Corbicula (Bivalvia: Sphaeriacea) vs. Indigenous Mussels (Bivalvia: Unionacea) in U.S. Rivers: A Hard Case for Interspecific Competition?

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SYNOPSIS. At a time when populations of indigenous river mussels have been dwindling and/or disappearing, the introduced Asian clam, Corbicula, has spread through many U.S. rivers from California to Florida. In the Arkansas River Navigation System, a heavily managed waterway, Corbicula presently has a different "competitive" presence than it does in the relatively unmanaged Buffalo River in Arkansas. Comparative studies of both Corbicula and indigenous bivalved mollusks reveal biological bases for the contrasting kinds of benthic faunal change. There are ecologically relevant, distinctive differences between the two kinds of animals: in mantle/shell and mantle/gill apparatus, in the reproductive complex and neuroanatomy, and in spawning and locomotor behaviors. It is argued that the conservative molluscan characteristics of Corbicula enable it to function in an exclusive, "contradictory" role with indigenous bivalves in a heavily managed waterway, and in a "contrary" competitive role elsewhere. Rationale is presented for incorporating organismic evaluation into studies of competition between distantly related taxa.

INTRODUCTION

The opportunities to investigate competition between distantly related taxa have increased substantially with the continuing introduction of exotic species into geographic areas previously inhabited only by indigenous species. These introductions may produce severe management problems and thus make their study even more critical. In this paper I will relate morphological and ecological factors which impinge upon the interactions of two freshwater mollusks (Corbicula and Lampsilis) in managed and unmanaged streams in Arkansas. Taxonomically, Corbicula represents a different mollusk superfamily (Sphaeriacea) than the indigenous river mussels such as Lampsilis (Unionacea).

Corbicula, the Asian Clam, was evidently introduced into the Columbia River on the west coast of the U.S. where it was first found in 1937 (Sinclair, 1971; Sinclair and Isom, 1963). By the 1950s it had moved into southern California. Since then it has spread through most of the heavily managed rivers in the southern U.S. from California to Florida. Eng (1975) reports a "biomass of 1.54 kg/0.25 ft²" for this clam in the huge Delta-Mendota Canal in California; and Gifford (1974) found Corbicula attaining a biomass of 500g live tissue/m² in the Cross-Florida Barge Canal. Corbicula is a serious concern to power companies on the U.S. rivers, as vast numbers of the clams regularly clog condensers and force plant shut-downs.

One expects that benthic assemblages in rivers will include an arthropod component (usually insect larvae) and a mollusk component (bivalves and/or gastropods), (Hynes, 1972). What is not expected is to find that one exotic mollusk will be more widespread and more numerous than all the dozens of indigenous benthic animal genera combined. A recent study of the benthos in the Arkansas River Navigation System (Kraemer, 1976) revealed that a single species (Mattice, 1978) of the introduced clam, Corbicula, showed higher incidence and far greater abundance than the next most prevalent group, comprised of 35 genera of midge larvae (Insecta: Chironomidae). In contrast, many indigenous species of mollusks (especially the unionacean river mussels) were scarcely represented in the bottom samples. The foregoing findings were based on evaluation of more than 500 ponar grab samples from Arkansas to Florida. Eng (1975) reports a "biomass of 1.54 kg/0.25 ft²" for this clam in the huge Delta-Mendota Canal in California; and Gifford (1974) found Corbicula attaining a biomass of 500g live tissue/m² in the Cross-Florida Barge Canal. Corbicula is a serious concern to power companies on the U.S. rivers, as vast numbers of the clams regularly clog condensers and force plant shut-downs.

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Grateful acknowledgment is made to Ms. Frances Waite, the illustrator who skillfully executed Figures 1, 2, 3, 4 and 6.
56 collection sites at 13 stations in a 240-mile long study reach (River mile 283 near Fort Smith, Arkansas, to River Mile 43, near Mud Lake). Sampling series were taken in October, 1974, January, 1975, and April, 1975. Despite its present ubiquitous presence in the Arkansas River, it seems highly unlikely that *Corbicula* was in the river bottom before the mid-1960s (Kraemer, 1976).

The prominent presence of *Corbicula* on the bottom of the Arkansas River Navigation System in Arkansas contrasts strongly with the establishment of this animal in the Buffalo River, a relatively unmanaged stream which flows into the White River in Northern Arkansas. I first found *Corbicula* in the Buffalo River in 1967. It is there still, but is not nearly as conspicuous a part of the benthos. Furthermore, many species of indigenous unionacean bivalves which I collected there in the early 1960s are still here.

