Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds

(geomorphology/sedimentation/*Margaritifera*/*Gonidea*)

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ABSTRACT   In the Salmon River Canyon, Idaho, the freshwater pearl mussel, *Margaritifera falcata*, attains maximum density and age in river reaches where large block-boulders structurally stabilize cobbles and interstitial gravels. We hypothesize that block-boulders prevent significant bed scour during major floods, and these boulder-sheltered mussel beds, although rare, may be critical for population recruitment elsewhere within the river, especially after periodic flood scour of less protected mussel habitat. Mussel shells in Indian middens adjacent to these boulder-stabilized areas suggest that prehistoric tribes selectively exploited the high-density old-aged mussel beds. Locally, canyon reaches are aggrading with sand and gravel, and *M. falcata* is being replaced by *Gonidea angulata*.

We studied bivalve molluscan fauna in the upper 40-km canyon reach of the "River of No Return" of the Salmon River, Idaho. This extremely rugged canyon section, that diverted Lewis and Clark in 1805 (ref. 1; see pp. 528–538), extends about 140 km from Shoup, Idaho, westward to the confluence with the Snake River. Our studies suggest that local lithology and fluvial geomorphic processes interact to regulate both population size structure and relative abundance of the two dominant mussels, *Margaritifera falcata* (Gould) and *Gonidea angulata* (Lea).

In canyon reaches of the Salmon River the distribution of fluvial bed structures (chutes, riffles, runs, pools, sand beaches, and terraces) appears structurally controlled (2) by exogenic factors, predominately by: (*i*) large block-boulders weathered from adjacent cliffs, (*ii*) outcrops of resistant bedrock, (*iii*) talus, and (*iv*) alluvial fans in the vicinity of steep tributaries that constrict the river channel and provide debris at a rate or caliber that exceeds river competence. These factors regulate, in large part, the distribution of mussel habitats in the canyon.

Lea (3) in 1839 reported the presence of *M. falcata* in the Pacific drainage from large samples of *G. angulata* collected by Nutall in the Columbia River. Although Gould recognized that Lea regarded the specimens as *Alasmodon margaritifera* (L.), he described in 1851 (4) the western species as *A. falcata* from material collected in California and Oregon. Ortmann (5) considered *falcata* as a subspecies *Margaritifera margaritifera* in 1913. This subspecies designation, based largely on the purple nacre, was even considered too trivial to warrant a varietal name as recently as 1964 (6). In a recent reevaluation of Unionacea by Heard and Guckert (7), the Pacific drainage populations were considered *M. falcata* and populations in the headwaters of the Missouri and from southeastern Pennsylvania to Nova Scotia as *M. margaritifera*. Both species of *Margaritifera* appear largely dependent upon salmonids for basin distribution of the parasitic, 3- to 5-week glochidium stage (8, 9), although glochidia

have been found on other fish (9, 10). The extreme longevity (40–100 years) of *M. margaritifera*, based upon apparent annuli exposed by saggital section of the ligament, has been widely reported (8, 10, 11) and is apparently similar for *M. falcata* in the Salmon River. The general ecology of *M. margaritifera*, including observations on *M. falcata* in Oregon streams, is detailed in a review by Roscoe and Redelings (6).

METHODS

River bed morphology and the distribution and abundance of mussels throughout the reach were studied by snorkeling and diving during summer low flow (60–90 $m^3 \cdot s^{-1}$). Mussel collections were made to determine species composition, population size structure (length, mm), and density (no. m^{-2}). Representative mussels were kept for evaluating shell weight, tissue biomass, and age; residual specimens were reimbedded at the collection sites. Other specimens were obtained for laboratory studies of vertical migration rates by individuals subjected to variable rates of sedimentation with sand and gravel. Specimens of *M. falcata* were air shipped to the Stroud Center, Avondale, PA, for sedimentation studies. These studies were conducted at ambient temperatures (10–18°C) in experimental streams constantly supplied with water from White Clay Creek. This creek supports a remnant population of *M. margaritifera* and is the southern limit in the eastern United States for this nearly circumboreal species. Comparative studies of vertical migration by natural populations of *G. angulata* and *M. falcata* were made in the Salmon River. For these studies portions of natural beds were surrounded by rock cribs or 30-cm sections of 45-cm-diameter steel culvert to retain added sediments.

