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Review of World Literature on Water Chestnut with Implications for Management in North America

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ABSTRACT

Water chestnut (*Trapa natans* L., *sensu lato*) is an annual, floating-leaved aquatic plant of temperate and tropical freshwater wetlands, rivers, lakes, ponds, and estuaries. Native to Eurasia and Africa, water chestnut has been widely gathered for its large nutritious seed since the Neolithic and is cultivated for food in Asia. Water chestnut is now a species of conservation concern in Europe and Russia. Introduced to the northeastern United States in the mid-1800s, the spread of water chestnut as a nuisance weed was apparently favored by cultural eutrophication. Water chestnut is considered a pest in the U.S. because it forms extensive, dense beds in lakes, rivers, and freshwater-tidal habitats. This results in displacement of submergent aquatic plants, interference with boating, fishing, and swimming, and depletion of dissolved oxygen which adversely affects fish communities. Dry weight phytomass ca. 100 to 1500 g/m^{-2} has been reported in native and introduced ranges. Water chestnut beds in the freshwater-tidal Hudson River support substantial phytophilous macroinvertebrate communities and a few species of small fishes. Larger fishes forage at edges of beds and penetrate into beds during favorable conditions, while birds forage on top of beds and rodents eat the seeds. Herbicides and manual or mechanical harvesting have been used for control. There has been no comparative study of water chestnut in native and introduced ranges, nor has the human food potential been investigated in the United States. Harvest of water chestnut for food, or for energy, might be compatible with local management for fish habitat and recreation.

Key words: Trapa natans, aquatic plants; invasive plants; noxious weed; vegetation management.

INTRODUCTION

Few plants incite as many contradictory perceptions as the water chestnut (*Trapa natans* L.). This floating-leaved aquatic plant is revered as an agricultural product in China and India, protected as a disappearing species in Europe, and despised as a nuisance in waterways of the northeastern United States. Because perceptions are so extreme, emotion sometimes clouds the issues. In this paper we provide an objective, comprehensive overview of water chestnut ecology and identify topics in need of further research. We refer to *Trapa natans* in North America unless stated otherwise. *Trapa* should not be confused with "Chinese water chestnut" (*Eleocharis dulcis* Burm. f., Cyperaceae), a spikerush with an edible tuber that is a common ingredient in Chinese food (Herklots 1972).

TAXONOMY

The genus *Trapa* is currently placed in the Lythraceae (purple loosestrife family; Angiosperm Phylogeny Group 1998) although previously segregated as the Trapaceae or Hydrocaryaceae. Some authors have split *Trapa* into numerous species distinguished by minute differences in the morphology of the fruits; Shishkin and Bobrov (1974) listed 25 species for the U.S.S.R. alone. Most botanists now recognize one species *T. natans* comprising two varieties: *T. natans* var. *natans* L. and *T. natans* var. *bispinosa* Roxb. (Integrated Taxonomic Information System 2003). *Trapa natans* var. *natans*, the water chestnut, water-nut, or water caltrop, now widely

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distributed in Eurasia, Africa, and the northeastern United States, bears a four-horned fruit (Crow and Hellquist 2000) whereas *T. natans* var. *bispinosa* Roxb. (= *Trapa bicornis* Osbeck, *T. bicornuta* L., and *T. japonica* Fler.), the water chestnut, singhara nut, or bull nut of China, Japan, India, and southeast Asia produces a fruit with two stout curved horns (Herklots 1972). The remainder of this paper addresses the nominate variety except as noted.

ANATOMY AND DEVELOPMENT

Water chestnut is an annual, floating-leaved aquatic plant found in freshwater wetlands, lakes, ponds, sluggish reaches of rivers, and fresh or slightly brackish reaches of estuaries. The plant has floating leaves that are broadly rhomboid, triangular, deltoid, or broadly ovate in outline, and broadly cuneate, truncate, or subcordate at base, up to 5 cm wide, with sharply, irregularly serrate or sinuate-dentate margins. Leaves are leathery, bright glossy-green above and below yellow-green and pubescent with prominent veins (Muenscher 1944, Hotchkiss 1972, Shishkin and Bobrov 1974, Gleason and Cronquist 1991). The petiole of each floating leaf has a spongy, swollen float that allows the foliage to form a rosette, up to 30 cm in diameter, on the surface of the water (Benson 1957, Gleason and Cronquist 1991, Crow and Hellquist 2000). A stem may produce several branches, each terminating in a rosette (Muenscher 1937). In May in the northeastern states, the small rosettes remain submerged as the stems elongate to reach the water surface; from June to September the rosettes are present on the water surface. Leaves are produced at a constant rate of one leaf per rosette per unit time, and leaf lifespan is approximately 1 month (Tsuchiya and Iwakuma 1993). Beneath the surface of the water is a flexible stem 1 to 5 m long that bears submersed, linear or spatulate leaves (Muenscher 1944, Gleason and Cronquist 1991; Kiviat, pers. obs.). These submersed leaves drop early and are replaced by pairs of fine, pinnate structures up to 8 cm long (Muenscher 1944, Gleason and Cronquist 1991, Crow and Hellquist 2000). These plumelike structures have been considered stipules, leaves, or adventitious roots (Vasilev 1978, Crow and Hellquist 2000, Rhoads and Block 2000). Nodes of the lower stem also bear slender, unbranched roots in the substrate and in the water above the substrate (Muenscher 1944, Crow and Hellquist 2000). The plant is secured in the mud by the lower roots and the fruit hull from which it originally grew (Smith 1955, Hall 1982).

Flowers are borne singly in the axils of floating leaves from late June to September in the Mohawk River and tidal Hudson River (Smith 1955, Seymour 1969, Countryman 1978, Kiviat 1993). The flower has four white, 8 mm long petals, four yellow stamens, and a two-chambered ovary (Muenscher 1944, Benson 1957, Seymour 1969, Gleason and Cronquist 1991). Pollination apparently occurs in the air; however, the pollen vector is unknown. Self-pollination possibly occurs before the flower opens (Shishkin and Bobrov 1974).