Introduction to this study

An evident contrast exists between the benthic role of the introduced *Corbicula* in "managed" and in "unmanaged" river bottoms. *Corbicula* is now producing a huge biomass in rivers which have a history of extensive management and a concomitant, depauperate fauna of indigenous river mussels. Relatively unmanaged rivers which still have autochthonous mussel populations now also have a *Corbicula* benthic component; but in such situations the introduced Asian clam does not seem to show a runaway distribution and biomass.

The following discussion briefly lists the results of my current studies on the life cycle, behavior, functional morphology and reproductive complex of *Corbicula*. *Corbicula* will be contrasted with *Lampsilis*, a highly evolved genus of the indigenous mussel group. Finally I will argue that at least in this instance, interplay between the selective process of the changing environment and the "random process" of (interspecific) variation (Mayr, 1978) can be understood. The outcome of this survival struggle can be predicted. Understanding and prediction are possible from a careful evaluation of the organisms in the distantly related taxa, the introduced *Corbicula* and the autochthonous *Lampsilis*.

Whether the findings reported here may be encompassed by the calipers of present day competition theory is certainly debatable. The reader may judge whether or not what follows constitutes a hard case for enlarging the data set presently included in competition theory. I think it does.

Summary of pertinent findings on *Corbicula*

1. The heavy protective shell holds the animal in a tight grip with its strong cardinal and distinctively serrated lateral teeth, (Kraemer, 1977a).

2. Mantle fusion is extensive in *Corbicula*. It narrows the pedal gape, protecting the animal from its environment. It makes a "foramen" around the posterior adductor muscle allowing for greater freedom of muscle-shell movement than is found in indigenous river mussels (Fig. 1). Mantle fusion provides a deep muscular siphonal pocket within which the siphons may withdraw, as into a vestibule of the mantle cavity; and from which juvenile *Corbicula* can be separately discharged (Fig. 3). Mantle fusion forms tubular, muscular anal and branchial siphons with a range and variety of movement greatly exceeding that of siphons of indigenous river mussels (Kraemer, 1977a, 1978b).

3. Hermaphroditism of *Corbicula* involves a reproductive complex comprised of seasonal and developmental changes in the digestive glands, female gonads, male gonads, differentiation of newly found follicular ganglia, and evidence of intrafollicular fertilization and early embryonic development (Kraemer, 1978b). Female gametes are the first to be discerned in developing gonads of young animals. A population of *Corbicula* could include individuals with alternative reproductive roles. En somme, features which seem to amplify the hermaphroditic reproductive complex of *Corbicula* are in strong contrast to the obligate parasitic glochidium larvae, dependent on fish hosts, and the dioecious habit of sexually mature, indigenous river mussels (Kraemer and Lott, 1977; Kraemer, 1978b).
FIG. 1. Corbicula. Drawing of a preserved specimen seen from the left side. Left shell valve removed, and left lobe of mantle partially pulled back to show enclosed structures. Note: (1) relatively small size of animal and prominent, heavy dentition (CT and LT); (2) thickened, fused portions of posterior mantle edge which enclose siphons within a protective muscular siphonal pocket (MA); and (3) adductor muscles (AA and PA) which pass freely through mantle lobes (e.g., MA). Mantle lobes do not adhere to the muscles. Compare with Figure 2. AA, anterior adductor muscle; CT, cardinal teeth; F, foot; IG, left inner gill; LP, left labial palps; LT, serrated lateral teeth on right shell valve; MA, thickened posterior region of left mantle lobe; OG, left outer gill; PA, posterior adductor muscle; U, umbo of right shell valve. (From Kraemer and Lott, 1977)
FIG. 2. *Lampsila ventricosa* (Barnes). Drawing of preserved mature female specimen seen from the left side. Left shell valve and most of left mantle removed. Note: (1) large size, lack of prominent dentition; (2) posterior mantles unthickened, unfused, modified portions form siphons, (AS, BS) and flared mantle flap, (T); and (3) adductor muscles (AA and PA) to which mantle lobes (MA) adhere. AA, anterior adductor muscle; AS, anal siphon (right side); BS, branchial siphon (right side); F, foot; IG, left inner gill; LP, left labial palps; M, posterior portion of left outer gill, permanently modified as marsupium for glochidium larvae; MA, part of left mantle lobe; OG, left outer gill; PA, posterior adductor muscle; T, "tail" of mantle flap on right lobe of mantle; U, umbo of right shell valve. (From Kraemer, 1970)
Fig. 3. *Corbicula*, drawn from rear, showing siphonal pocket. Thickened muscular posterior portions of mantle lobes form a pocket within which the anal and branchial siphons can be withdrawn, (see MA on Fig. 1). Distal edges of pocket have been drawn apart. In living animal these edges close to form a vestibule. AS, anal siphon (opening of anus is visible within); BS, branchial siphon; FU, papilla-studded midline fusion of mantle lobes; LM, edge of siphonal pocket formed by left mantle lobe; RM, edge of siphonal pocket formed by right mantle lobe.
4. The byssal holdfast thread of juvenile Corbicula (Fig. 5), allows the animals to populate a shifting, sandy river bottom (Kraemer, 1976, 1977b). No comparable structure is developed in free-living stages of indigenous young river mussels, or in pill clams.

