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Camuri Grande, Federal District, on the north coast of Venezuela.

Sassia lewisi Harasewych and Petuch, 1980

Mexico and Barbados—Specimens of this recently described species, were originally dredged off Contoy Island, Quintana Roo, Mexico, in 60-80 metres, and off St. James, Barbados in 140 metres.

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THE OCCURRENCE AND SPREAD OF THE INTRODUCED ASIATIC FRESHWATER CLAM, CORBICULA FLUMINEA (MÜLLER), IN NORTH AMERICA: 1924-1982

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ABSTRACT

The distribution and dispersal of Corbicula fluminea (Müller) in North America were examined on the basis of all available published reports of new populations from 1924 through 1982. The dispersal of C. fluminea in North America has proceeded from two epicenters of artificial introduction, the first a result of an introduction from southeast Asia into the northwestern United States, and the second from a population in the Ohio River (probably a result of introduction of specimens from populations earlier established in western United States). The dispersal from these two sites of introduction has been marked by a progressive invasion of adjacent drainage systems, high downstream rates of dispersal and inability to breach barriers to dispersal such as mountain ranges. The very high natural dispersal powers of C. fluminea appear to be associated with its invasive nature and have been previously overlooked as the basis for this species' extraordinarily rapid invasion of North American fresh waters.

Corbicula fluminea (Müller) is a freshwater clam (Family Corbiculidae) (Newell, 1969) endemic to southeast Asia (Morton, 1979). This

species was introduced to North America near the end of the 19th century. It was first recorded from the northwest corner of the United

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States and has since spread rapidly over many parts of the United States (Cherry, *et al.*, 1980a, 1980b). *C. fluminea* has now been reported in 35 of the continental states, the exceptions being Montana, Wyoming, North Dakota, South Dakota, Nebraska, Kansas, New York, Connecticut, Rhode Island, New Hampshire, Maine, Massachusetts, and Vermont (Cherry, *et al.*, 1980a, 1980b). It has also been reported from fresh waters in northern Mexico (Taylor, 1981; B. Morton, personal communication).

C. fluminea has become an important member of many benthic communities in North American fresh waters. Its high growth rates and extraordinary reproductive capacity (Aldridge and McMahon, 1978) allow it to reach very high densities soon after establishment of a new population (McMahon, 1983).

By sheer weight of numbers *C. fluminea* has become one of the most important aquatic pest species in the United States. Its shells accumulate in and obstruct irrigation canals and underground pipes (Eng, 1979; Fitch, 1953; Ingram, 1959; Prokopovich, 1969; Prokopovich and Hebert, 1965). It enters and fouls municipal water treatment facilities (Ingram, 1959; Sinclair, 1974; Smith, *et al.*, 1979). *C. fluminea* also renders dredged river sand and gravel unfit for use as aggregation material in cement (Sinclair and Isom, 1961, 1963). This species has also been reported to outcompete native unionid and sphaeriid bivalves, many of which are presently endangered (Boozer and Mirkes, 1979; Cooper and Johnson, 1980; Fuller and Imlay, 1976; Gardner, *et al.*, 1976; van der Schalie, 1973; Sickel, 1973; Taylor and Hughart, 1981). The most serious aspect of *C. fluminea* as a pest species is its ability to foul the service water systems and steam condensers of electrical generating stations, causing extensive damage to equipment and expensive shut-downs for manual removal of shells (Boozer and Mirkes, 1979; Cherry, *et al.*, 1980a, 1980b; Diaz, 1974; Goss and Cain, 1977; Goss, *et al.*, 1979; Harvey, 1981; Ingram, 1959; McMahon, 1977; Mattice, 1979; Sinclair and Isom, 1961, 1963; Smith, *et al.*, 1979; Thomas and MacKenthum, 1964; Thomerson and Myer, 1970). Perhaps of even greater concern, *C. fluminea* has not only been

reported to foul the steam condensers of nuclear power stations, but, also, to enter and obstruct the emergency reactor cooling systems of these facilities (Parsons, 1980).

While there have been several recently published accounts of the distribution of *C. fluminea* in the United States (Britton and Morton, 1982; Cherry, *et al.*, 1980a, 1980b), there is little published information regarding the actual pattern and pace of the spread of this important pest species in North American fresh waters. Since its probable introduction by Chinese immigrants who may have carried it to North America as a conveniently transported food item (Britton and Morton, 1979; Counts, 1981), it has been presumed by the majority of investigators that the spectacularly rapid spread of this species through North American fresh waters has been the result of human activities including: its use as fish bait (Ingram, 1959); utilization by tropical fish hobbyists as an aquarium specimen (Abbott, 1975); transport of juveniles in the bilge water of pleasure craft or as a tourist curiosity (Britton and Morton, 1979); and, perhaps, unknowingly by fish stocking programs and with transported river sand and gravel used as cement aggregation material (Britton and Morton, 1979; Sinclair and Isom, 1961, 1963).