After pollination, one of two locules and its ovule abort and the peduncle bends down into the water where a unilocular, one-seeded fruit develops (Muenscher 1944, Benson 1957, Gleason and Cronquist 1991, Cronk and Fennessy 2001). The seed has two unequal cotyledons: a large, starchy cotyledon within the endocarp and a small, scale-like cotyledon that grows out through the terminal pore of the fruit left by abscission of the style (Gleason and Cronquist 1991). The fruits mature from mid-July into September and are released by the rotting peduncles (Winne 1950, Smith 1955, Countryman 1978, Cronk and Fennessy 2001). Each rosette produces 10 to15 nuts, each ca. 6 g wet mass (2.1 g dry mass) and 2 to 4 cm wide (excluding the barbed portions of the horns) at maturity (Countryman 1978, Gleason and Cronquist 1991, Kiviat and Beecher 1991). Production of few, heavy seeds is unique among aquatic plants and indicates adaptation to stable environments where persistence is more important than dispersal (Kurihara and Ikusima 1991). Referred to as a "turbinate drupe" or "nut," the fruit has a short-lived, fleshy exocarp (pericarp) that disintegrates to reveal the persistent, hard endocarp (Muenscher 1944, Benson 1957, Gleason and Cronquist 1991, Crow and Hellquist 2000). The nut is tetrahedral, black, hard, and woody with four sharp spines, formed from the persistent sepals of the flower, that bear recurved barbs (Muenscher 1944, Benson 1957, Gleason and Cronquist 1991, Crow and Hellquist 2000). The nuts are 20% heavier than water upon maturity, and sink rapidly to the bottom where they overwinter in the sediment (Muenscher 1937, Bogucki et al. 1980). The parent plant is killed by frost in autumn and decomposes quickly. Seeds are capable of remaining dormant in bottom sediments for up to 10 years; however, seeds quickly lose viability if allowed to dry out (Muenscher 1944, Winne 1950, Beaven 1959).

When water temperatures rise to 12 C or higher in the spring, the bristle-bordered terminal pore of the fruit begins to rot; within a month the seed starts to germinate (Muenscher 1944, Countryman 1978, Vuorela and Aalto 1982, Mazumdar 1985, Kurihara and Ikusima 1991). At high temperatures in the laboratory seeds germinated more synchronously in a shorter period; however, temperature did not influence the final or maximum germination rate (Kurihara and Ikusima 1991). By the end of the 2nd week after germination the first and second cotyledons and the hypocotyl are fully formed, and during the 3rd week secondary roots develop from the hypocotyl. Unbranched roots grow down toward the substrate while a filamentous root reaches up and out (Muenscher 1944).

The nut hulls that remain in the sediment after germination are resistant to decomposition and can persist for many years, giving the appearance of a more substantial seed bank than is actually present. Samples taken from the Watervliet Reservoir near Albany, New York, showed that more than 90% of apparent fruits were empty hulls (Madsen 1993). Nut hulls also form conspicuous windrows at the high water line of infested water bodies.

GROWTH REQUIREMENTS

Water chestnut requires full sun, sluggish, nutrient-rich, fresh waters, and soft substrate (Winne 1950, Kiviat 1993). Water chestnut grows in waters 0.3 to 3.6 m deep but is most abundant in sheltered bodies of water about 2 m deep with soft, muddy bottoms (Muenscher 1937, Countryman 1978, Bogucki et al. 1980). Water chestnut rarely grows where the substrate is low in organic matter; in addition, swiftly flowing water and sharp fluctuations in water level can be detrimental to its survival (Winne 1950, Vuorela and Aalto 1982). In the Hudson River, some water chestnut plants are rooted slightly above low tide level such that they are stranded on the substrate at low tide. Water chestnut dominates Tivoli South Bay, a tidal freshwater wetland on the Hudson River in New York State, whereas adjacent Tivoli North Bay has little water chestnut. Tidal fluctuations of 1.2 m and water chemistry are similar in both bays, but South Bay lacks well developed tidal creeks whereas the tidal creeks in North Bay create higher velocity flows and scoured substrates that apparently inhibit establishment of water chestnut. Predation by muskrat (*Ondatra zibethicus* Linnaeus) might also be a factor.

The roots of water chestnut absorb dissolved inorganic nitrogen (DIN) from the water and from the sediment. In the laboratory, Tsuchiya and Iwakuma (1993) found that maximum leaf area index and maximum net productivity were positively correlated with nitrogen absorption. Increased nitrogen influx resulted in increased petiole and fruit biomass and decreased stem and root biomass in the mud (Tsuchiya and Iwakuma 1993). This occurs because more nitrogen can be allocated to fruit production while fewer roots are required for nitrogen uptake; leaf lifespan, however, was independent of nitrogen influx (Tsuchiya and Iwakuma 1993).

Substrate pH affected water chestnut germination and growth in the laboratory. Seeds germinated most quickly in a substrate with a pH of 7.9 to 8.3, and more slowly at a pH of 4.2 to 5.2; slowest germination occurred in sediments with a pH of 5.3 to 7.8. After 2 weeks, however, seedlings grown in both alkaline and acidic substrates died, but those grown in moderately acidic to neutral substrates developed well (Apinis 1937). Winne (1950) suggested that increased alkalinity from sewage inputs to the Sudbury River could have favored water chestnut. The wide distribution of subfossil and modern water chestnut indicates tolerance to a wide range of pH values (Vuorela and Aalto 1982).

Water chestnut is restricted to fresh waters because its seeds fail to germinate when NaCl concentrations exceed 0.1% (Vuorela and Aalto 1982). The southernmost occurrence of water chestnut in the Hudson River is in brackish tidal marsh at Iona Island with a maximum salinity of about 7 ppt where water chestnut is limited to an area apparently receiving fresh groundwater. The plant is also intolerant of $Ca(HCO_3)_2$ and $Mg(HCO_3)_2$ (Vuorela and Aalto 1982).

Plant density affects nearly every facet of water chestnut growth and vigor. Water chestnut competes for two-dimensional water surface space rather than three-dimensional canopy space as do terrestrial plants. Plants in plots with 5 to 15 rosettes/m^2 were larger, more productive, and longer-lived than plants in plots with about 100 rosettes/m^2. Water chestnut in low-density plots had 5 times as many rosettes and 8 to 10 times the biomass of plants in high density plots, and low density planting resulted in greater allocation to reproduction and larger leaf size. Rosettes of low-density plots showed practically no mortality until the entire plant senesced in September, whereas the rosettes of plants in high-density plots suffered continuous mortality through the growing season (Groth et al. 1996).

Table 1 contains estimates of peak standing crop biomass of water chestnut. Estimates from a freshwater-tidal marsh (Tivoli South Bay of the Hudson River) are about 400 to 500 g/m^2, estimates from lakes in more northern latitudes and an estimate from the nontidal Hudson River are less than a third of the Tivoli values, and a single estimate from a lake in northern India is more than twice the Tivoli values. The estimate from Watervliet Reservoir, a lake less than 100 km north of Tivoli, seems anomalously high and may represent an unusually favorable habitat. If we assume that methodological differences are unimportant, it appears from these limited data that water chestnut biomass declines with increasing latitude, but that "shelter" (i.e., reduced hydrodynamic energy level) and higher fertility allow greater accumulation of biomass. Besha and Countryman (1980) reported dry mass as 17.6% of wet mass.

TABLE 1. PEAK ABOVEGROUND BIOMASS REPORTED FOR WATER CHESTNUT (*TRAPA NATANS*). ALL HABITATS ARE NONTIDAL EXCEPT TIVOLI SOUTH BAY.