Age determinations were made by the technique described by Hendelberg (8), in which the valves of each mussel were cut along the ligament, producing a sagittal section. Apparent annuli were counted, using a dissecting microscope at ×25. Annuli were counted from the posterior tip of the ligament back to the point of umbo erosion. The age equivalent of the eroded ligament was estimated by correlating the length of the eroded section, measured in mm, to the average length and age of young mussels with intact ligaments. This additive method for estimating age has been used with apparent success by others (8, 10, 11). The theory of growth line formation in mollusca has been described recently (12).

Particle size of substrate in mussel beds was measured by three techniques. The length (*a*), intermediate axis (*b*), and width (*c*) of block-boulders were measured with tape or meter stick to the nearest cm. We define block-boulder as particles >1 m in length, of local origin, and having only minor evidence of fluvial abrasion. The cobble and gravel surface armorment was measured by Leopold's pebble count method (13). The size distribution of underlying sand and gravel was estimated by the weight of dry sieved (half phi units) samples.

Table 1. Population characteristics of mussel communities in three major habitats

Characteristic	Large, block-boulder-controlled reaches		Cobble/boulder-shielded runs		Sand and gravel bars	
	Living population	Buried relic population	Living population	Buried relic population	Living population	Buried relic population
Margaritifera falcata						
Species composition, %	94.9	—	60.0		2.9	
Population density, no. m^{-2}	192	—	8.3	97.0	5.4	89.8
Valve length, cm: mean ± SD	12.94 ± 1.91	—	7.66 ± 1.10	455	7.93 ± 1.63	220
range	6.0–16.1	—	4.4–9.4	11.86 ± 2.10	6.7–11.0	12.50 ± 2.83
Tissue biomass, g*: mean	14.2	—	3.2	5.0–14.5	3.6	5.3–15.1
Age, years: modal range	60–100	—	25–40		30–40	
Gonidea angulata						
Species composition, %	5.1	—	40.0		97.1	
Population density, no. m^{-2}	10.4	—	5.5	3.0	183	10.2
Valve length, cm: mean ± SD	8.26 ± 0.80	—	7.98 ± 1.12	13.9	8.31 ± 1.25	25
range	5.9–10.4	—	5.3–10.4	9.41 ± 0.81	2.4–11.0	9.18 ± 0.65
Tissue biomass, g*: mean	3.8	—	3.4	7.2–10.8	4.0	4.8–10.5
Age, years: modal range	10–22	—	12–18		12–24	

* Ash-free dry weight of average individual in population sample.

RESULTS AND DISCUSSION

In the canyon-dominated river we identified and sampled four types of mussel communities; two were alive and two were relic. Live mussel beds were (i) high density communities dominated by large, old-age *M. falcata* and (ii) young communities of variable density and species composition, but characterized by an approximately normal size distribution. Relic beds were structurally similar to the live, old-age communities but were either: (i) buried under sand and gravel; or (ii) recently exposed on the surface after erosion of overlying sediments.

