*, had low fecundity. There was a significant interaction between

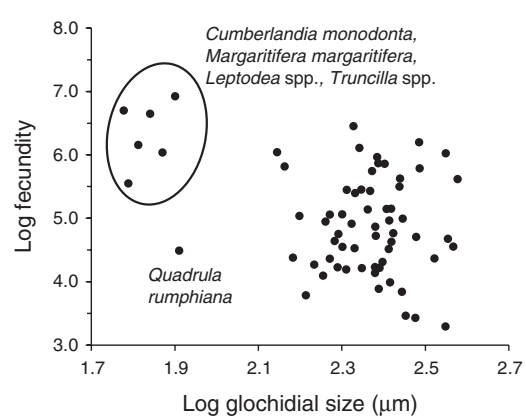

Fig. 4. Relationship between offspring (glochidia) size and fecundity in North American freshwater mussels. Points within the ellipse are six species with small glochidia and high fecundity (see text).

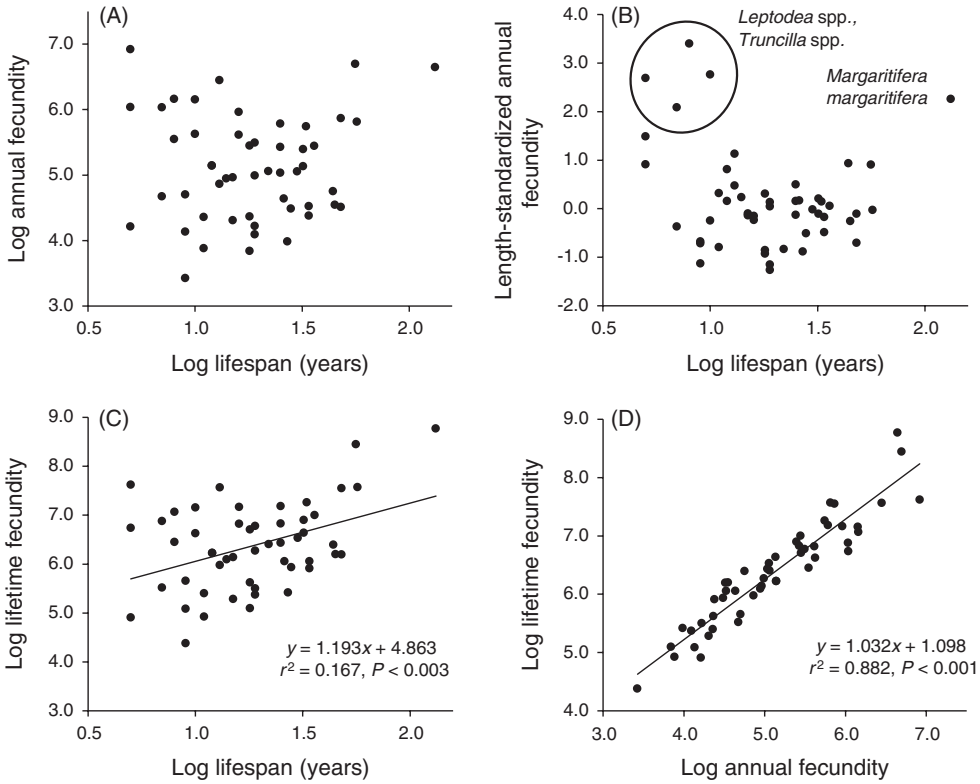

Fig. 5. (A–D) Relationships between lifespan and fecundity in North American freshwater mussels.

glochidial size and adult shell length (ANOVA, $F = 5.99$, $P < 0.0178$), showing that, across all species, the relationship between fecundity and length was confounded by variation in glochidial size. After omitting from the analysis the six species with small glochidia and high fecundity, glochidial size was not related to fecundity (Fig. 4; $P < 0.1995$, $r^2 = 0.033$, $N = 61$) and there was no interaction between glochidial size and length ($F = 0.16$, $P < 0.6907$). Further, there was no relationship between glochidial size and length-standardized fecundity (ANCOVA, $F = 2.03$, $P < 0.1604$).