Location	Variety	Biomass, g/m^2 dry mass
Watervliet Reservoir, New York	*natans*	1575[1]
Tivoli South Bay, Hudson River, New York	*natans*	357[2]
Tivoli South Bay	*natans*	530[3]
Tivoli South Bay	*natans*	570[3]
Tivoli South Bay	*natans*	389-510[4]
Thompson Island Pool, Hudson River	*natans*	104[5]
Fishponds, Č. Budějovice-Vodňany basin, Czech Republic	*natans*	107[6]
Bada tal Reservoir, northern India	*bispinosa*	994[7]
Lake Kasumigaura, Japan	*bispinosa*	160[8]

[1]Besha and Countryman 1979 (n not stated), calculation from Kiviat 1987.
[2]Kiviat and Beecher 1984 unpublished (mean of 10 samples along transect).
[3]Findlay 1986 and 1987 unpublished data (values of ca. 400 and ca. 425 g/m^2 were estimated for rosettes and the top ca. 40 to 50 cm of stems only; thought to be 70 to 80% of total aboveground phytomass).
[4]Schmidt and Kiviat 1988 (range of three means, five samples each, 28 July, 14 Aug., 31 Aug. 1987).
[5]Feldman 2001 (mean of six, 1 m^2 samples).
[6]Květ and Husák 1978.
[7]Unni 1984 (Maximum phytomass of cultivated water chestnut in a small reservoir).
[8]Tsuchiya and Iwaki 1979 (Presented as dry weight of 8.93×10^5 kg in 56.7 ha).

NATIVE RANGE AND HABITAT

Water chestnut is native to temperate and tropical Eurasia and Africa (Muenscher 1944, Gleason and Cronquist 1991, Crow and Hellquist 2000). *Trapa* fossils as old as the Cretaceous are known from the former U.S.S.R. (Shishkin and Bobrov 1974). Analysis of Neolithic (3300 to 2800 BC) sediment collected from archeological sites in the village of Pannala, Orimattila, southern Finland revealed that the dominant aquatic plant of the lake basin was water chestnut in association with floating-leaved species of *Potamogeton*, *Nymphaea*, and *Nuphar*. The plant remains suggest an environment rich in nitrogen, which may have been the result of human activity (Vuorela and Aalto 1982). The drastic increase in water chestnut populations along the Sudbury River in the 1940s was apparently associated with increased soluble nitrate levels in the stream (Burk et al. 1976); furthermore, the decline of water chestnut in the Sudbury and Concord Rivers has been attributed more to improved water quality resulting from waste treatment facilities in the watersheds than to the ineffective eradication efforts of years past (Countryman 1970).

Kurihara and Ikusima (1991) noted that the species was "... encountered in lakes, ponds, and ditches all over Japan" and that Lake Inba-numa, which lost most of its aquatic plants due to pollution, was almost completely covered with water chestnut. Water chestnut was considered a noxious weed because it impeded fishing, transport, and leisure activities in many Japanese waterways (Kurihara and Ikusima 1991).

By the late 1970s water chestnut was common in almost all states of northern India (Little 1979). The species grew wild in some regions, was extensively cultivated in others, and presented problems of excessive growth in still other areas. Kaul et al. (1976) noted water chestnut inhabited water bodies of the Valley of Kashmir in the Himalayas where lakes, ponds, ditches, and streams at 1600 to 2500 m elevation had nutrient-rich waters and supported several species of aquatic plants. Kaul et al. (1976) suggested that shrinking of the Kashmir lakes was mostly attributable to the profusion of aquatic plant growth, which may have resulted from increased water pollution. Water chestnut under favorable conditions quickly forms a stable floating mat, which hinders navigation and interferes with recreational activities (Kaul et al. 1976).

Water chestnut was among a suite of 17 aquatic plants of oxbow lakes in the vicinity of Cracow, Poland, that declined due to urbanization, hydrological alterations, water pollution with sewage and industrial waste, and natural infilling (Dzwonko and Plazińska 1977). Water chestnut was extirpated from the Třeboň basin of the southern Czech Republic, probably due to fish pond management during the late 1900s, according to a brochure of the Institute of Botany, Academy of Sciences of the Czech Republic, Division of Plant Ecology. Water chestnut is now very rare in Europe where it is considered endangered or extirpated in many countries (Zvelebil 1987, Cronk and Fennessy 2001). The plant is conspicuously absent from the comprehensive text River *Plants of Western Europe* (Haslam 1987).

INTRODUCTION AND SPREAD IN NORTH AMERICA

Water chestnut was introduced from Europe as an ornamental. Dispersal is limited because of the large, sinking nuts, but water chestnut has persisted and spread in the northeastern states. The barbed spines of the nuts enable them to cling to moving objects, including the plumage of Canada geese (*Branta canadensis* [Linnaeus]) (Mirick 1996; Robert L. Bard, pers. comm.), mammal fur, human clothing, nets, wooden boats, construction equipment, and other vehicles. Mature seeds are also sometimes produced by rosettes which have broken free and drifted to new areas (Bickley and Cory 1955).

The most effective form of dispersal of water chestnut is human introduction. The species was first introduced to North America in Middlesex County, Massachusetts, ca. 1874, and by 1877 was cultivated in Asa Gray's botanical garden at Harvard University in Cambridge, Massachusetts (Countryman 1978). Davenport (1879) found water chestnut growing wild in Fresh Pond not far from the University; he traced the plant to Louis Guerineau, the gardener at the botanical garden, who threw water chestnut seeds into this and nearby ponds. Davenport and his friend Minor Pratt further distributed the seeds to at least one pond in Concord near the Sudbury River, and in 1879 Davenport reported that several specimens of water chestnut brought to him for identification from the Boston area likely resulted from his introductions. Davenport (1879) commented "... that so fine a plant as this, with its handsome leafy rosettes, and edible nuts, which would, if common, be as attractive to boys as hickory nuts now are, can ever become a 'nuisance' I can scarcely believe." Water chestnut was found in the Concord River in Concord, Massachusetts in 1886 and grew to nuisance proportions, covering 40 ha by 1899 (Burk et al. 1976, Countryman 1978). By the mid-1940s water chestnut populations exploded and became a nuisance in the Sudbury River. In the 1900s the Sudbury and Concord rivers suffered increasing eutrophication from domestic sewage pollution, which could at least partially account for the profusion of water chestnut in these water bodies (Countryman 1970).

