

SHELL DISSOLUTION AS A SIGNIFICANT CAUSE OF MORTALITY FOR
CORBICULA FLUMINEA (BIVALVIA: CORBICULIDAE)
INHABITING ACIDIC WATERS

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ABSTRACT

Dissolution of the shell in the umbonal region is a major source of mortality for *Corbicula fluminea* inhabiting acidic waters. Resistance to similar dissolution among the Unionidae may be explained in part by greater rates of compensatory nacre deposition, but seems to occur primarily because of the presence of thick conchiolin layers within the shell.

INTRODUCTION

Corbicula fluminea (Müller 1774) has gained considerable notoriety as one of the most successful introduced species of mollusk, having spread across a wide geographic range in a short time, and building up populations of up to 25,000 individuals per sq ft (juveniles?) along the way (Sinclair, 1971). Although *Corbicula* has some natural vertebrate predators (Britton & Murphy, 1977), increases in geographic range and population numbers seem to continue unabated, causing widespread concern about the effect of this invasion on native aquatic bivalves. Although direct evidence has not been presented to support claims of spatial competition between *Corbicula* and autochthonous bivalves, competitive interactions are inferred since increases in population size of this genus are usually accompanied by decreases in unionid populations (Fuller & Imlay, 1976; Gardener et al., 1976; Fuller & Richardson, 1977). An alternative explanation of this "competitive" effect may be suggested by the observation that *Corbicula* can tolerate the ubiquitously deteriorating environmental conditions of aquatic habitats better than can unionids (Habel, 1970; Diaz, 1974; Kraemer, 1976; Horne & McIntosh, 1979) and hence increase in relative abundance (Kraemer, 1979). *Corbicula* seems to be exhibiting the classic exponential population increase characteristic of species introduced into essentially open habitats (from which unionids have been or are being excluded). Interestingly, some populations seem to be experiencing drastic fluctuations in population numbers which also has followed such logistic growth in both laboratory and natural single species assemblages (Murie, 1934; Hickie, 1936; Sinclair & Isom, 1963; Horning & Keup, 1964; Bickel, 1966; Krebs, 1972; Sickel & Heyn, 1980).

Personal observations, however, indicate that *Corbicula* does not always establish numerical superiority over unionid populations where they co-occur, even in areas where *Corbicula* has been established for a number of years (e.g., branches of the Ocmulgee River, Georgia; branches of the Suwannee River, Florida; Lake Waccamaw, North Carolina; see also Kraemer, 1979). One habitat type where abundances of *Corbicula* are consistently below those of unionids can be characterized by both low pH of the water and low levels of habitat disturbance. It is the purpose of this paper to document shell dissolution as a major source of mortality for *Corbicula* inhabiting such acidic waters.

METHODS

Corbicula specimens were collected on January 10, 1980, from Mosquito Creek below the Florida State Hospital dam, Chattahoochee, Gadsden Co., Florida. This site, although relatively disturbed, was

was chosen because of the ease by which living and dead specimens of *Corbicula* could be collected. The bottom was composed of a sand/clay mix with bare rock in areas of scour. Water depth varied from 0.3 to 0.8 m, and the current was approximately 0.4 m/sec. The pH of the water was 5.6 at the time of sampling. Densities of *Corbicula* were locally very high, especially in depressions in the stream bottom, where the bivalves occurred in a layer 7-10 cm above the substratum in densities of approximately 580/m². The unionid assemblage, consisting mainly of *Elliptio arcata* (Conrad 1834), with some *Carunculina parva* (Barnes 1823) and *E. icterina* (Conrad 1834), was characterized by much lower densities, on the order of 2-5 individuals/m². Extent of shell dissolution on these unionids was not different from that occurring in other moderately acidic habitats. Specimens of *E. complanata* (Lightfoot 1786) exhibiting similar amounts of shell dissolution were used for comparative purposes in this study, and were collected from branches of the Chester River, Kent Co., Maryland. Voucher specimens of the species used in this study have been deposited in the collections of the Academy of Natural Sciences of Philadelphia.

Shells were embedded in clear plastic, sectioned, polished with carborundum and diamond grit, and acid etched (5% HCl) for Scanning Electron Microscopy. Histological examinations were performed on five *Corbicula* specimens ranging in size from 20-25 mm which showed evidence of recent shell dissolution but were still alive. These bivalves carefully were excised from their shells, fixed in 10% formalin (for 24 hr), embedded in paraffin, sectioned at 6 μ m, stained with Harris hematoxylin, and counterstained with eosin Y.