We found *M. falcata* and *G. angulata* to be widely distributed throughout the canyon reach; however, contiguous beds generally were restricted to cobble and boulder "ramp-like" runs connecting deep pools to riffles or rapids. As water flows over a ramp it becomes progressively shallower and swifter, averaging about 1 m·s^{-1} at base flow and 3–4 m·s^{-1} over extant mussel beds at bankfull discharge. This incline bed form may be preferred habitat because: (i) the rate of seston transport in close proximity to mussels increases as river depth gradually decreases yet laminar flow predominates, thus valve orientation may be optimized towards the flow of food resources in contrast to rapids where turbulent, omnidirectional current vectors compromise a selected orientation; and (ii) the high energy dissipation and scour that occurs on the bed of pools during flood, alternating with periods of sedimentation during flow recession and baseflow, is avoided. Beds of both species were usually aligned parallel to the shore, at a base flow depth of 1–2 m and commonly extended to midchannel or edge of the thalweg in areas of high current velocity. Individuals or groups of mussels occupied gravel-filled interstices of the tightly jointed cobble pavement or collected in dense clumps in a series of large wave-generated scour depressions or in smaller gravel-filled pockets behind large boulders (11). Table 1 summarizes the population characteristics for both living and buried, relic mussel communities and Table 2 contrasts the geomorphic structure of live mussel beds.

M. falcata was predominant (>90% of total mussel community) when interstitial sediments were gravel and attained high density (mean = 192 m^{-2}), large size (maximum = 16.2 cm), and old age (maximum aged individual 114 years) in cobbled habitats where interstitial gravels were protected by fields of block-boulder (Fig. 1A). *M. falcata* were absent from deep

Table 2. Geomorphic structure of river bed in major habitats from which living mussel populations (Table 1) were examined

	Block-boulder	Cobble/boulder	Gravel
Characteristics of bed control structure			
Source of material	Local canyon wall, cliff or alluvial debris fan	Bedload transport	Bedload transport
Particle shape or bed form	Rectangular, blocky	Rounded blocky to spherical	Sand and gravel bars
Fluvial control process	Generate internal turbulence: reduction in bed shear	Tightly jointed armorment of the river bed: reduction of bed roughness	Hydraulic: eddy currents; reduction in velocity
Particle size, cm*: mean ± SD	66.8 ± 23.8	32.5 ± 16.9	4.9 ± 2.0
range	30–250	15–45	0.2–6
Mussel bed structure			
Surface sediments	Rounded cobbles and boulders	Rounded blocky cobbles and boulders	Very coarse blocky and angular gravel
Interstitial sediments	Medium gravel	Medium sand	Sand and fine gravel
Gravel size, mm*: mean ± SD	12.3 ± 8.9	7.2 ± 5.3	3.5 ± 1.6
Sand size, mm: median D$_{50}$	†	0.28	0.17
Sorting coefficient	†	1.30	1.76

* Intermediate axis (*b*).
† Insufficient material for analysis.

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pools, except within gravel-filled fractures on bedrock ledges, and from riffles. *G. angulata* was predominant (>90%) and possessed high density (average = 183 m^{-2}) on stabilized sand and gravel bars (Table 1). On cobble runs unprotected by block boulders, most *M. falcata* populations were relatively young (20–40 years) and had an approximately normal size distribution, with a modal size ranging between 6 and 8 cm (Fig. 1A). For this genus, the 16.2-cm valve length for *M. falcata* is the largest specimen recorded from either the United States or Europe. An Asian subspecies [*M. m. dahurica* (Middendorff)] from the Amur River was 17.7 cm (14).

We suggest the following model concerning the long-term population dynamics of *M. falcata*: The bed of the Salmon River is highly variable, with mussel beds largely limited to relatively stable, cobbled runs. Depending upon bed resistivity, periodic floods, perhaps approaching a 50- to 100-year event, may cause high mussel mortality by bed scour in most canyon habitats. This periodic scour keeps populations relatively young with an approximately normal size distribution. Modal size may reflect time since recolonization, and size range may be indicative of the duration of recruitment necessary to achieve local carrying capacity. (Size, however, is not necessarily a good predictor of age and correlation of age with channel disturbances needs to be established.) In contrast, where mussel beds are protected by a field of large block-boulders, the dissipation of kinetic energy during floods is primarily through turbulence within the water column rather than bed shear. In these rare but highly stable habitats *M. falcata* attains maximal density, old age, and a population size structure that is highly skewed towards large individuals (Fig. 1A). These few, uniquely structured populations may be critical in providing long-term recruitment for reestablishing populations in main channel and tributary areas vulnerable to periodic scour.