Father J. Hermann Wibbe, a Polish Catholic priest, toured Europe in the 1880s shortly before coming to Schenectady, New York, to assume religious duties. Father Wibbe was a plant lover and brought with him seeds he had gathered in Europe. In 1886 Father Wibbe reported that water chestnut he had transplanted from Europe into Sander's Lake in 1884 was growing luxuriantly. Sander's Lake, now known as Collins Lake, in Scotia, New York, drains into the Mohawk River via Collins Creek (Winne 1950, Countryman 1978). Locks and dams of the New York Barge Canal system caused flooding from the Mohawk River into Sander's Lake, allowing water chestnut to escape (Winne 1950). The species was well established in the Mohawk River by 1920 and in 1934 was estimated to cover 405 to 486 ha of the Mohawk River and 16 km of the Barge Canal (Muenscher 1937). No live plants were found in the Hudson River at that time, but water chestnut slowly spread down the Mohawk and reached the Hudson River at Cohoes by the late 1930s (Muenscher 1937, Winne 1950). By 1952 the total New York infestation was estimated at 1,416 ha (Countryman 1978). Water chestnut is still well established along the Hudson River from Saratoga County south to Putnam and Orange Counties (Lamont and Fitzgerald 2001); in the freshwater-tidal Hudson River it forms dense beds in virtually all sheltered subtidal shallows (Kiviat, pers. obs.). Additional infestations include Watervliet Reservoir, a marshy waterfowl impoundment, numerous artificial or partly natural ponds, and a major tributary, all within 30 km of the Hudson River in Columbia, Ulster, and especially Dutchess County, New York (Besha and Countryman 1980, Kiviat 1993 and pers. obs., Tiner 2000). Water chestnut was discovered in the western end of Oneida Lake in central New York, in 1999 where it is the subject of intensive control efforts (Anonymous 2002).

Water chestnut probably reached Lake Champlain from the Hudson River via the Hudson-Champlain Canal, possibly by means of fruits clinging to boats. The species was first discovered in shallow bays of the southern end of Lake Champlain in the 1940s; in 1978 water chestnut was spreading northward (Countryman 1970, 1978). Despite control efforts, the range now extends over 84 km of Lake Champlain and populations have been discovered in four other bodies of water in Vermont (Bove and Hunt 1997). About 1997, water chestnut was discovered in the Richelieu River system, draining Lake Champlain, in southern Québec, Canada (Aquatic Nuisance Species in Vermont 2003). This was possibly the first reported Canadian population.

Water chestnut was observed in a Potomac Park fish pond prior to 1919, and in 1923 a 0.8 ha patch was discovered in Oxen Run across the Potomac River from Alexandria, Virginia (Gwathmey 1945). The colony grew to 36 ha within 3 years and several smaller infestations were found nearby. By 1940 the total infestation of the Potomac River was ca. 3642 ha, extending 64 km downriver and 8 km upriver from Washington, D.C. (Gwathmey 1945, Countryman 1978). In August 1954, U.S. Fish and Wildlife Service staff discovered four beds totaling 4 ha in the tidal sections of the Bird River, a tributary of the Gunpowder River (Bickley and Cory 1955, Countryman 1978). By 1964 ca. 4 ha were found in the Sassafras River and Turner's Creek (Countryman 1978); all four of these Maryland waterways are tributaries of Chesapeake Bay.

Control efforts were successful in the Potomac River and Chesapeake Bay, where water chestnut beds were maintained at a level that required only hand removal (Rawls 1964). Water chestnut, however, still proliferates in the Concord River (Goettel 1998). Crow and Hellquist (2000) referred to water chestnut as "locally aggressive" from southern New Hampshire, Massachusetts, western Vermont, and eastern New York to Maryland and northern Virginia.

DETRIMENTAL EFFECTS

Aquatic Vegetation

Water chestnut is capable of covering nearly 100% of the water surface when conditions are favorable. High density growth results in the interception of 95% of incident sunlight, which severely affects plants beneath the water chestnut canopy, and causes shading out of submerged vascular plants and their associated microscopic flora and fauna (Winne 1950, Kiviat 1987, 1993, Groth et al. 1996). Water chestnut was considered "destructive to important submerged duck-food beds" (Martin and Uhler 1939). Displacement of submersed plants by water chestnut is believed to cause the loss of many animal species and their replacement by more tolerant, more common, and in some cases non-native species (Beaven 1955).

In the tidal Hudson River, water chestnut has apparently replaced water celery (*Vallisneria americana* Michx.), clasping pondweed (*Potamogeton perfoliatus* L.), introduced Eurasian watermilfoil (*Myriophyllum spicatum* L.), and other submergent plants in many areas; the only water celery beds that thrive in the Tivoli Bays, a semi-impounded wetland of the Hudson, are where current and wave action exceed tolerance of water chestnut. Duckweeds (*Lemna minor* L., *Spirodela polyrhiza* L., *Wolffia* spp.) and filamentous algae grow among the rosettes, taking advantage of the shelter from winds and currents. Narrowleaf cattail (*Typha angustifolia* L.), pickerelweed (*Pontederia cordata* L.), and spatterdock (*Nuphar advena* [Aiton] Aiton f.) seem unaffected by the presence of water chestnut, which cannot compete with tall emergent species that grow above the low tide level (Kiviat 1987, 1993). Water chestnut was recently discovered in the Connecticut River, and there is concern about its spread in the tidal marshes which have exceptional significance for rare plants and animals (Derman 2000).

Animals

Quantitative studies of animal use of water chestnut beds have been limited to invertebrates and fishes. Cattaneo et al. (1998) studied Lago di Candia, a shallow, highly vegetated lake in northern Italy with a surface area of 152 ha, a mean depth of 4.7 m and with aquatic vegetation occupying >90% of shoreline, and compared epiphyton development on submersed vegetation with that of water chestnut. All descriptors of epiphyton including algae, cyanobacteria, and macroinvertebrates were significantly higher on submersed plants than on water chestnut. The positive relationship between other epiphyton and macroinvertebrate abundance suggests that epiphyton plays a role as a food source for epiphytic fauna and, by extension, associated fish and waterfowl (Cataneo et al. 1989).

Feldman (2001) sampled phytophilous macroinvertebrate communities on water chestnut and water celery at two sites in the nontidal upper Hudson River. Macroinvertebrate density per m^2 leaf surface and per m^3 water was substantially greater on water celery. Overall, however, there were 34 macroinvertebrate taxa on water celery vs. 40 taxa on water chestnut. Community composition of invertebrates was quite different in the two plant communities. Larger macroinvertebrates were more abundant on water chestnut, possibly due to less fish predation in the denser vegetation mass. Biomass of invertebrates was not measured.

The effects of water chestnut on animals are not limited to reductions in wildlife food plant populations. Dissolved oxygen (DO) under dense water chestnut beds was consistently low in laboratory experiments (Tsuchiya and Iwakuma 1993). A recent study of Tivoli South Bay suggests a direct relationship between native water celery biomass and the benthic and phytophilous invertebrate density, while the inverse was true for water chestnut. Lutz and Strayer (2000) proposed that depressed DO levels in water chestnut beds at low tide could account for the inverse relationship. Caraco and Cole (2002) compared DO in a 60-ha water celery bed and a 90-ha water chestnut bed in Inbocht Bay of the freshwater tidal Hudson River during the growing season. Measurements taken by centrally moored instruments showed that DO never dropped below 5 mg/L in the water celery bed, but DO values <2.5 mg/L were produced 42% of the time by the water chestnut bed. Dissolved oxygen below 5 mg/L negatively affects sensitive fishes and invertebrates; when DO is less than 2.5 mg/L most fishes are negatively affected (Frodge et al. 1990).