RESULTS

Shell dissolution in *Corbicula fluminea* from Mosquito Creek is restricted to the umbonal regions of the shell where the periostracum has worn off. Holes eventually appear in the umbo as a result of this dissolution, but bivalves with intact shells in advanced stages of dissolution showed a number of other associated effects, including breakage and weakening of the ligament and dissolution of dentition (Fig. 1A). It is probable that these associated effects are sublethal since they negatively affect normal functioning of the shell.

Size-frequency diagrams of valves of living and dead bivalves show five peaks which correspond well to age classes suggested by previous authors (Sinclair & Isom, 1963; Gardener et al., 1976) (Fig. 2). While bivalves in the first two size classes often showed signs of some dissolution in the umbonal region, complete dissolution was not observed before the bivalves attained a minimum shell length of about 22 mm, which corresponds to an age of about three years (complete umbonal dissolution may well have occurred before this: small empty shells probably are differentially transported by the fast current). Frequency of complete dissolution increases in the fourth size class, and few bivalves in the fifth size class remain alive. Life expectancy of *Corbicula* is thus limited to a maximum of five years, with probable debilitating sublethal effects appearing in the first and second years. Of the 150 articulated valves of dead specimens examined, only 4% did not show complete umbonal dissolution and are presumed to have died from other causes.

Histological examination of mantle tissues of live individuals in which complete umbonal dissolution had occurred revealed the pathological effects of shell dissolution (Fig. 1D). The mantle generally had ruptured, and cells composing the mantle were necrotic, often showing signs of cell wall disintegration and pycnotic nuclei. Amoebocytes were common among the mantle cells. Tissues underlying the mantle showed similar pathological effects, and massed amoebocytes were common. It is assumed that the bivalves are attempting to cope with an invasion of microorganisms following shell dissolution, but absence of any shell repair in other animals with similar umbonal dissolution make it clear that the animals will not be able to counter the effects of such an invasion.

Scanning Electron Microscope (SEM) examination of *Corbicula fluminea* revealed a shell composed entirely of complex cross lamellar crystals. Counts & Prezant (1979) mentioned that the periostracum is tightly bonded to the shell by a rugose inner surface, but shell dissolution appears to proceed rapidly where the periostracum is worn away: once a small hole is formed in the periostracum, a pit rapidly forms underneath it and further loosens the periostracum from below (Fig. 1C). Organic layers (conchiolin) are narrow (Counts & Prezant, 1979).