Fecundity showed little relationship with lifespan (Fig. 5). Annual fecundity was not related to lifespan, either for all species ($P < 0.6189$, $N = 51$), or for the dataset excluding species with high fecundity and small glochidia ($P < 0.1274$, $N = 46$). Similarly, there was no relationship between length-standardized fecundity and lifespan ($P < 0.1538$, $N = 51$). There was an apparent trend of higher length-specific fecundity in short-lived species, driven by *Leptodea* spp. and *Truncilla* spp., but long-lived *Margaritifera margaritifera* also had high length-specific fecundity. Lifetime fecundity was positively related to lifespan, but lifespan explained little of the variation in fecundity; omitting species with high fecundity and small glochidia improved the explanatory power of this model by only a small margin ($r^2 = 0.2014$, $P < 0.004$). However, this relationship was apparently an artifact of the weak, but positive relationship between size and lifespan (see Section II.3 and Haag & Rypel, 2011). After removing the effect of size on lifetime fecundity, lifetime fecundity was not related to lifespan (ANCOVA, $F = 0.88$, $P < 0.3537$, $N = 51$). Rather, lifetime fecundity was simply a strong function of annual fecundity (Fig. 5).

Fecundity was weakly related to brooding period. Total fecundity did not differ between long-term and short-term brooders (ANOVA, $F = 0.15$, $P < 0.7009$, $N = 71$). Length-standardized fecundity differed significantly between brooding strategies but explained very little variation in fecundity (ANCOVA, $F = 5.30$, $P < 0.0244$, $r^2 = 0.071$, $N = 71$; no interaction between log length and brooding, $F = 2.41$, $P < 0.1258$). Mean length-standardized fecundity was higher for long-term brooders but confidence intervals overlapped [least-square mean (95% confidence interval): long-term brooders = 120216 (80716–179045); short-term brooders = 56453 (33742–94450)], and in general, data scatter for the two strategies was similar (Fig. 6A). Removing species identified previously as outliers had no substantial effect on relationships between fecundity and brooding period.

There was little relationship between fecundity and the area of the gills used for brooding. Total fecundity was not related to gill brooding area (ANOVA, $F = 0.05$, $P < 0.8217$, $N = 71$). Length-standardized fecundity differed significantly among brooding area classes (ANOVA, $F = 7.26$, $P < 0.0003$; Fig. 6B). Fecundity was significantly higher for species that brood glochidia only in the posterior half of the outer gills (i.e. class 0.25, including most species in the Lampsilini) than species that brood glochidia in the entire outer gills (i.e. 0.50; Anodontini, *Elliptio* spp., *Pleurobema* spp.), but did not differ among the other brooding groups.

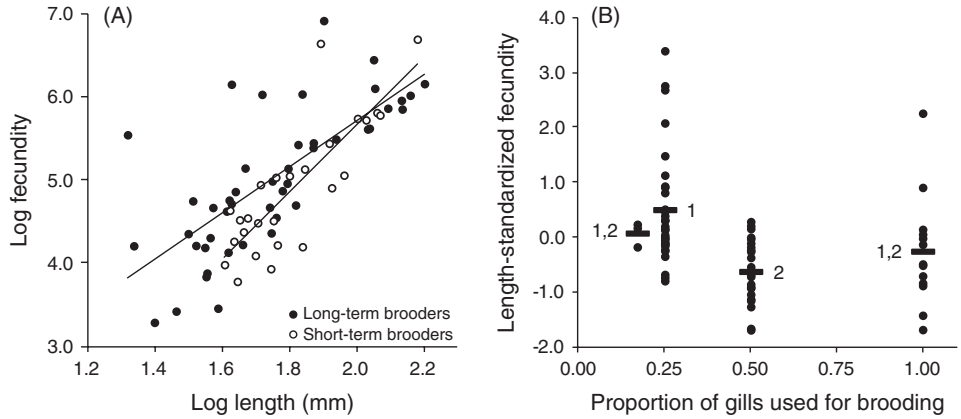

Fig. 6. (A,B) Relationship between brooding traits and fecundity in North American freshwater mussels. In (B), horizontal bars are mean length-standardized fecundity for each brooding area class; classes with the same number are not significantly different ($P > 0.05$).

Despite these significant differences, total and length-specific fecundity overlapped greatly among brooding classes (Fig. 6).