It was thought that depression of DO to lethal levels at low tide in large Hudson River water chestnut beds would force resident fish into open water, a phenomenon that commonly draws local fishermen to water chestnut bed edges where larger predatory fish feed. Further study of Inbocht Bay revealed, however, that fish moved uniformly out of the bed with the ebbing tide regardless of DO levels (Coote et al. 2001).

The coupling of decreased epiphyton abundance and low DO could be responsible for the low diversity of fish communities that inhabit water chestnut beds. Several studies have investigated species composition and abundance of fishes in water chestnut beds of the Hudson River. Most concluded that although fish do inhabit water chestnut beds, the species found in greatest abundance are common ones with wide tolerance for adverse environmental conditions that include water pollution, turbidity, and low DO (Schmidt and Kiviat 1988, Pelczarski and Schmidt 1991, Schmidt et al. 1992, Gilchrest 1998). Resident fish communities in these studies mainly consisted of fourspine stickleback (*Apeltes quadracus* [Mitchill]), juvenile banded killifish (*Fundulus diaphanus* [Lesueur]), spottail shiner (*Notropis hudsonius* [Clinton]), tessellated darter (*Etheostoma olmstedi* Storer), and the introduced common carp (*Cyprinus carpio* Linnaeus) (Schmidt and Kiviat 1988, Pelczarski and Schmidt 1991, Schmidt et al. 1992, Gilchrest 1998). These are not important sport or commercial species, but in the Hudson are important forage fishes for which water chestnut beds provide significant nurseries. Adult spottail shiners, banded killifish, and tessellated darters are not found in dense water chestnut beds, but are common in water celery beds (Schmidt and Kiviat 1988).

Connor (1978) rescued an osprey (*Pandion haliaetus* Linnaeus) in juvenal plumage that was found entangled in water chestnut in Tivoli South Bay, apparently exhausted and unable to take flight. The bird presumably became entangled when it dove into the water to catch prey.

Human Activities

Water chestnut receives a great deal of attention because of impact on commercial and recreational activities. Bickley and Cory (1955) stated the formation of "dense masses capable of supporting large birds" over vast areas of open water interferes with boating, fishing, swimming, and duck hunting in the Chesapeake Bay. Swimming and other beach-related activities are also hindered by the sharp nut hulls that accumulate on shores and cause painful injuries when stepped on, sometimes penetrating shoes (Gwathmey 1945, Winne 1950, Beaven 1955, 1959, Countryman 1978, Bogucki et al. 1980, Giddy 2003). Barbed spine-tips break off in the skin and cause infection (Kiviat, pers. obs.). Water chestnut may have played a role in the drowning deaths of a woman and two children in the Hudson River in July 2001 (Bonopartis 2001). An investigation by the Ulster County Sheriff's office was not conclusive, but evidence was consistent with the idea that tidal currents or a ship wake swept one or more of the drowned persons into a water chestnut bed and initiated their entanglement in the plants (Undersheriff Wood and Captain van Vliet, pers. comms.).

The Asian custom of eating raw water chestnut contributes to the ingestion of the giant intestinal fluke (*Fasciolopsis buski* [Lankaster]) larvae that cause fasciolopsiasis (Gangstad and Cardarelli 1990). In addition, water chestnut beds are regarded as potential breeding habitat for mosquitoes (Gwathmey 1945). O'Malley (1989) stated that "mosquito larvae are usually found where surface vegetation and debris are present," but we have seen no documentation of mosquitoes in water chestnut beds in North America.

Water from water chestnut beds of the nontidal Mohawk River and the tidal Hudson River was higher in dissolved organic carbon (DOC) and more acidic than in nearby open water habitats (George and Alben 2000). There has been concern that increased DOC in reservoirs due to water chestnut could be a precursor to toxic chlorinated organic compounds in drinking water (Besha and Countryman 1980).

POSITIVE ASPECTS

Water Quality Improvement

Aquatic plants are important in water purification as they reduce current velocity and allow deposition of sediment and nutrient removal (Karpati and Pomogyi 1979). Tsuchiya and Iwakuma (1993) showed that 84 to 96% of dissolved inorganic nitrogen entering water chestnut-filled tanks was fixed, and only a small amount of nitrogen was discharged in outflow water from the tanks. This suggests that water chestnut beds in the field may remove a great deal of nitrogen from runoff waters, thus potentially reducing eutrophication of downstream sites. This function, however, can only be performed before plants begin to decay in the fall or if the plants are harvested and removed from the system before senescence. There may be an impact on water quality of rapid decomposition of water chestnut material in fall (Besha and Countryman 1980, Derman 2000).

Water chestnut is capable of accumulating heavy metals. Analyses of whole plants sampled in association with a remedial investigation of the Marathon Battery Federal Superfund site at Foundry Cove on the Hudson River demonstrated that cadmium and nickel concentrations in plants from the outfall area were significantly higher than concentrations in plants from a control site; the level of cadmium in samples decreased with increased distance from the outfall. The overall range for whole plants ($n = 9$) on a dry weight basis was 1.6 to 420 ppm cadmium, 0.96 to 180 ppm nickel, and 1.2 to 13 ppm cobalt. Concentrations of all three metals, however, were consistently higher, location by location, in water celery than in water chestnut (Acres International Corp. 1985). The fate of accumulated metals after water chestnut decomposition or ingestion by animals is unknown.

Uses by Wildlife

Aquatic plants often provide habitat with a high surface area per ha ratio that is favorable to numerous species of invertebrates. In Tivoli South Bay, Findlay et al. (1989) found the mean density of invertebrates in water chestnut beds was 12,300 individuals/m^2, with 55% chironomids and 24% oligochaetes. Invertebrate densities in water chestnut of Tivoli South Bay, however, were not high compared to other studies (Findlay et al. 1989). Chironomids eat the debris that collects on the surface of water chestnut leaves; this cleans the leaf and may allow increased light absorption and gas exchange (Kelly and Perrotte 1989). Chironomids are important food for fishes (Coote et al. 2001) and chironomid density was reduced when juvenile fishes arrived in the South Bay (Findlay et al. 1989). It is unclear whether submersed plant beds would support similar invertebrate communities in the absence of water chestnut. Yozzo (1990) analyzed stomach contents of larval and juvenile fishes in Tivoli South Bay and found that ostracods and other microcrustaceans were frequently eaten by inhabitants of water chestnut beds such as banded killifish, fourspine stickleback, spottail shiner, and golden shiner (*Notemigonus crysoleucas* [Mitchill]). These findings suggest that water chestnut provides significant foraging habitat for fishes and may enhance total fish production in the Hudson River Estuary (Yozzo 1990).