Mussel shell middens and rock pictographs of prehistoric Sheepeater Indians (15) adjacent to mussel beds protected by block-boulder deposits suggest a selective tendency toward long-term or repeated harvest of mussels from river reaches of sufficient resistivity to support dense old-age populations of *M. falcata*. The apparent selective exploitation of mussel beds presently supporting a predominance of large (12- to 15-cm) old mussels suggests an alternative to Ortmann's hypothesis (16) that Indians avoided harvesting the large, tough mussels. We believe small shells predominate in middens located adjacent to present day old-age populations because intense use maintained young and perhaps more productive populations in these habitats.

Locally, canyon reaches in the Salmon River are aggrading with sand and gravel due to a 100-year episode of mining, logging, irrigation diversion, and grazing. In addition, massive slope failure and erosion from Dump Creek, caused by hydraulic mining activities beginning in 1897, alone contributed an estimated 7 × 10^6 m^3 of material to the upstream end of the canyon (17). The increased influx of sediments appears to be shifting community structure from predominance by *M. falcata* to increased numbers of *G. angulata*. Where sand replaces or covers interstitial gravels, *G. angulata* progressively replaces *M. falcata* (Table 1). Presently, translatory waves (18) of sand and gravel are moving through the canyon powered by the annual flood. This material forms bars and submergent and emergent sand beaches or is broadly spread along the channel as shoals during flow recession and may be stabilized by armorment with cobbles or boulders or gradually reworked during flow recession and dissipated downstream (Fig. 2). In aggraded channel areas, relic mussel beds on cobbled runs are commonly covered with 30–100 cm of sediment where beds happen to coincide with the depositional zone.

We sampled five relic mussel beds having high density and dominated by old individuals of *M. falcata* (Table 1; Fig. 1B). Two beds were exposed or partially exposed at the surface of the streambed; two were buried up to 1 m in sand and gravel and armored with a tightly jointed, cobble pavement; and a single bed was buried in well-sorted sand with no armorment. Buried populations of *M. falcata* were found intact, in the normal vertical position, in beds up to about 10 × 100 m. Some mussel beds were apparently inundated by sand and gravel bars that were either simultaneously or subsequently stabilized with cobbles. The relic surface populations resulted from similar burial followed by erosion of overlying sediments. Both exposed and buried relic populations had remarkably similar size structure, with a predominance of old-age individuals (Fig. 1), which also corresponded closely to the structure of living populations in boulder-protected habitats. Particle size, degree of sorting, or absence of surface armorment apparently had little effect on the ability of *M. falcata* to maintain its position at the stream bed surface in an aggrading channel.

To explore the reason for entombment and the apparent shift in dominance to *G. angulata* in reaches aggrading or inundated with sand, we conducted studies of vertical migration under varying rates of sedimentation. Our field and laboratory experiments showed that *G. angulata* readily moved vertically (5 cm·hr^{-1} at 20°C) under both sudden (30 cm·hr^{-1}) and gradual (1–10 cm·hr^{-1}) burial by sediments. Large *M. falcata* (>10 cm) failed to migrate regardless of sedimentation rate and remained buried until they died. Small *M. falcata* (≤8 cm) migrated vertically about 0.2 cm·hr^{-1}. Reasons for failure of large *M. falcata*
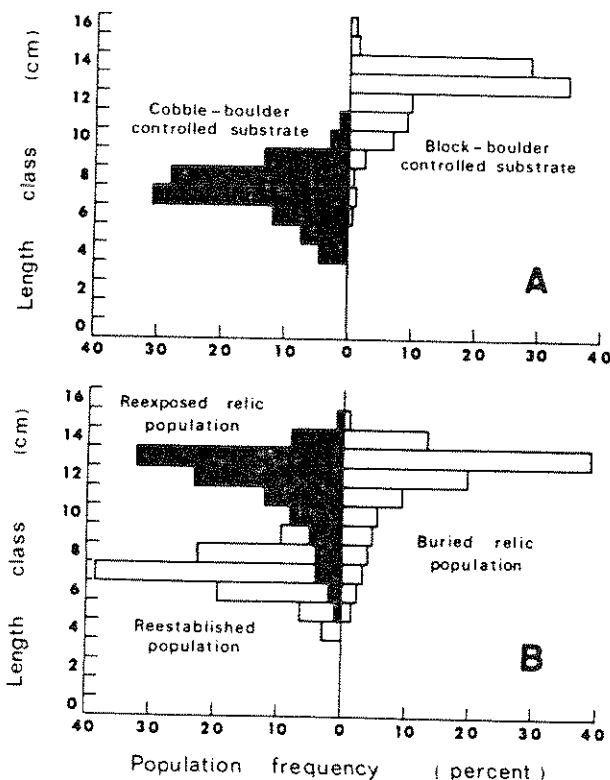