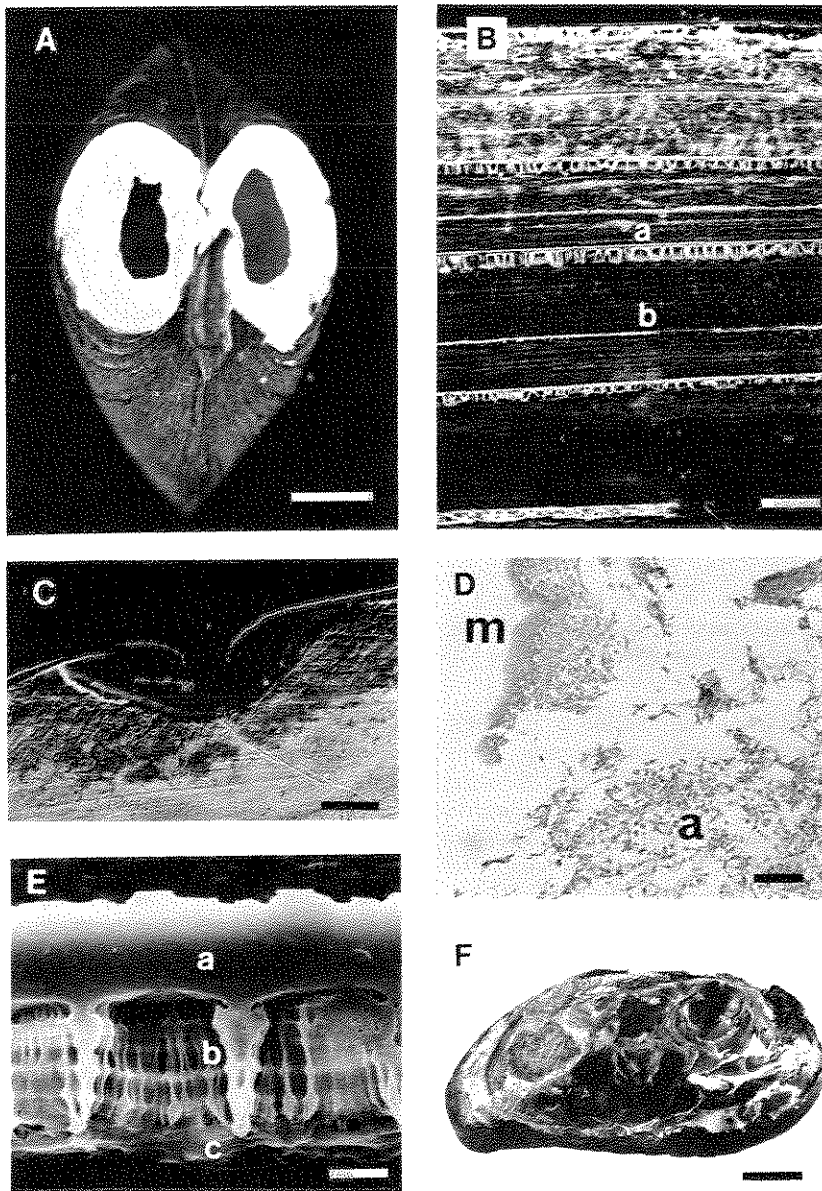


FIG. 1. A, Complete dissolution of the umbonal region in *Corbicula*, with breakage of the ligament and dissolution of dentition. Scale bar = 5 mm. B, Scanning electron microscope (SEM) photograph of the naacre of *Elliptio complanata*, showing thick conchiolin layers (a) alternating with thinner bands (b). Dissolution has loosened the uppermost conchiolin layers; a partial layer can be seen at bottom left. Scale bar = 200 μ . C, SEM photograph of the shell of *Corbicula* showing pits forming in the area where the periostracum has worn away (top). Scale bar = 200 μ , specimen size = 23 mm. D, Effects of complete dissolution on the mantle and underlying tissues in *Corbicula*. The mantle (m) is necrotic, and massed amoebocytes (a) are common. Scale bar = 100 μ , specimen size = 23 mm. E, SEM photograph of the thick conchiolin layer of *E. complanata*. Note the structure of the reticulate band (b), and the rugose surfaces of the upper and lower homogeneous bands in contact with the naacre (a and c). Scale bar = 5 μ . F, Extensively dissolved specimen of *E. complanata* from Newville Lake, Halfway River East, Cumberland Co., Nova Scotia. Dark areas on the shell are successive organic layers protecting the underlying naacre. Scale bar = 2 cm.

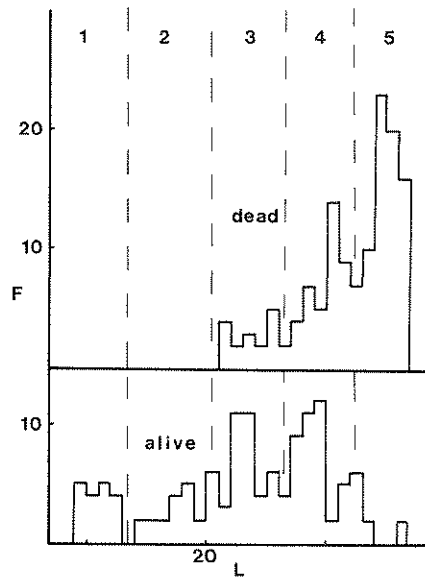


FIG. 2. Size frequency diagram of dead and living specimens of *Corbicula* collected from Mosquito Creek. Dashed lines indicate approximate age classes; shell length (L) is in mm.