Juvenile blueback herring (*Alosa aestivalis* [Mitchill]) in Inbocht Bay fed preferentially on insects within a water chestnut bed; ready movement of the herring out of the bed suggested water chestnut was not used as protection from predators (Coote et al. 2001). Behavior and community composition of fishes vary in different Hudson River water chestnut beds; bed area and exposure to currents are believed to be important factors shaping this habitat (Gilchrest 1998, Coote et al. 2001).

Adult water-lily leaf beetles (*Galerucella nymphaeae* [Linnaeus] = *Pyrrhalta nymphaeae*) overwinter in empty water chestnut hulls in the shoreline wrack of Tivoli South Bay (Fritzi Grevstad, pers. comm.; Kiviat, pers. obs.) and adults and larvae of this species feed extensively on the water chestnut leaves (Countryman 1978, Schmidt 1986). The above-water portions of water chestnut also provide cover or substrate for water-measurer bugs (*Hydrometra* Latreille), water striders (Gerridae), big bluet damselfly adults (*Enallagma durum* Hagen), lady beetles (*Coleomegilla maculata* DeGeer), and wolf spiders (*Lycosa helluo* Walckenaer), while underwater portions host flatworms (*Dugesia*), hydra (*Hydra*), water-fleas (Cladocera), copepods (Copepoda), seed shrimp (Ostracoda), scuds (*Gammarus*), mayfly nymphs (Ephemeroptera), big bluet nymphs, and snails (Gastropoda) (Kiviat 1993; Hummel, pers. obs.). We have observed snapping turtles (*Chelydra serpentina* [Linnaeus]) and blue crabs (*Callinectes sapidus* Rathbun) in Hudson River water chestnut beds, and zebra mussels (*Dreissena polymorpha* Pallas) on submerged leaves and stems. Lists of invertebrate taxa associated with water chestnut are in Yozzo and Odum (1993), Findlay et al. (1989), and Feldman (2001).

Various marsh and water birds walk on water chestnut mats and probably forage there. European coots (*Fulica atra* Linnaeus) forage for beetles, dragonfly nymphs, snails, and leeches associated with floating-leaved plants including water chestnut in western France (Paillisson and Marion 2001). Cedar waxwings (*Bombycilla cedrorum* Vieillot) hawk or glean insects, probably water-lily leaf beetles, from water chestnut beds on the Hudson River (Kiviat, pers. obs.). In the former U.S.S.R., black tern (*Chlidonias niger* [Linnaeus]) was reported nesting on water chestnut beds, and common white-cheeked tern (= whiskered tern, *Chlidonias hybridus* Pall.) constructed floating nests of water chestnut "stalks" (Dement'ev and Gladkov 1969). Wood ducks (*Aix sponsa* [Linnaeus]) sometimes ingest whole water chestnuts; it is not known whether this results in injury to the ducks (R. L. Bard, pers. comm.).

Muskrats gnaw one side of the hull to eat the nuts in the Sudbury River, Potomac River, and Hudson River (Muenscher 1937, Winne 1950, Kiviat 1993). Beavers (*Castor canadensis* Kuhl) eat the nuts and vegetative parts of the plant (T. Welling, pers. comm.). Norway rats (*Rattus norvegicus* [Berkenhout]) cross dense water chestnut mats to collect the nuts for food (R. L. Bard, pers. comm.). Eastern chipmunks (*Tamias striatus* [Richardson]) eat water chestnuts along the Hudson River (Robert E. Schmidt, pers. comm.; Rachel Stevens, pers. comm.). Gray squirrels (*Sciurus carolinensis* Ord) eat both the nuts and the "core" of the rosette (Erin O'Hare, pers. comm.; Kiviat, pers. obs.). Red squirrels (*Tamiasciurus hudsonicus* [Bangs]) cache water chestnuts and eat them in winter (Kiviat, pers. obs.). White-tailed deer (*Odocoileus virginianus* Zimmerman) graze on vegetative material of water chestnut in the Hudson River (Robert E. Schmidt, pers. comm.).

Human Use

The Maglemosian people of northern Europe ate water chestnuts during the period 8000 to 6000 BC (Zvelebil 1986). This is possibly the oldest known human use of water chestnut. Excavations in southern Finland and the east Baltic region have revealed that cultural layers commonly coincide with highly productive phases of peatland development characterized by extensive beds of vegetation such as water chestnut which are indicative of eutrophic conditions (Zvelebil 1987). Cracked, sharp-edged water chestnut hull fragments found at a study site in southern Finland indicate human consumption in the Neolithic period (3300 to 2800 BC) (Vuorela and Aalto 1982). Enormous quantities of water chestnut were present in sediments of the Neolithic settlement in Moor, Austria (Coles and Coles 1989), and excavations at a study site in Molino Casarotto in subalpine Italy revealed remnants of water chestnut fruits that date their consumption as far back as 4000 BC (Dennell 1992). At the Robenhausen site in Switzerland, the best-preserved settlement of Neolithic Europe, water chestnut was apparently stored for winter use. Shelled, pounded, and cooked water chestnut provided flour for Neolithic wetland dwellers that did not grow cereals, such as Robenhausen inhabitants, and supplemented the diets of drylanders who did, such as the Moor inhabitants (Coles and Coles 1989).

Waters of the Neolithic lakeside settlements of northwest Russia provided stable food supplies, including water chestnuts (Coles and Coles 1989). At Sarnate, Latvia, and similar sites in the east Baltic region thick deposits of water chestnut hulls around hearths and inside dwellings, burned remains in ashes, and fragments embedded in work surfaces and mallet heads suggest that processing of water chestnut with specialized tools was a widespread activity (Zvelebil 1987). Increasing abundance of water resources during the late Atlantic period allowed water chestnut to flourish; in addition freshwater fishes proliferated and people became increasingly settled (Coles and Coles 1989). Deteriorating climatic conditions at the end of the Sub-Boreal and Sub-Atlantic periods caused the gradual disappearance of water chestnut from Finland, northern Russia, and the east Baltic. Some archeologists believe water chestnut was such an important food source for prehistoric peoples of northwestern Russia that the disappearance of the plant contributed to the shift from hunting and gathering to agriculture (Zvelebil 1986, 1987).