While human mediated dispersal of *C. fluminea* certainly has occurred, investigators appeared to have generally overlooked this species' great inherent natural powers of dispersal which are associated with its invasive habit and are an apparent adaptation to its preferred disturbed, highly variable, temporally unstable, lotic habitats, from which most unionids and sphaeriids are excluded (Kraemer, 1979; McMahon, 1983). Indeed, the high dispersal powers of the genus, *Corbicula*, are illustrated by the fact that it has a recent fossil history in North America and by fossil record and aminostratigraphic shell dating evidence that indicate that a species of *Corbicula* has reinvaded the fresh waters of southeastern England during each of the last three or four interglacial periods (Miller, *et al.*, 1978).

If the spread of *C. fluminea* in North America was primarily the result of human activity one

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would expect that the appearance of new populations would have a largely random component, with upstream invasion rates being equal to or greater than downstream rates, with reports of new populations occurring in habitats great distances outside the previously known species' range and with a marked dispersal of new populations across natural barriers, as mountain ranges, that bisect drainage systems. On the other hand, if the majority of dispersal in this species was by natural means then dispersal would be characterized by a steady, progressive expansion of its range from one closely adjacent drainage system to the next, with no anomalous reports of high upstream invasion rates or the breaching by new populations of natural barriers to dispersal.

In order to better understand the pace, pattern and modes of dispersal of *C. fluminea* in

North America all available literature on this species was surveyed for reports of new populations (primarily in *The Nautilus*) as part of a more extensive review of the biology of this species in North America (McMahon, 1983). The location of each new population and the date on which it was first observed were recorded on an outline map of the United States (Fig. 1). This information was then utilized in the following analysis of the distribution and spread of *C. fluminea* in North American fresh waters.

The first specimens of *C. fluminea* found in North America were recorded as empty shells in Namaino, Vancouver Island, British Columbia in 1924 (Counts, 1981). The first living population was discovered near the mouth of the Columbia River separating Washington and Oregon in 1938 (Burch, 1944) (Fig. 1). From this apparent point of original introduction, *C.*



FIG. 1. Occurrence and spread of *Corbicula fluminea* in North America from 1924 to 1982. Published population records for *C. fluminea* are indicated by the stars and dates on which they were first observed. Probable patterns of dispersal by natural means are indicated by solid arrows while those patterns of dispersal associated with human activity and vectors are indicated by dashed arrows.

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fluminea dispersed throughout North American fresh waters at an extraordinary rate, primarily by successive invasion of adjacent drainage systems (a pattern characteristic of dispersal by natural means). *also char. of human dispersal*

C. fluminea spread southwards in West Coast drainage systems from the Columbia River, reaching the San Joaquin River Drainage System near San Francisco, California, by 1946 (Ingram, 1948). By 1952 it was recorded from drainage systems in extreme southern California (Fitch, 1953) (Fig. 1). During this period of southward expansion on the West Coast no *C. fluminea* populations were reported from east of the Rocky Mountains, which formed an effective barrier to its dispersal (Fig. 1). Only after reaching the southern portions of California, did *C. fluminea* spread to the east, probably through a network of interconnecting irrigation canals into the Colorado River Drainage System where it was first recorded in irrigation canals near Phoenix, Arizona, as early as 1956 (Dundee and Dundee, 1958). From the Colorado Drainage System *Corbicula* spread to the adjacent drainage system of the Rio Grande River, the most likely mode of dispersal again being through irrigation canal systems, where it was first observed in the Rio Grande River near El Paso, Texas, in 1964 (Metcalf, 1966) (Fig. 1). *C. fluminea* quickly extended its range to the downstream portions of the Rio Grande, being reported near the mouth of the river at Brownsville, Texas, in 1969 (Murray, 1971). From the Rio Grande the range of *C. fluminea* expanded rapidly northwards through several closely adjacent Texan river drainage systems reaching northeastern Texas by 1972 (Britton and Murphy, 1977; Aldridge and McMahon, 1978; Pool and McCullough, 1979) (Fig. 1).