FIG. 1. Size frequency distribution of live and relic populations of *M. falcata* in the Salmon River, Idaho. (A) Comparison of average population structure of living mussels found on cobble armored river beds with populations in river reaches when the cobble bed structure is stabilized by an overburden of large block-boulders. (B) Size distribution of a young replacement population on cobbled-boulder substrate compared to that of a sand/gravel-buried relic population 0.6 m below the extant population and that of a reexposed relic population.
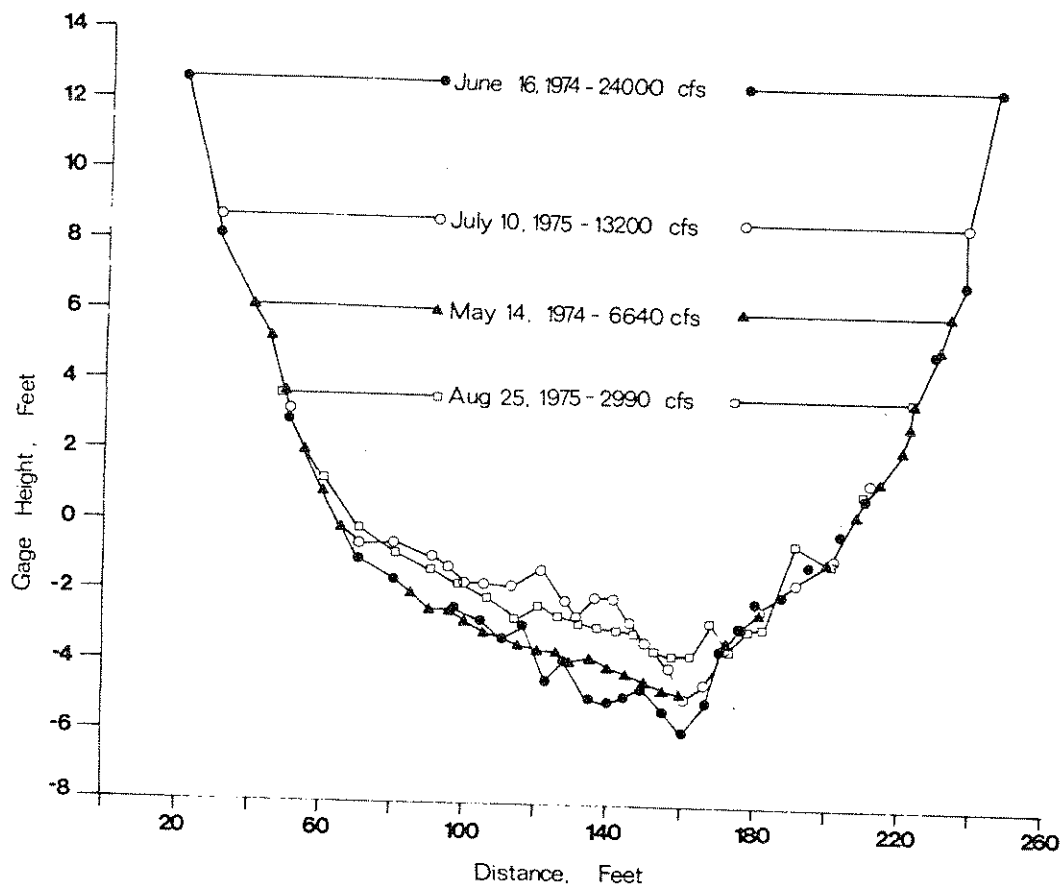
FIG. 2.   Changes in bed elevation of the Salmon River at the Shoup, Idaho, gaging station (U.S. Geological Survey no. 13-3070.00) during the flood of record (June, 1974) and the apparent passage of a sand–gravel wave through the pool during the recessional stage of the 1975 annual flood. By October, 1975, the transitory bar was no longer evident and the river bed coincided with the boundary denoted by solid triangles (May, 1974). This boundary is interpreted as the equilibrium channel configuration and was observed in 1978 to be composed of a closely jointed armorment of rounded cobbles and boulders. The caliber of bed armorment may reflect earlier climatic and flow regimes and apparently was not significantly disturbed by the flow of record. One foot = 0.305 m; 1 cfs (cubic foot per s) = 0.0283 $m^3 \cdot s^{-1}$.