Water chestnut is valued for its nutritional and medicinal properties in modern India. The fresh nuts have a high moisture content and are in demand for quenching thirst (Mazumdar 1985). Raw *T. natans* var. *bispinosa* Roxb. nuts were commonly sold in the markets of Hong Kong, Malaya, and Thailand; however, they contain substances harmful to the alimentary canal and must be boiled to be edible (Herklots 1972). Dried water chestnuts were ground into flour and used to make various foodstuffs (Mazumdar 1985). In China water chestnut was extensively cultivated and the fruits were commonly sold in markets (Pemberton 1999). The flour and the nuts of *T. natans* var. *bispinosa* were eaten in Hong Kong at the Festival of the Full Moon (Herklots 1972). The species was used for medicine widely in Asia (Khatib 1934, Herklots 1972). Water chestnut kernels were used to treat rabies, poisonous animal bites, diarrhea, amoebic dysentery, and other conditions in the U.S.S.R. (Shishkin and Bobrov 1974). Proximate composition of Russian water chestnut nuts (presumably fresh) was 15% protein, 7.5% fat, 52% starch, 3% sugar, and 22.5% water (Shishkin and Bobrov 1974).

The singhara nut is a valuable agricultural product, commercially cultivated in many parts of India, particularly in the eastern and southern regions (Mazumdar 1985). Singhara was extensively grown in Uttar Pradesh, Madhya Pradesh, Bihar, and Orissa, where high rainfall was conducive to successful cultivation (Little 1979). Harvesters on rafts picked the fruits and sell them at market while still fresh; average yields of 260 to 370 g/m^2, and up to 550 g/m^2 were harvested from beds in West Bengal (Mazumdar 1985). The Indian Agricultural Research Institute of New Delhi studied methods to control the agricultural pests that threatened water chestnut crops. The singhara beetle (*Galerucella birmanica* Jacoby, Chrysomelidae) was particularly damaging to both the foliage and fruits of the plant and was resistant to traditional chemical pesticides (Pradhan et al. 1964).

In addition to serving as food for people and animals, water chestnut has been recommended for paper pulp, fertilizer, fish food, compost, and biogas fuel (i.e., methane generated from organic material via anaerobic digestion). Besha and Countryman (1980) analyzed the efficiency of anaerobic digestion of water chestnut to produce methane as a fuel for generating electricity. They estimated a potential yield of 1.16×10^{11} kJ (1.29×10^4 MW of electricity) annually from the 2000 ha of water chestnut in New York State, and stated that the residue after anaerobic digestion could be used as a cattle feed supplement (Besha and Countryman 1980).

Water chestnut has been composted on a small scale for garden fertilizer, which raised the question of contamination. A 1980 sample of water chestnut from the Hudson River at Beacon, New York, contained 0.8 ppm cadmium, 0.05 ppm mercury, and 0.15 ppm PCBs (dry weight basis). Ward Stone (NYS DEC, letter to Pete Seeger dated 23 September 1980) stated that application of 90 kg (wet mass) of water chestnut to a vegetable garden would not add dangerous amounts of toxic substances and would add less cadmium than commercial fertilizer.

We have heard of individual water chestnut hulls being sold in New York City, and have seen a variety of jewelry, curios, and sculpture incorporating the hulls. Bailey and Bailey (1976) stated the nuts were used in rosaries. *Trapa natans* var. *bispinosa* nuts are said to have been used in offerings to the "darker gods," and the nuts are advertised on the Internet as charms to ward off evil (Yronwode 2002). Due to the hulls in shoreline wrack, water chestnut is one of the most asked-about species along the tidal Hudson River, and names such as "devil-nut" are sometimes used. Water chestnut is sold internationally as an aquarium plant and for garden pools (Herklots 1972, Derman 2000), and is used for these purposes in North America although it is considered weedy and troublesome in gardens (Bailey and Bailey 1976).

CONTROL

Legislation

On 1 July, 1949 New York State enacted a law prohibiting transport of water chestnut. Chapter 40, §1, paragraph 170 of the Laws of New York states "No person shall plant, transport, transplant or traffic in plants of the water chestnut or in the seeds or nuts thereof nor in any manner cause the spread or growth of such plants. Any person aiding in any manner in such prohibited acts shall be deemed to have violated this section." In some cases more than 50 years passed before other states such as Maine, Minnesota, North Carolina, New Hampshire, South Carolina, Florida, and Vermont followed suit with similar noxious weed laws that specifically list *Trapa natans* as posing an ecological or economic threat. In those states it is a misdemeanor offense to possess, import, transport, sell, distribute, or cultivate the plant or plant parts except for permitted scientific or educational purposes. Persons found in violation of these restrictions are subject to fines of up to hundreds of dollars. Minnesota regulations are a preventive control measure as the plant has not yet been found in that state. The National Invasive Species Act of 1996 specifically mentions *Trapa natans* as a species of concern, but imposes no restrictions or penalties on actions involving the plant, making its efficacy questionable (USDA 2003).

Existing laws and classifications, however, do not stop dealers of exotic plants from advertising both *T. natans* var. *natans* and *T. natans* var. *bispinosa* seeds in nationally distributed mail-order catalogs and on websites for use in garden ponds and household aquaria (Oregon Exotics 2003). Unregulated sale to the general public is risky due to the potential for establishment in much of North America.

Legislation, education, and removal efforts are often combined. Water chestnut was first detected in Oneida Lake in 1999, and since then a federally funded inter-municipal effort to educate and mobilize the public in control efforts has been in effect. These include the formation of the Central New York Water Chestnut Task Force, hand-pulling workshops, mechanical harvesting, and lakeside educational signs (Central New York Regional Planning and Development Board 2002).

Chemical Control

The herbicide 2,4-dicholorophenoxy acetic acid (2,4-D) was used successfully in the Mohawk River, the Hudson River, and Lake Champlain to reduce dense water chestnut populations (Greeley 1960, Countryman 1978). Only 242 L (8 bushels) were found in all of Lake Champlain in 1967 (Countryman 1978). Although 2,4-D in high concentrations is an effective control for water chestnut, many native wetland plants are also susceptible (Cronk and Fennessy 2001). In 1976 the NYS DEC became concerned about the potentially harmful side effects on fish and aquatic invertebrates; because lesser applications of 2,4-D and alternate herbicides were known to be ineffective and a massive hand-pulling effort was deemed too costly the NYS DEC terminated its water chestnut control program after the 1976 season (Countryman 1978, Kiviat 1993).

Physical Control

Physical control methods are often coupled with chemical control. Water chestnut is an annual; therefore, successful eradication depends on removal of rosettes before fruits mature. This can be accomplished with machines such as underwater cutters and harvesters or by hand-pulling smaller colonies; regardless of removal method, all plant parts must be taken to the shore so they can decompose. Harvested material may be placed to decompose in cribs in the water but local depletion of DO may result from this practice (Countryman 1978). Care must be taken to ensure the removal of the entire plant so damaged or fragmented plants do not continue to mature fruits, and harvesting efforts must outlive any potentially viable seeds in bottom sediments (10 to 12 years) to ensure successful control (Elser 1964). Countryman (1978) recommended that control activities occur before 10 or 15 July when mature fruits may begin to drop.