Length-standardized fecundity (residuals of log fecundity regressed on log length) was significantly different among host-infection strategies (ANOVA, $F = 23.86$, $P < 0.0001$, $N = 58$). Length-standardized fecundity was higher for broadcasters than for all other infection strategies, but did not differ significantly among any other strategies (Fig. 7). Among putative broadcasters, only *Potamilus purpuratus* had length-standardized fecundity that was similar to species with other infection strategies. Even though length-standardized fecundity did not differ among the remaining strategies, residuals were centered nearly on zero only for species that displayed mantle lures. For conglutinates, mucus webs, and mantle magazines, most residuals were < 0, indicating a weak trend for lower length-specific fecundity in these strategies. Within the mantle lure strategy, length-standardized fecundities were lowest in *Epioblasma*, which uses a host-trapping infection strategy in conjunction with lure display (see Section IV). Overall, the lowest observed values of length-standardized fecundity were for three species that produce conglutinates (*Fusconaia burkei*, *F. ozarkensis*, and *Pleurobema collina*), and two species that apparently release glochidia in mucus webs (*Alasmidonta heterodon*, *Elliptio complanata*).

Patterns of length-standardized fecundity and host use were similar to those for infection strategy and differed significantly among groups (ANOVA, $F = 10.10$, $P < 0.0001$, $N = 59$). Length-standardized fecundity was significantly higher for species that use freshwater drum than for all other host groups; among other groups fecundity differed only between species that use bass and those that use minnows (Fig. 7). In addition, length-specific fecundity was high for each of the single species in the dataset that use gar (*Lampsilis teres*) and salmonids (*Margaritifera margaritifera*). Residuals were centered nearly on 0 for bass, sunfish, darter, sculpin, skipjack herring, mudpuppy, and sauger, suggesting that mussels using these hosts have similar length-specific fecundities. Most residuals for minnows, catfishes, and generalists were < 0, suggesting a weak trend of lower length-specific fecundity for mussel species using these host groups. Despite these patterns, fecundity overlapped greatly for all host strategies.

(4) Relationships of reproductive effort and life-history variables

Reproductive effort was not related to length, fecundity, or glochidial size, either for the combined dataset of observed and estimated values ($P < 0.138–0.891$, $r^2 = 0.001–0.107$), or for observed values only ($P < 0.850–0.960$, $r^2 = 0.001–0.005$). For observed and estimated RE combined, RE was strongly negatively related to lifespan (Fig. 8). For observed values only, lifespan explained an even higher percentage of the variation in RE ($P < 0.0001$, $r^2 = 0.861$). Reproductive effort also differed significantly among brooding strategies and was higher in long-term brooders (ANOVA: $F = 40.84$, 1 d.f., $P < 0.0001$; Fig. 8).

(5) Models with multiple life-history variables

The multiple regression model including length, glochidial size, lifespan, brooding period, and host infection strategy supported results of bivariate relationships and the primary importance of size in predicting fecundity. For the full dataset, size was clearly the most important variable determining fecundity, and this model explained a large percentage of the variation in fecundity (Table 4). However, glochidial size and host-infection strategy were also significant factors although their sums of squares were much smaller than for length. Lifespan and brooding period were not significant factors. In the dataset excluding the five species identified as significant outliers (*Leptodea* spp., *Margaritifera margaritifera*, and *Truncilla* spp.; see Section III.3), length was the only significant factor but infection strategy was marginally significant; this model explained a similar proportion of the variation in fecundity as the full dataset (Table 4). For the 40 species in this dataset, length alone explained 73% of the variation in fecundity. This suggests that knowledge of infection strategy could