to migrate are unknown. However, the possibility of rock binding due to long-term growth in high-density beds (220–450 m^{-2}) was excluded because mussels experimentally isolated, both in laboratory streams and the Salmon River, failed to migrate. We found no previous report on vertical migration rate by this species, but the mechanics of burrowing and surface horizontal movements on sand in aquaria have been described for *M. margaritifera*, as have field observations of little or no lateral movement on rocky bedded rivers (19). Vertical movement by *M. falcata* into overlying aggrading sand may be fatal if the supporting sand is subsequently removed by erosion. Our studies show that large individuals cannot regain an upright position in the cobbled river bed after falling on their sides, and rarely do so in sand or silt. In laboratory studies, large *M. falcata* (>10 cm) appeared to have little ability or inclination to return to a normal vertical position. Observations of *M. margaritifera* in both European (10) and Northern American (11) rivers suggest that dislodgement and failure to regain a vertical position in rocky rivers is not unusual.

Morphologically and behaviorally, *G. angulata* appears better adapted for aggrading rivers; it has well-formed distal inhalent and exhalent siphons and the entire shell except for siphons commonly is buried in sediments, apparently without affecting filtration (feeding). Furthermore, *G. angulata* is strongly angular and wedge shaped, and the foot is commonly positioned into the substrate at a right angle to the shell ridge. In contrast, *M. falcata* forms no distinct siphons and inhalent

water is drawn in over the entire posterior half of the valve. When the animal is partially buried in sand, the siphon opening is restricted to the uncovered portion. In nonaggrading gravel habitats, *M. falcata* rarely burrows into the substrate more than 25–40% of valve length.

The periodic local aggrading of the Salmon River undoubtedly is related to recent landscape disturbances associated with resource use in a fragile semi-arid region. However, the trade-off in relative dominance of these two species due to fluvial and geomorphic processes has occurred for millenia as revealed by stratigraphic studies of fossil populations in sandstone and conglomerates (20–23). However, when similar population changes are correlated with contemporary activities that accelerate habitat shifts at rates beyond which these and other populations can adjust, there is need for concern. Finally, preservation of the unique, old-aged mussel populations in the Salmon River requires identification and protection of structural features that maintain habitat stability. Road building or indiscriminant clearing of large boulders from canyon roads along the river can jeopardize the local high-density mussel populations by creating new depositional zones in proximity to existing beds. Flood control measures and channel reconstruction after major flood disturbances frequently involve channel enlargement and removal of block-boulders (e.g., segments of Big Thompson Creek, Colorado; Teton River, Idaho); this activity alters current patterns, turbulence, and sediment storage and thus dramatically affects ecological relationships.

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