A similar SEM examination of the shell of *Elliptio complanata* revealed a shell of different structure composed of aragonitic prismatic and laminar crystals. Thick conchiolin layers are common, and each consists of three separate bands (Fig. 1B). The upper band is composed of a rather thick ($9\ \mu\text{m}$) homogeneous layer of conchiolin with a rugose upper surface, which is in contact with the laminar crystals forming the nacre (Fig. 1E). Below this lies a reticulate band ($\pm 10\ \mu\text{m}$ thick) composed of tightly packed, dagger-shaped laminae which seem to enclose rounded chambers (Fig. 1E). The bottom of the conchiolin layer is composed of another, thinner sheet of conchiolin measuring about $1\text{--}2\ \mu\text{m}$ in thickness. This band also exhibits a rugose surface where it comes in contact with the nacre. It is probable that the reticulate portions of the conchiolin layer contain calcareous structures which dissolved away when the specimen was etched with HCl. Thick conchiolin layers seem to alternate with thinner layers composed of homogeneous sheets, and may end rather abruptly (Fig. 1B). It may well be that the microstructure of these conchiolin layers can be used as a taxonomic character.

DISCUSSION

Dissolution of shell in the umbral region is a major source of mortality for *Corbicula fluminea* inhabiting the acidic waters of Mosquito Creek. Debilitating associated effects such as breakage of the ligament and dissolution of dentition occur before complete dissolution of the umbo. Mortality presumably results from an invasion of microorganisms.

Personal observations indicate that unionids in similar environments rarely suffer mortality from shell dissolution except at an advanced age. Extensive shell dissolution can take place (Fig. 1F) without lethal effects, even though ligament and dentition functions are adversely affected as in *Corbicula*. Breakage of extensively dissolved shell usually occurs in the area of the adductor muscles, possibly as a result of excessive strain imposed on the thin

shell layers. Resistance to shell dissolution may be explained in part by greater rates of compensatory nacre deposition on the inner surface of the unionid shell, but seems to occur primarily because of the existence of thick conchiolin layers within the shell.

While the existence of these and similar layers in the Unionidae has been documented for some time (e.g., Gray, 1833; Tolstikova, 1974), their function has remained obscure. Tevesz & Carter (1980: 315-316) have termed them "adventitious conchiolin layers" and mentioned that they occur sporadically through the nacre in the umbonal region, but they are uncertain as to what actuates their formation. These layers also exhibit remarkable convergence with the conchiolin layers described for the Corbulidae (Lewy & Samtleben, 1979), in which they are hypothesized to deter boring as well as shell dissolution. While unionids do not have to cope with predatory boring gastropods, any unionid shell which exhibits extensive dissolution reveals successive calcareous layers protected by these organic sheets (Fig. 1F). Unlike *Corbicula*, once the unionid periostracum has worn away, shell dissolution in similar acidic waters may be sufficiently retarded by these conchiolin layers to permit compensatory shell deposition, depending on environmental conditions. Unionids probably will be excluded from very low pH conditions not only due to rapid rates of shell dissolution, but also because of the difficulty of concentrating calcium carbonate under those conditions (see also a discussion of the other effects of low pH on unionids in Fuller, 1974).

Members of the family Corbiculidae have a much shorter evolutionary history in aquatic habitats than unionids: fossil forms are fully marine, and some Recent species are restricted to brackish water (Moore, 1969). Kraemer (1979) found *Corbicula* conservative in a number of characters, mentioned that unionids are better adapted to river life, and doubted that *Corbicula* can outcompete unionids in undisturbed environments. (A disturbed environment generally can be defined as one in which ecological conditions have been modified by human activities, including introduction of pollutants, increases in sediment loads, maintenance dredging of shoals, bank stabilization projects, constructions of dams, etc.) The results of this study indicate that the conchiolin layers in unionid shells might be adaptive in that they retard rates of shell dissolution in lotic habitats of low pH. However, early reproduction, viviparity, possible self-fertilization (McLeod & Sailstad, 1980) and a simpler life cycle than found among unionids characterize *Corbicula* as an opportunistic species capable of rapid colonizations and population buildups. This led Gardener et al. (1976), among others, to express concern over population sizes of *Corbicula* in their study area (the Altamaha River), largely because of the danger this posed to survival of endemic unionids in the drainage. Survival of such endemics may well depend on the availability of both undisturbed and low pH habitats (Mosquito Creek is an example of a low pH *disturbed* habitat, in which *Corbicula* densities can be high despite low individual fitness), from which recolonization could proceed once *Corbicula* populations have stabilized and environmental deterioration of such drainages is reversed.

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