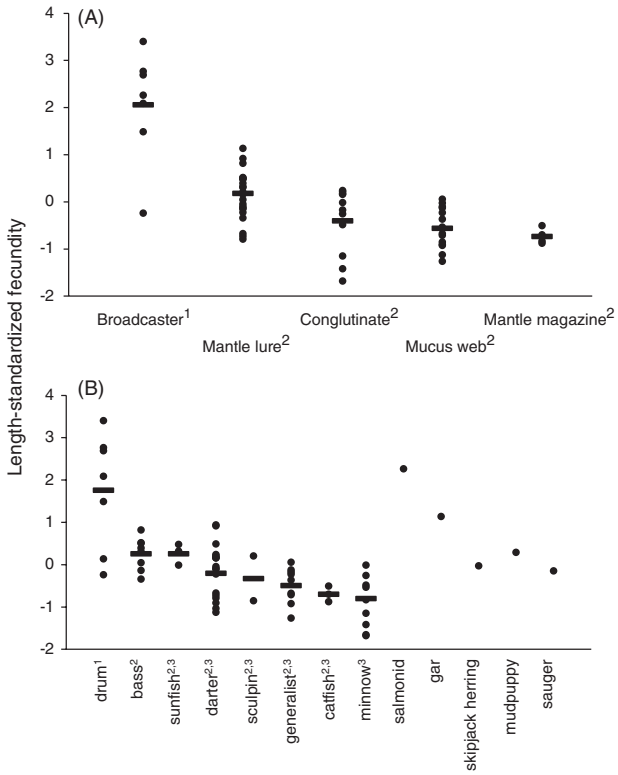

Fig. 7. Patterns of fecundity among host strategies of North American freshwater mussels. (A) Shows variation in fecundity among host-infection strategies and (B) shows variation among host-use strategies. For both (A) and (B), length-standardized fecundity was obtained as the residuals of fecundity regressed on length (both log-transformed). Horizontal bars are mean residuals for each group; groups with the same number are not significantly different ($P > 0.05$); on the (B), host groups without numbers were not included in the analysis.

provide at best only a small improvement in prediction of fecundity compared to length alone.

IV. DISCUSSION

Like many organisms, fecundity of mussels is strongly related to body size, both within and among species. Within a population, a high proportion of variation in fecundity among individuals is accounted for by shell length. Because fecundity increases as a power function of length in most species, large individuals are expected to contribute a disproportionately high fraction of reproductive output in a population. Age is typically a poorer predictor of mussel fecundity (Haag & Staton, 2003), suggesting that fecundity is determined primarily by energetic constraints related to body size. Although shell volume and mass were roughly equivalent to length as predictors of fecundity, female body mass or condition may explain some of the variation in fecundity unaccounted for by length. In *Margaritifera margaritifera*, heavier females produced more glochidia per unit length, and there was an apparent body mass threshold below which other females did not reproduce (Bauer, 1998).

The extent to which fecundity varies among populations and the significance of this variation remains poorly known. In *Elliptio arca*, *Fusconaia cerina*, and *Quadrula asperata*, mean fecundity and length-specific fecundity did not differ among populations in a river or among nearby rivers (see Haag & Staton, 2003). In other cases, mean fecundity differed widely between populations, but length-fecundity relationships were similar, and differences in fecundity were simply a result of population differences in adult size (e.g. *Obliquaria reflexa*, *Pyganodon grandis*). Growth rate and body size can be influenced to a large extent by environmental factors (see Haag & Rypel, 2011), and concomitant differences in fecundity are an expected consequence of this plasticity. More interesting are cases in which length-specific fecundity differs among populations, indicating different levels of energetic allocation to reproduction. Such differences have been documented among populations in different water bodies (*Amblema plicata*, *Pyganodon cataracta*), and even among populations in a river (*Actinonaias ligamentina*, *Pleurobema decisum*; see Paterson & Cameron, 1985; Haag & Staton, 2003; Moles & Layzer, 2008). The potential adaptive significance of these differences is unknown, but some also may be simple responses to variation in body size. For example, even though length-specific fecundity differed widely among populations of *P. cataracta*, these populations also differed in length-specific body mass, and fecundity did not differ when expressed as a function of mass (Paterson & Cameron, 1985). Despite these examples, no studies have examined patterns of fecundity and reproductive allocation at large scales, such as across the geographic range of a species or across broad environmental gradients.

The great variation in fecundity among mussel species suggests that this may be an important trait for describing divergent life-history strategies within the group. However, similar to within- and among-population variation, variation in fecundity among species was explained primarily by body size and there was little evidence of trade-offs between fecundity and other life-history traits. For most species, there was no evidence of a trade-off between fecundity and offspring size, and little evidence of a trade-off between fecundity and lifespan. The degree of parental care invested in offspring was opposite to that predicted by life-history theory: species that brood glochidia for extended periods (long-term brooders) had on average significantly higher fecundity than short-term brooders.