5. Comparatively rapid locomotion through the substrate is achieved by Corbicula. Rapid foot movements may be at least partially coordinated by the unusual, conjoined statocysts recently discovered in these animals, (Kraemer, 1978a).

Summary of pertinent findings on Lampsilis

1. Lampsilis possesses a typical unionacean dentition comprised of pseudocardinal teeth and non-serrated laterals.

2. In Lampsilis there is no median suturing of the mantle lobes. To the contrary, each mantle lobe adheres closely to the adductor muscle (Fig. 2). Lampsilis, like other indigenous river mussels, has almost no mantle edges (Fig. 4). During siphoning the animal literally "makes" its anal and branchial siphons by bringing together the appropriate portions of its left and right mantle lobes, and holding them in siphoning position (Kraemer, 1969, and in preparation).

3. Lampsilis, like most other indigenous river mussels, is dioecious, and its zygotes develop within modified, marsupial portions of the female's gills (Fig. 2) into specialized glochidium larvae. The glochidium larvae must parasitize particular fish-host species before metamorphosing into free-living adult river mussels.

4. In the highly evolved and sexually dimorphic group within the Unionacea to which Lampsilis belongs, distal portions of the mantle lobes are further flared into fish-like mantle flaps (Figs. 4, 6). In mature "flapping" females, the pulsing flaps resemble small swimming fish, with conspicuous eyespots and elaborate "tails." Gravid females exhibit prolonged flapping behavior as part of their spawning complex. During flapping periods, the mussels are extremely exposed to the river bottom environment (Kraemer, 1970).

5. Movement of Lampsilis through the substrate is not nearly as rapid as that of Corbicula. Foot movements appear to be coordinated by a pair of statocysts, each widely separated from the other, and each being separately innervated by a bilateral cerebral ganglion and statocyst nerve, (Kraemer, 1970, 1978a). Lampsilis statocysts conform to those described for other mollusks (Bullock and Horridge, 1965; Barber, 1968).

SUMMARY, CONCLUSIONS AND DISCUSSION

In the foregoing section on the introduced sphaeriacean calm, Corbicula, and the indigenous river mussel, Lampsilis, I have listed findings regarding their contrasting life cycles, locomotor behavior, reproductive complex, mantle fusion and neuroanatomy. Though these two distantly related animals are both filter-feeding bivalves inhabiting river bottoms, an evaluation of the foregoing characteristics helps to account for both the dwindling presence of the indigenous river mussels and for the great spread of the introduced Asian clam. Lampsilis and its related genera typically live on shoals in the river bottom. They characteristically populate a shoal substrate of large (cobble or larger) particle size. Their flared, unfused mantles render them more exposed to the environment during feeding and/or siphoning activity periods. In spawning of larvae the female mussels are especially exposed. Suitable fish hosts are also required for larval attachment, and for subsequent continuation of mussel generations in the river bottom. Fish host travels have served for millennia to extend distributional range of indigenous species (van der Schalie, 1945). As long-lived species (25 years or more), the reproductive capacity of a mussel is potentially enormous.

Corbicula presents a far more conservative anatomy than the river mussel. There is extensive mantle fusion, muscular thickening of the mantle, development of the siphonal pocket, of mobile tubular siphons. There is the heavy, ridged shell which, with its strong dentition, tightly grips the animal...
FIG. 4. *Lampsilis ventricosa* (Barnes). Drawing of preserved mature female specimen removed from shell, mantle lobes spread apart, and viewed from the rear. Note that siphons (AS and BS) are just modified portions of distal edges of the left and right mantle lobes. Note almost total lack of fusion between distal portions of left and right mantle lobes, and flaring of posterior portions of mantle lobes due to special mantle flaps. (Compare with Fig. 3). A, region of anus; AS, anal siphon; BS, left and right portions of branchial siphon; F, foot; IG, inner gill (right); M, posterior portion of right outer gill serving as marsupium for glochidium larvae; PA, posterior adductor muscle; RF, right mantle flap; RM, right mantle lobe; T, tails of left and right mantle flaps.
**Fig. 5. Corbicula.** Photomicrograph of preserved juvenile from Arkansas River benthic sample, with distinctive byssal thread still attached to several sand grains. Length of shell: 1.5 mm.