While the range of *C. fluminea* was expanding into southern California on the West Coast of the United States, a second, unexpected infestation of this species was recorded in 1957 in the Ohio River, near Paducah, Kentucky (Sinclair and Isom, 1961, 1963). This anomalous population was recorded at a time when the range of *C. fluminea* in the western United States had apparently extended no further east than the Colorado Drainage System in Arizona, 3100 km

southwest of Paducah (Fig. 1). As such, it almost certainly represents an unnatural extension of the range of *C. fluminea* in North America, associated with an, as yet, unidentified human vector. It is highly unlikely that this new infestation was the result of specimens being carried to the Ohio River from western populations by migratory waterfowl as *C. fluminea* cannot survive in their digestive tracts (Dreier, 1977; Thompson and Sparks, 1977).

This artificially introduced population of *C. fluminea* in the Ohio River formed the epicenter of a second major expansion of this species' range in the eastern half of the United States (Fig. 1). From Paducah it spread rapidly downstream in the Mississippi River, reaching the lower portions of the river itself and adjacent Gulf Coastal drainage systems extending into western Florida as early as 1960 (Dundee and Harman, 1963; Schneider, 1967) (Fig. 1). The rapid downstream advance of *C. fluminea* in the Ohio and Mississippi Rivers was almost certainly associated with the ability of its small juvenile stage (~ 0.2 mm in shell length, Aldridge and McMahon, 1978) to be passively transported by water currents (Goss and Cain, 1977; Goss, *et al.*, 1979; Sickel, 1979; Sinclair, 1964; Sinclair and Isom, 1961, 1963; Smith, *et al.*, 1979). As did the Rocky Mountains on the West Coast, the Appalachian Mountains seemed to have formed an effective barrier to the expansion of *C. fluminea* into the drainage systems of the Atlantic seaboard (Fig. 1). Instead, only after it reached the lower portions of the Mississippi River, did the range of *C. fluminea* expand greatly in an easterly direction, progressing successively across the closely adjacent drainage systems of the lower elevations of the Southern Coastal Plain, extending into extreme southern Florida, by 1969 (Clench, 1970). During this period of range expansion across the Gulf Coastal States, a second anomalous range extension of *C. fluminea* was reported in Lake Overholser, Oklahoma, in 1969 (Clench, 1972) (Fig. 1). Specimens were taken from this lake long before *C. fluminea* had extended into north central Texas and either represent an incredibly rapid upstream expansion in the Arkansas River Drainage System, or, as appears more likely, an artifi-

cial introduction by a human vector (Fig. 1).

From the drainage systems of the eastern Gulf Coastal Plain, *C. fluminea* extended into the adjacent fresh waters of the Atlantic Coastal States, being reported from the Atlantic drainage system of Georgia by 1971 (Fuller and Powell, 1973) and reaching as far north as Virginia and New Jersey by 1972 (Diaz, 1974; Fuller and Powell, 1973). Thereafter, the northern expansion of *C. fluminea* slowed greatly with the species still reported to be slowly extending its range in New Jersey (Trama, 1982). The present northern limit of *C. fluminea* in the eastern United States is marked by a marginal population in Lake Erie, Michigan, first recorded in 1980 (Clarke, 1981) (Fig. 1).

C. fluminea has now probably reached the extent of its northern distribution in North America. It is apparently excluded from more northern fresh waters by its intolerance of low winter temperatures. Laboratory studies have shown the absolute lower thermal limit of *C. fluminea* to be 2°C (Mattice and Dye, 1976), a minimum temperature exceeded by most bodies of water in the higher latitudes of North America for several months during the winter. Indeed, massive mid-winter mortalities induced by unusually cold ambient water temperatures (< 2°C) have been reported for a *C. fluminea* population in the Ohio River near Cincinnati (Horning and Keup, 1964). In this regard, it is highly significant that populations on the northern edge of the range of *C. fluminea* in the eastern United States appear to be restricted to and to only survive in areas receiving thermal discharges from power stations during winter months (Dreier and Tranquilli, 1981; Eckbald, 1975; Rodgers, *et al.*, 1979; Thomas and MacKenthum, 1964).

The upstream invasion rate of *C. fluminea* appears to be far slower than downstream rates in the major drainage systems in which it has become established (Fig. 1). Of particular interest is the slow upstream expansion of *C. fluminea* in the Ohio River from its point of probable origin near Paducah, Kentucky, around 1957, from which it reached the upstream limit of its range in the Ohio River Drainage System in the Kanawha River, West

Virginia, by 1963 (Thomas and MacKenthum, 1964) (Fig. 1). During the same period this species spread downstream a much greater distance into Louisiana, Mississippi and Alabama (Fig. 1). The upstream dispersal of *C. fluminea* in the Mississippi River was similarly slow, with populations reaching Allamakee County, Iowa, in the river proper by 1974 (Eckbald, 1975) and Lake Sangachris, Illinois, by 1973 (Dreier and Tranquilli, 1981) (Fig. 1).