The strongest evidence for a fecundity trade-off are the diminutive glochidia of *Margaritifera margaritifera*, *Leptodea* spp., and *Truncilla* spp., which are less than one third the size of most other species. Even though they have extraordinarily high fecundity, RE of these species is lower than, or comparable to, many other species. This suggests that reduced energetic investment in individual glochidia allows maximization of total glochidial output as predicted by life-history theory. A cost of small glochidia may be the requirement for an extended period of glochidial development on hosts (Howard

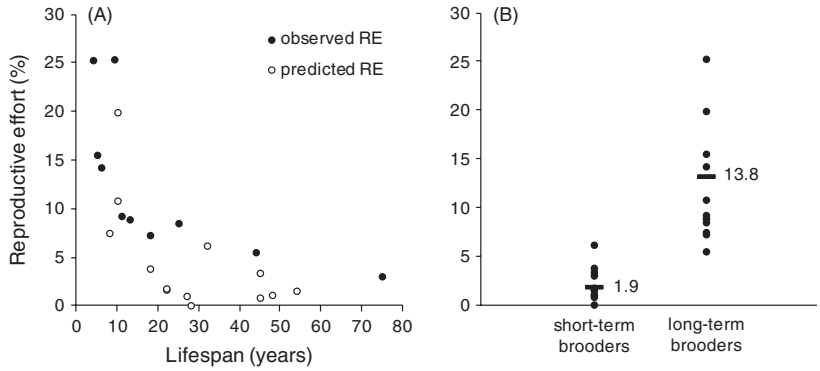

Fig. 8. Relationship between reproductive effort (RE), lifespan, and brooding period. (A) Regression equation is arcsin RE = −16.564(log lifespan) + 35.254; $P < 0.0001$, $r^2 = 0.632$ (observed and predicted RE combined), but data are plotted untransformed. (B) Horizontal bars indicate mean values back-transformed from arcsin-transformed data.

Table 4. Results of multiple regression models for predicting fecundity of freshwater mussels based on life-history variables

Variable	d.f.	Partial sums of squares	F	$P <$	r^2
Full dataset ($N = 46$)	8	24.470	30.29	0.0001	0.871
Length	1	11.010	109.04	0.0001	—
Glochidial size	1	1.575	15.60	0.0003	—
Lifespan	1	0.003	0.03	0.8646	—
Host-infection strategy	4	1.101	2.73	0.0444	—
Brooding period	1	0.081	0.80	0.3766	—
Dataset without outliers ($N = 40$)	8	15.697	21.98	0.0001	0.850
Length	1	9.731	109.00	0.0001	—
Glochidial size	1	0.213	2.39	0.1326	—
Lifespan	1	0.010	0.12	0.7355	—
Host-infection strategy	4	0.884	2.47	0.0648	—
Brooding period	1	0.001	0.01	0.9096	—

& Anson, 1922; Young & Williams, 1984; Steingraeber *et al*., 2007; Barnhart *et al*., 2008), during which the chances of glochidial or host death are increased. Despite the costs of small glochidia, the host-infection strategy of these species may place them under strong selective pressure to maximize fecundity. *Margaritifera margaritifera* broadcasts free glochidia into the water column where host infection apparently is largely a matter of chance and may be strongly dependent on high glochidial abundance in the drift (Murphy, 1942). In *M. margaritifera*, small glochidia are further thought to allow high fecundity despite the low productivity of streams in which it typically occurs (Bauer, 1998). Host-infection strategies of *Leptodea* spp. and *Truncilla* spp. are unknown, and the forces that may have selected for small glochidia and high fecundity in these species are unclear. Gravid female *Truncilla* spp. show subtle mantle movements that are absent in males (B. Sietman, personal communication), but otherwise, both genera lack conspicuous mantle lures, conglutinates, or other obvious host attraction adaptations, suggesting that they also may broadcast free glochidia. Alternatively, it is proposed that their host, the molluscivorous freshwater drum, becomes infected with glochidia by feeding on gravid female mussels (Coker *et al*., 1921; Howard & Anson, 1922; Barnhart *et al*., 2008). This host-infection mode has not been documented directly, but small glochidia may make possible the unusually high glochidial infestations typically seen on drum (e.g. Surber, 1915; Coker *et al*., 1921; Weiss & Layzer, 1995) therefore maximizing the benefits of female sacrifice. Regardless, the occurrence of this trait in two disparate mussel lineages (Margaritiferidae and Lampsilini) suggests that it is an adaptive trade-off rather than a phylogenetic artifact.

Diminutive glochidia also occur in the *Quadrula quadrula* group (including *Q. rumphiana*) and in *Quadrula verrucosa* (Barnhart *et al*., 2008). These species attract and infect hosts with mantle magazines, but this trait is shared with other members of the Quadrulini that do not have diminutive glochidia (*Cyclonaias tuberculata*, *Quadrula metanevra* group, *Q. pustulosa* group; Barnhart *et al*., 2008; Sietman, Davis & Hove, 2012). Unlike other species with diminutive glochidia, fecundity is low in *Q. rumphiana* and is comparable to *Q. asperata* and *Q. pustulosa*, and much lower than *Q. cylindrica*, all of which have glochidia that are nearly three times larger than *Q. rumphiana*. Consequently, the presence of small glochidia in the Quadrulini clearly does not represent a trade-off allowing higher fecundity, and the potential adaptive significance of this trait is unexplained.