Physical control methods have been employed with variable success in the Potomac River, Lake Champlain, Chesapeake Bay, the Sudbury River, the Concord River, and the Hudson River. High-speed cutting techniques employed in the Watervliet Reservoir proved very effective in reducing seed production. Madsen (1993) calculated that water chestnut produced 19 seeds/m^2/year in a control area and 1.4 seeds/m^2/year were lost from the seed bank in a treated area. Control was largely successful on the Potomac River but took more than 20 years and several hundred thousand dollars (Martin et al. 1957, Madsen 1993).

Few observations have been reported of native plant establishment following chemical and mechanical control of water chestnut. Species mentioned were water celery, duckweeds (Lemnaceae), and wild-rice (*Zizania aquatica* L.) (Gwathmey 1945; R. L. Bard, pers. comm.). We have found no quantitative studies, however, of vegetation development after water chestnut removal.

Biological Control

Repeated stocking of grass carp (*Ctenopharyngodon idella* [Valenciennes]) has controlled water chestnut, as has a single stocking of 300 to 400 3-year-old carp in a 1 to 1.5 ha area (Krupauer 1971). The diet of grass carp, however, is not restricted to water chestnut and introduction of this foreign fish species must be carefully monitored and managed to avoid detrimental side effects such as loss of rare plant species or escape into other bodies of water.

A pathogenic fungus (*Sclerotium hydrophilum* Sacc.) cultured from a diseased plant in the Watervliet Reservoir has potential for biocontrol. The fungus is capable of killing young rosettes; to be effective, however, fungus populations would have to be artificially increased in the spring during rosette formation (Hall 1982).

Herbivorous insects such as beetles in the genus *Galerucella* (Family Chrysomelidae) provide yet another control possibility. The water-lily leaf beetle is native to North America, commonly grazes water chestnut leaves, and occasionally kills patches of water chestnut in the tidal Hudson River. This insect was investigated as a potential control agent and it was thought the beetle would be effective if its populations were artificially increased in the spring when rosettes are most vulnerable to beetle herbivory. Without augmentation, however, the beetles only chewed ca. 25% of the leaf tissue; because 100% leaf damage is necessary to significantly reduce the number or mass of water chestnut fruits, the water-lily leaf beetle would probably not provide effective control (Hall 1982, Schmidt 1986).

Pemberton (1993, 1995, 1999, 2002) investigated natural enemies of *Trapa* in northeast Asia and western Europe. Countries visited include China, Japan, eastern Russia, South Korea, France, Germany, Italy, Poland, and Switzerland. These surveys were unsuccessful in finding an insect suitable for biological control because the highly damaging insects such as the leaf beetle (singhara beetle) and the *Nymphula* moth species had broad host ranges and the host-specific insects such as the *Nanophyes* and *Bagous* weevils were not very damaging. There are several insects that should be investigated further as potential control agents for water chestnut in warm climates. Weevils include *Bagous tersus* Egorov et Gratshev of Russia, *B. trapae* Prashad of India, *B. vicinus* Hustache and *Nanophyes rufipes* Motschulsky of India. Other beetles include *Galerucella singhara* Lefroy and *Haltica cyanea* Weber of India and *Galerupipla* of Thailand. Moths include *Nymphula gangeticalis* Lederer of India and *N. crisonalis* Walker of Thailand. A fungus which attacks the leaves that should be considered is *Bipolaris tetramera* (McKinney) Shoemaker of India (Pemberton 1995, 1999, 2002).

DISCUSSION

Water chestnut invasion alters the vegetation composition and structure to a variable degree. Water chestnut beds may support significant numbers of invertebrates, fishes, and other animals, yet denser beds exclude most native plants. More important waterfowl foods such as water celery are unable to compete with water chestnut in lower-energy habitats. Denser, larger beds in the Hudson River cause seasonally low dissolved oxygen and impoverished fish communities while supporting abundant aquatic and terrestrial invertebrates.

Natural enemies are believed to regulate populations of many aquatic plants in their native ranges, but this has yet to be demonstrated for water chestnut. Water chestnut forms extensive, dense beds and is even considered a pest in portions of its native range, whereas in many areas it is a component of diverse aquatic floras. In its introduced range in the United States, water chestnut is a nuisance weed with the potential to cover hundreds of ha in some waterbodies. Yet there are some pond, river, and tidal marsh habitats in which the abundance of water chestnut is very restricted. Highly dominant populations of water chestnut appear to be commonly associated with culturally eutrophic, low-energy waters. The possibility that predators, parasites, and competitors such as muskrat, water-lily leaf beetle, fungi, and native aquatic plants play a role in suppressing water chestnut populations in the U.S. requires study.

Water chestnut might be managed as a resource instead of a nuisance in some water bodies. If water chestnut became an economically viable source of food or energy, harvesting could thin or fragment beds while providing an economic incentive to sustain management. Thinning or fragmentation should alleviate oxygen depletion and improve fish habitat while maintaining the functions of water chestnut as habitat or food for many other vertebrates and invertebrates. Economic use of water chestnut, however, could lead to cultivation and protection of the plant rather than its eradication. Increased physical disturbance from harvesting, pesticide application, hydrologic alterations, or fertilization could occur. Contaminant levels and microbiology (pathogens and parasites) of North American water chestnut fruits have not been studied and might limit use for food.

RECOMMENDED RESEARCH

Most of the quantitative data on water chestnut are from the tidal Hudson River and a few localities in the native range. Studies comparing water chestnut in U.S. lakes and nontidal rivers to tidal rivers, and studies comparing water chestnut ecosystems in the introduced and native ranges, would be illuminating. The role of cultural eutrophication and habitat alteration in water chestnut invasion needs study. Few data are available on effects of water chestnut invasion on submersed plant communities and their invertebrate and fish faunas. Fish communities vary in different water chestnut beds and populations are probably dependent on bed size, density, interspersion with other plant communities, and exposure to currents. Importance of water chestnut beds as nursery habitats and the extent to which the resident fishes are prey for piscivorous fishes, reptiles, and birds, have not been thoroughly investigated. Data on density and species composition of fishes in water chestnut compared to alternate plant communities need to be augmented by studies of fish productivity, health, and fitness which may be affected by water chestnut differently than density. Impacts of water chestnut on animals and animals on water chestnut need assessment to enable better management strategies. Mosquitoes and other biting flies in water chestnut beds need study. The ecology of the duckweeds associated with water chestnut beds and the ecology of nut hull wrack and other decomposing plant materials merit investigation. Lastly, there is a need to develop innovative management, including biological control, mechanical alteration of beds to improve habitat for certain species, and uses of harvested plant matter. Educating landowners, managers, and recreationists to recognize and remove water chestnut when new infestations first establish in ponds and estuaries should also be a priority.

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