If the majority of dispersal of *C. fluminea* in the United States was mediated by human vectors the upstream dispersal rate should be similar to the downstream rate. Instead, the downstream rate is many times that of the upstream rate in most drainage systems, presumably the result of passive downstream transport of newly released juveniles over relatively large distances on water currents. However, rapid upstream invasion has been recorded for *C. fluminea* in the Tennessee River, where it was found in the river's upper reaches by 1959, only two years after it was recorded at the river's mouth in the Ohio River in 1957 (Sinclair and Isom, 1961, 1963), indicating that human activity may have been implicated in its dispersal in this drainage system.

It appears that much of the dispersal of *C. fluminea* in North America has occurred by natural means. It can be demonstrated that mountain ranges appear to form effective barriers to the extension of the range of *C. fluminea*, and that downstream dispersal rates are generally much more rapid than upstream rates, two factors that would not be characteristic of the more random dispersal patterns that should be associated with human vectors. Upstream dispersal may be the result of transport of specimens in fish digestive tracts as many species are known to feed on smaller (shell length < 5.0 mm) individuals of *C. fluminea* (Britton and Murphy, 1977; Dreier, 1977; Grantham, 1967; Ingram, 1959; Rinne, 1974; Sinclair and Isom, 1961, 1963). A more likely vector for the transport of *C. fluminea* are wading shore birds and waterfowl. Juveniles of *C. fluminea* (< 5.0 mm shell length) have been observed to produce a mucilaginous byssal thread with which they attach themselves to sand grains (Kraemer, 1979) and

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particularly to filamentous green algae (McMahon, unpublished observations). Such sand grains and especially filamentous green algae could easily become attached to or entangled in the feet of wading birds or ducks (many species of which feed on *C. fluminea*, Dreier, 1977; Thompson and Sparks, 1977, 1978) and be subsequently transported into upstream habitats. Obviously, it is also highly likely that such transport by bird vectors may be the major mode of dispersal between closely adjacent drainage systems and could, therefore, along with passive dispersal of juveniles by water currents, account for most of the rapid range expansion of this species in North American freshwaters. In contrast, longer-term migratory flights would expose juveniles to lethal levels of desiccation and would, therefore, prevent transportation across mountain ranges.

Consequently, it appears that while there have been several obvious instances of human mediated introductions of *C. fluminea* into North American freshwater habitats, the majority of the dispersal of this species appears to have been by natural means from perhaps two major epicenters of artificial introduction, one in the Northwest corner of the United States and a second in the Ohio River. The dispersal of *C. fluminea* from these two sites of introduction has been marked by a steady progression of its range through adjacent drainage systems, higher downstream than upstream invasion rates and the obstruction of its dispersal by mountain ranges, a pattern of range expansion generally associated with natural modes of dispersal.

Of apparent high importance in the rapid expansion of the range of *C. fluminea* in North America is the passive transport of its juvenile stage over large distances on water currents. In this regard, human activities in the navigable waterways of the United States as dredging and canalization not only appear to jeopardize native unionid and sphaeriid species (Kraemer, 1979; McMahon, 1983) but, also, to optimize conditions for passive dispersal of *C. fluminea* on water currents.

Certainly, the extraordinary rate at which *C. fluminea* has spread through North American

fresh waters (Fig. 1) no longer requires explanations based solely on human vectors. Rather, it may have occurred primarily by natural means that are clearly associated with the highly invasive nature of this species and with the remarkable capacities for dispersal, as evidenced in the fossil record (Miller, *et al.*, 1979), of freshwater members of the genus, *Corbicula*, as a whole.

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HERMAPHRODITISM, SEXUALITY AND SEX RATIO IN THE SURF CLAM, *SPISULA SOLIDISSIMA*, AND THE SOFT-SHELL CLAM, *MYA ARENARIA*

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ABSTRACT

In the surf clam, Spisula solidissima and soft-shell clam, Mya arenaria, hermaphroditism is an anomalous condition of very low prevalence (ca. 0.13% for surf clams and 0.35% for soft-shell clams). No conclusive evidence was found that environmental stress caused the condition or influenced the sex ratio, which was approximately equal for both species.

Accidental functional hermaphroditism in the dioecious surf clam, *Spisula solidissima* Dillwyn, was reported by Ropes (1968a) from a

single individual taken from off False Cape, North Carolina. He pointed out that this anomaly is rare, in part because the gonadal tissues