There were no strong differences in fecundity among other host-infection strategies suggesting that differences in efficiency among these strategies have not been large enough to exert substantial selective pressure on fecundity.

Nevertheless, differences among or within some strategies could reflect the relative efficiency of host infection. For example, the lower length-specific fecundity of *Epioblasma* spp. compared to other species with mantle lures may be due to the unusual host trapping behaviour exhibited by these species. Females trap hosts (darters) between their shell valves and pump glochidia over the fish's gills (Barnhart *et al*., 2008); this behaviour may be highly efficient in transferring glochidia to hosts thus relaxing selection for high fecundity. For mantle-lure strategies that do not include host trapping, it is more difficult to propose that their generally high length-specific fecundity reflects lower infection efficiency compared with conglutinate, mucus web, and mantle magazine strategies that are typically associated with low length-standardized fecundity. First, pelagic conglutinates are composed of a large number of unfertilized eggs that provide structure to these conglutinates (Barnhart *et al*., 2008). These structural eggs represent an energetic cost to females and necessarily lower fecundity dramatically in these species. Second, most species that produce mucus webs are host generalists. Rather than reflecting the efficiency of the web strategy itself in infecting fishes, lower fecundity may be possible in these species because of a greater chance of infecting hosts brought about by a broadening of the host resource. Finally, there is likely a phylogenetic component to some of these patterns. For example, all species that use mantle magazines to infect hosts are in the Quadrulini, and lower fecundity for this strategy may be simply a shared, inherited trait within this lineage.

Other shared traits within lineages may be responsible for differences in fecundity among species or tribes. Brooding period and the area of the gill used for brooding have a strong phylogenetic component and may not be easily modified by selection. Brooding glochidia in the gills likely decreases feeding and respiratory efficiency. In the Anodontini and Lampsilini, glochidia are brooded for an extended period, and gravid gills are greatly distended to several times their normal thickness leaving little or no space for water circulation. This problem is dealt with in the Anodontini by the development of accessory gill water tubes in gravid females (Richard *et al*., 1991; Tankersley & Dimock, 1993; Tankersley, 1996) and in the Lampsilini by using only a small portion of the total gill area. In species that use the entire length of the gill for brooding and lack accessory water tubes (Margaritiferidae, Pleurobemini, Quadrulini), gills are usually incompletely filled with glochidia and are not greatly distended. This condition has been interpreted as a result of poor fertilization success or female energetic status (Haggerty *et al*., 1995; Bauer, 1998). However, incompletely charged gills seems to be a characteristic of these species (Coker *et al*., 1921; Haag & Staton, 2003) and, along with a short brooding period, may be necessary to maintain filtering and respiratory efficiency. Such constraints could partially explain the low fecundity of most Pleurobemini and Quadrulini.

In contrast to fecundity, patterns of variation in reproductive effort among species showed evidence of a strong trade-off with lifespan as predicted by life-history theory. A central tenet of life-history evolution is that, when resources are limiting, organisms with longer life spans should devote less energy to reproduction per unit time compared with short-lived organisms (Williams, 1966; Stearns, 1992; Charlesworth, 1994). High and early investment in reproduction can decrease lifespan because of diversion of resources from somatic maintenance, and also because of adult mortality associated with reproductive behaviours. In addition to differences among species, this trade-off also appears to be manifested among populations of a species. Reproductive effort of *Amblema plicata* from a long-lived population in the Sipsey River (54 years) was about half that of a short-lived population in the Little Tallahatchie River (18 years; see Haag & Rypel, 2011). Among 13 Finnish populations of *Anodonta piscinalis*, there was a negative correlation between RE and lifespan in one year when food resources appeared to be limiting, but this trade-off was not apparent when resources were more abundant (Haukioja & Hakala, 1978). One unusual feature of RE in mussels is the higher reproductive effort of long-term brooders, which presumably invest more energy in parental care than short-term brooders and would be expected accordingly to devote less energy to offspring production. Factoring in potential costs of brooding may further widen differences in RE among species.