and yet maintains an independent relationship with the adductor muscle allowing freedom of movement. The size of mature *Corbicula* is intermediate between the larger indigenous river mussels and smaller, thin-shelled pill clams. The hermaphroditic process of *Corbicula* involves seasonal and maturational changes in digestive system, development of "indifferent" gonadal tissue, then oogenic follicles, then spermatogenic follicles, then differentiation of follicular ganglia. Oogenic follicles multiply, fill with gametes, empty, and then seem to contain young embryos. Juvenile clams, released onto the river bottom (from the siphonal pocket, a muscular vestibule), develop a long strong byssal thread, a holdfast mechanism. Rapid movement of organisms through the substrate is facilitated by the unusually mobile foot, which has been found to have a conjoined statocyst apparatus evidently well suited to sensing quick movements.

*Corbicula* is able to maintain vast populations in harsh environments (Gifford, 1974; Eng, 1975; Sinclair and Isom, 1963). In the Arkansas River Navigation System large numbers were recovered from benthic samples containing only fine to medium sand and a few midge larvae. Reduced numbers of *Corbicula* were found even in samples from sites subjected to repeated dredging (Kraemer, 1976).

As noted in the introduction to this paper, the molluscan component of the relatively "unmanaged" Buffalo River in Arkansas has included *Corbicula* for at least 10 yr. The clam does not have a conspicuous presence there, and is abundant only in some sandy patches of the river bottom where indigenous mussels are rare. In contrast, in the Arkansas River in Arkansas, benthic studies indicate that in not more than ten years, *Corbicula* has become the most abundant, ubiquitous benthic animal there. It seems likely that current management practices may have unwittingly aided the establishment and spread of *Corbicula*. Maintenance dredging of shoals to maintain navigation channels, allocation by permit to commercial companies for dredge mining of sediments along many miles of the Arkansas river (Kraemer, 1976), bank stabilization projects—all tend to decrease available habitat for indigenous river mussels even though mussel fish hosts are still there (Buchanan, 1976). Extensive dredging tends to homogenize and decrease particle size (Cummins, 1966) resulting in substrate upon which *Corbicula*, but not the indigenous mussels can live. Substrate movement in regular dredging operations may well aid distribution of sand-grain-size juvenile *Corbicula*, each attached by its byssal thread to small substrate particles.

Biologists have assumed that filter-feeders do not partition the environment for feeding. This may not be true. Green (1971) used multiple discriminant function analysis of bivalved lake mollusks, including mussels (*Anodonta, Lampsilis, Lasmigona, Amblema*) and fingernail or pill clams (*Sphaerium, Pisidium*). His results led him to conclude that distribution separation among 10 indigenous species in the defined ecological space was primarily on a trophic
**Fig. 6.** *Lampsilis ventricosa* (Barnes). Drawing of living female (from left side) engaged in spawning behavior. Animal is in “headstand” in substrate, foot serving as prop for the shell valves. A marsupium (i.e., one of the posterior outer gills charged with glochidia larvae) is pushed out between the two fish-like mantle flaps. During this spawning (“flapping”) behavior, the interior of the animal is extremely exposed to the aquatic environment. The mantle flaps are extensions of the left and right mantle lobes and are not anatomically connected, (see Fig. 4). Nonetheless, the mantle flaps exhibit paired, pulsing movements at rates up to three per second. Glochidia are eventually discharged from the water tubes of the gill-marsupia to make their necessary contact with specific host fish. When the gill-marsupia are emptied, “flapping” behavior ceases. AS, anal siphon; BS, branchial siphon; E, eyespot of (left) mantle flap; F, foot; M, posterior portion of outer gill, charged with larvae and serving as marsupium; T, tail of (left) mantle flap; U, umbo of (left) shell valve. (From Kraemer, 1970)
basis. In his evaluation of reproduction in fingernail clams (Sphaeriidae: *Sphaerium* and *Musculium*), Heard (1977, p. 453) concludes that in streams

". . . where representatives of *Pisidium* and *Sphaerium* occur together, the larger animals of the latter might out-compete those of the former for food or space (i.e., be K-strategists). If so, *Pisidium* (r-strategists) would gain advantage by producing larger broods to counteract possibly lower survivorship."