Trade-offs among life-history traits are depicted by the concepts of the fast-slow continuum and *r*- and *K*- selection (Pianka, 1970; Promislow & Harvey, 1990; Bielby *et al*., 2007). In a fast life history (generally corresponding to *r*-selected species), high or variable extrinsic mortality is thought to favour fast growth and early and high investment in reproduction, which results in decreased lifespan. Low or constant mortality and increased competition selects for the opposite suite of traits represented by a slow life history (*K*-selected species) (Arendt, 1997; Cichon, 1997).

In addition to the apparent trade-off between reproductive effort and lifespan, relationships among other mussel life-history traits are emerging that suggest a broad range of life-history strategies in the group. Lifespan varies widely among mussel species, ranging from < 5 to > 100 years, and is strongly negatively related to growth rate such that species that invest heavily in growth have predictably short lives (Haag & Rypel, 2011). Similarly, age at maturity ranges from < 1 to 20 years and also is negatively related to growth rate but positively related to lifespan (Haag, 2012). Together, these relationships depict a continuum of life-history diversity with at least two endpoints corresponding to *r*-selected species with fast growth, short lifespan, high annual reproductive investment, and early maturity, and *K*-selected species with the opposite suite of traits. Among species in the present study, *r*-strategists include the lampsiline *Leptodea fragilis*, and the anodontines *Anodonta anatina*, *Pyganodon* spp., and *Utterbackia imbecillis*. Species at the *K*-selected end of the continuum include the Pleurobemini (*Fusconaia* spp., *Pleurobema* spp.), Quadrulini, slow-growing populations of *Amblema plicata*, and potentially lampsilines such as *Obliquaria reflexa* and *Obovaria unicolor*. Despite its high fecundity, *Margaritifera margaritifera* has low reproductive effort, late age

at maturity, and a long lifespan concordant with a *K*-selected life-history strategy (Bauer, 1998). Other species in this study fall at intermediate positions along the continuum, and for some, such as *Amblema plicata*, life-history traits may be plastic resulting in variable expression of life-history strategy among populations in different environments (Haag, 2012). Particularly interesting is the very low reproductive effort of *Quadrula rumphiana*, which was at least an order of magnitude lower than all other species. This species has only a moderate life span (~28 years), but its low reproductive effort and diminutive glochidia suggest that it represents a unique life-history strategy.

V. CONCLUSIONS

(1) Fecundity of North American mussel species spans nearly four orders of magnitude, but most species have considerably lower fecundity than previous characterizations for the group (e.g. > 200000; McMahon & Bogan, 2001). Nevertheless, the primary role of body size in predicting fecundity suggests that glochidial production is mainly determined by physical and energetic constraints rather than trade-offs among life-history traits. For species that broadcast free glochidia, extraordinarily high fecundity at the cost of reduced glochidial size may be selected for to maximize chances of host infection in the drift. However, for most other species with more elaborate host-infection strategies, differences in fecundity among species may have little adaptive significance. The high fecundity seen in some mussel species has been explained as an adaptation associated with their parasitic life cycle (McMahon & Bogan, 2001). Parasites were long considered to have higher fecundity than free-living organisms to compensate for the high mortality that typically occurs during transmission to hosts (Poulin, 1995; Whittington, 1997). However, recent studies have shown that, similar to mussels, fecundity of many parasites is primarily a function of body size, and length-specific fecundity of parasitic organisms is not different from free-living relatives (e.g. Trouvé & Morand, 1998). Glochidia experience extremely high mortality (≫ 99%) between release from the female and recruitment to the benthic juvenile stage, and recruitment can be highly variable among years probably according to environmental factors (Jansen, Bauer & Zahner-Meike, 2001; Haag, 2012). Accordingly, variation in fecundity has little influence on population growth compared to adult survival (Haag, 2012). Despite the traditional focus on fecundity as a measure of fitness, changes in adult survivorship are increasingly viewed as having a much greater effect on population growth in a wide range of organisms (Crone, 2001). For mussels, as in other organisms, differences among habitats in the relative importance of environmental stochasticity and its effects on adult survivorship may be primary drivers of diversification in life-history strategies, which in turn, influence species responses to human impacts (Haag, 2012).

(2) Unlike fecundity, the relative allocation of energy to reproduction, as measured by reproductive effort, appears to be an important variable for understanding mussel life-history evolution. The negative relationship between RE and lifespan, as well as apparent trade-offs among other life-history traits, indicates a range of divergent life-history strategies with endpoints similar to those described for many other organisms (Haag, 2012; see also Winemiller & Rose, 1992; Grime, 2001).

(3) Despite its strong relationship to other life-history variables, RE of freshwater mussels is generally low (mean = 7.2% in this study for dry-mass estimates) compared with marine bivalves, in which RE commonly exceeds 40% (Dame, 1996). Further, estimates of RE that do not include the inorganic fraction of glochidial mass are about half of estimates based on total dry mass, indicating even lower investment in reproduction. This could suggest that production of glochidia incurs comparatively little cost to female mussels, and consequently, patterns of reproductive allocation may have had little role in shaping life histories (see Tuomi, Hakala & Haukioja, 1983). This idea is supported by the observation that transplanting freshwater mussels among sites with apparently varying productivity resulted in large changes in growth but only slight or no changes in reproductive output (Jokela & Mutikainen, 1995). An alternative explanation for this result is that allocation to reproduction is a high-priority heritable trait that is influenced by environmental variation to a lesser extent than phenotypically plastic traits such as growth (Glazier, 2002). Additional studies of RE in mussels, particularly those addressing the influence of environmental and biotic factors and accordant variation in RE among populations, will be valuable in elucidating mechanisms of life-history diversification.

(4) Measures of RE based on biomass can be a useful index of relative differences among species or populations, but this method has several shortcomings (Roff, 1992). First, it does not account for potential differences in caloric content of reproductive *versus* somatic tissues. Second, it is not based on actual production and cannot account for differences in reproductive allocation over the life of an individual. In most bivalves, allocation of production to gonads increases with age and often approaches 100% in older individuals with slow growth (Thompson, 1984; Nakaoka, 1994; Gosling, 2003). In addition, differences in age at maturity among species will influence schedules of reproductive allocation and their demographic consequences.

(5) Several issues specific to mussels also complicate accurate estimation of RE. First, in the method used by Bauer (1998), measurements of adult female body mass included the mass of the soft tissue and the organic fraction of the shell only, but glochidial mass included these components as well as the inorganic fraction of glochidial shells. In my dataset, the mean inorganic fraction of glochidial mass across species was 62% – nearly three times higher than for adult tissue mass (mean = 22%) – resulting in estimates of RE based on ash-free dry mass that were about half of those based on total

dry mass. However, the inorganic fraction of glochidia may not be completely cost-free for female mussels. For example, maternal carbon and calcium is transferred to developing glochidia (Wood, 1974; Silverman, Kays & Dietz, 1987), but the magnitude of these and other contributions is unknown. Second, other aspects of reproduction likely incur as yet unspecified costs. Unfertilized structural eggs, membranes and pigments associated with complex conglutinates such as those in *Ptychobranchus* spp., copious mucus produced in association with glochidia in many species, and reductions in filtering efficiency associated with brooding all have an energetic cost that must be accounted for. Production and display of complex mantle lures in the Lampsilini doubtless requires considerable energy, and display of these lures may expose females to higher predation risk (Jones & Neves, 2011). Third, reproductive periodicity is poorly known for many species and it is possible that some, particularly short-term brooders, produce multiple broods in a year (e.g. Price & Eads, 2011; see Haag, 2012). Frequent multiple-brood production would substantially alter the low annual fecundity and RE apparent for the Pleurobemini and Quadrulini under the assumption of single broods. Finally, population dynamics of most mussel species, particularly short-lived species, are poorly known. Short-lived species are expected to have higher rates of instantaneous mortality, which is expected to influence reproductive allocation (Haukioja & Hakala, 1978; Heino & Kaitala, 1997, 1999; Haag, 2012).

(6) The apparent breadth of mussel life histories contrasts with traditional depictions of the group as uniformly long lived and with typically high fecundity. Effective conservation efforts will need to consider fundamental ecological differences among species because strategies designed for long-lived, slow-growing species at the *K*-selected end of the life-history continuum may be ineffective for species with *r*-selected traits. For example, efforts to reestablish extirpated populations of short-lived species with high RE may require very large initial introductions to offset the high natural mortality typically associated with this life history. Short-lived species with high growth rates and high RE also may be dependent on high food availability making them more susceptible to food competition in dense mussel assemblages. Understanding the evolution of mussel life histories and the factors that shape mussel assemblages is ultimately dependent on specifying the selective forces that regulate populations, particularly the roles of mortality and density dependence.

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