Some workers (Britton, 1979; Mattice, 1975–1978) are examining physical and chemical parameters which may affect populations of *Corbicula* in rivers. The foregoing constitutes the slender bulk of studies I have found which may relate to relationships between the introduced *Corbicula* and indigenous river mussels such as *Lampsilis* in U.S. rivers today.

One might argue that *Corbicula* is less a competitor of *Lampsilis* than it is an opportunistic colonizer of disturbed habitat. It seems more likely, however, that *Corbicula* is a "sometime" competitor of *Lampsilis*; and that benthic substrate is a critical factor in their competitor/non-competitor relationships. I should like to suggest an analogy here. In the Aristotelian Square of Opposition critical distinction is made between contradictions and contraries. An A proposition, "All S is P," is contradicted by the O proposition, "Some S is not P." In contrast, the E proposition, "No S is P," is not a contradiction of the A proposition, but is contrary to it.

By analogy, might it be that in the greatly altered habitat of the Arkansas River Navigation System, faunal exchange is occurring because the introduced *Corbicula* can live in nearly all the substrate (altered); and little substrate remains in which *Lampsilis* and its relatives can live, (i.e., a contradictory, faunally exclusive situation)? In contrast, in the (relatively unaltered substrate) Buffalo River, the introduced *Corbicula* in many instances is present not as the chief species in the benthic community, but as one of many bivalved mollusk species. Here it may occupy the substrate in a contrary (and competitive) role, where its differently organized reproductive complex, its conservative fused mantle and its distinctive nervous apparatus all provide it with an Innenwelt and an Umwelt (von Uexkull, 1909) qualitatively different from the indigenous species.

In both altered and unaltered habitat, peculiar biological characteristics of *Corbicula* help to explain its presence. The meaning of the *Corbicula* presence is different in the two situations, however. In the Arkansas River (altered habitat) physical/chemical environmental factors appear to be of overriding importance for *Corbicula*. In the Buffalo River, (unaltered habitat) interspecific competition between *Corbicula* and the indigenous bivalves may shift between K and r strategies from one season of the year to another, much as Heard (1972) postulated for *Pisidium* and *Sphaerium*.

Reviewing the theoretical basis for biological change in changing environments, Levins (1968) made use of contrasting trophic and other population characteristics between species of organisms. Examining problems of competition in variable environments when populations are caught in an "ecological crunch," Wiens (1977) argued that such circumstances may actually nullify assumptions of competition theory.

Reproductive and trophic capabilities evolved by the large superfamily (Unionacea) of freshwater mussels over millions of years, have proved very effective in the mussels' distribution, colonization and establishment as a significant component of river bottom communities throughout the world. It would be foolish to conclude that they are no match for the introduced organism, *Corbicula*. Field and laboratory studies are enabling me to realize that unionacean bivalves such as *Lampsilis* are better adapted for life in a river than is the introduced *Corbicula*. It is now clear that *Corbicula* has more conservative structure/function/behavior than indigenous river mussels. *Corbicula* is built for hard times. In many details *Corbicula* resembles bivalves of marine intertidal habitat. From studies such as this it is possible to predict conditions in which relationships between indigenous and introduced organisms may be
tilted to favor one species or the other. Certainly the drastic faunal exchange seen in the present case in heavily "managed" habitat can thereby be anticipated, minimized, reversed, and/or perhaps even avoided.

Finally, what has the foregoing to offer modern competition theory? It offers a hard case in which two taxa display these attributes: (1) taxa which are distantly related; (2) taxa which occupy similar habitat and both utilize and affect that habitat in similar ways; (3) taxa which exhibit comparable reproductive capabilities; (4) taxa which include both an indigenous and an introduced species; (5) taxa which differ markedly with regard to their response to ecological crunch; (6) taxa which include animals with a sensory world and complex behavior very different from our own. In the hard case characterized by the above features, the outcome is not in doubt. It is obvious. This seems to be a case, then, for widening the perspective of competition theory, and for consulting with other biological disciplines to examine the means by which the outcome has been produced. "Complicating the data" (Castaneda, 1978) by including information about the structure, function and behavior of animals should make possible the construction of more parsimonious hypotheses. Then improved means for testing competitive and/or non-competitive relationships between species may be sought.

Consequently stressed and strengthened, competition models may be expected to have increased predictive value in real situations. I propose that the data presented here constitute a substantial and urgent case for the study of interspecific competition.

REFERENCES


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Ibid.


