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Introduction of nonindigenous aquatic vascular plants in southern New England: a historical perspective

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Abstract

Aquatic plants comprise few species worldwide, yet introductions of nonindigenous hydrophytes represent some of the most severe examples of biological invasions. Often innocuous in their indigenous regions, many aquatic plant species have caused extreme ecological and economic consequences when introduced into nonindigenous habitats. Typically, aquatic plant invasions are unnoticed or overlooked until they are perceived as problematic. By then, plants are virtually impossible to eradicate and negative ecological impacts caused by their spread into natural communities are irreparable. We present criteria to facilitate decisions whether a species should be characterized as nonindigenous or invasive. Historical data are used to clarify methods of introduction, avenues and means of dispersal, and extent of invasiveness of the following aquatic plants in southern New England: *Acorus calamus*, *Butomus umbellatus*, *Cabomba caroliniana*, *Callitriche stagnalis*, *Egeria densa*, *Hydrilla verticillata*, *Limnobium spongia*, *Marsilea quadrifolia*, *Myriophyllum aquaticum*, *Myriophyllum heterophyllum*, *Myriophyllum spicatum*, *Najas minor*, *Najas guadalupensis*, *Nasturtium officinale*, *Nymphoides peltata*, *Potamogeton crispus*, *Trapa natans* and *Veronica beccabunga*.

Introduction

Nonindigenous plant introductions have significantly impacted biological communities worldwide. Historical literature gives insight into means of introduction, dispersal patterns/mechanisms, and rapidity with which nonindigenous ranges expand. Such information is useful for evaluating past introductions, and possibly for predicting potential future introductions. Here we review the history of nonindigenous predominantly submersed aquatic plants in southern New England. Many nonindigenous wetland species (e.g. *Iris pseudacorus*, *Lythrum salicaria*) occur in this region, but are not the focus of this study.

We first clarify our use of several terms. *Nonindigenous* species are *those species that did not occur geographically within a particularly defined region prior to some predetermined period*. We arbitrarily circumscribe the southern New England region as the southernmost portions of Vermont and New Hampshire, the southeastern portion of New York State (including Long Island), Connecticut, Massachusetts and Rhode Island. A predetermined time period is also necessary, given that plant migrations are incessant, their communities are dynamic, and it is difficult to conceptualize what any truly 'original' flora might be for a given area. Our reference frame for indigenous species is the period immediately preceding the European settlement of southern New England. Simply, a species is indigenous if it occurred in southern New England prior to 1496 when John Cabot became the first European explorer to set foot in New England (Newby 1982). It is virtually impossible to obtain evidence of nonindigenous species introductions to the northeast prior to that time. 'Norsemen' may have brought certain plants to northeastern North America in the 11th

century (Fernald 1910), but it is doubtful that they introduced any of the aquatic plants discussed here.

Our definition of 'nonindigenous' may be awkward, but it avoids problems dealing with (1) general geographical designations and (2) ancient plant migrations or community changes. The former problem is illustrated by species native to a broadly defined region (e.g. 'eastern North America'), but not native to a specific portion of that area (e.g., 'northeastern North America'). Another problem involves comparisons between the extant flora of a region and past 'fossil' communities. Defining the indigenous flora as the vegetation in place at a specific date clarifies what should be considered as nonindigenous. We are concerned mainly with impacts resulting from plant introductions subsequent to European settlement. Our definition is complicated by introductions of nonindigenous genetic races of species that are otherwise native to an area, which is not an issue for species discussed here. Species whose origin cannot be confidently ascertained can be categorized as 'cryptogenic' (Carlton 1996).

The terms 'weed' and 'invasive' deserve clarification because of their varied usage. *Weeds* are *those plants that interfere with management or appreciation of natural resources*. Essentially, weeds are plants growing where they are perceived as undesirable. Although certain biological characteristics can be associated with different weedy species, there is no universal way to define weeds strictly using biological criteria. An important corollary is that weeds can include nonindigenous or indigenous species. The term 'invasive' is similar but has a different focus. We consider *invasive species* as *nonindigenous species capable of establishing and spreading significantly within natural communities*. Whether an invasive species is perceived as weedy depends on individual assessment. Furthermore, our definition takes into account the explosive growth of native species (e.g., bursts of fireweed, *Epilobium angustifolium*, following fires) without characterizing them as invasive, which seems illogical. *Naturalized* species are *species capable of reproducing and persisting in a nonindigenous region*. A distinction between 'invasive' and 'naturalized' is difficult; however, *all* invasive species are naturalized. *Cultivated* describes *plants grown intentionally in intensively managed habitats*. These can include indigenous species as well as nonindigenous species that may or may not be naturalized.

Countryman (1970) summarized the introduction and spread of *Trapa natans*, *Nymphoides peltata*, *Butomus umbellatus* and *Egeria densa* in New England. Several additional nonindigenous aquatic species have since been recorded from southern New England. This paper expands and updates the summary by Countryman (1970), providing information that should facilitate nonindigenous species management.

Nonindigenous aquatic species in southern New England

As defined above, we assembled a list of nonindigenous aquatic plants in southern New England (Table 1). These species are arranged in three categories: (1) native to southern New England but perceived as nonindigenous, (2) native to North America but nonindigenous to southern New England, and (3) nonindigenous to North America. We acknowledge exclusion of certain species. *Hydrocharis morsus-ranae* (European Frogbit) is a nonindigenous aquatic in northern New England but has not yet been observed in southern New England. Principally wetland species (e.g. *Iris pseudacorus, Lythrum salicaria*) are excluded for brevity. The aquatic *Eichhornia crassipes* and *Pistia stratiotes* may escape from cultivation during the growing season, but are not known to overwinter in southern New England. *Azolla pinnata* was reportedly introduced to Springfield, Massachusetts; however, specimens were later identified as *A. caroliniana*, a North American native of uncertain status in New England.

In Appendix I we review literature, herbarium specimens, personal observations and other records that furnish information on the dispersal, introduction and spread of the species listed in Table 1. Herbarium acronyms follow Holmgren et al. (1990): CONN (University of Connecticut, Storrs, Connecticut); GH (Gray Herbarium, Harvard University, Cambridge, Massachusetts); MASS (University of Massachusetts, Amherst, Massachusetts); NASC (North Adams State College, North Adams, Massachusetts); NEBC (New England Botanical Club, Harvard University, Cambridge, Massachusetts); YU (Yale University, New Haven, Connecticut).

Insights on invasiveness from historical collection data

Nonindigenous aquatic species have persisted in southern new England and their introduction continues (Table 1; Figure 1). The number of nonindigenous

Table 1. Major nonindigenous aquatic plants in southern New England. Within categories, species are listed chronologically by their earliest reliable record for North America ('earliest NA'). Dates for the earliest reliable record in southern New England ('earliest SNE') and the most recent collection in southern New England ('recent SNE') are provided (see Appendix I). References are footnoted. 'Recent SNE' dates were obtained from specimens collected by the authors or available in New England herbaria.

List of species	Earliest NA	Earliest SNE	Recent SNE
Category I: Probably native but known only from recent historical records			
Najus guadalupensis	Native	Native? (1904, Nantucket I.)[a]	1998
Category II: Native to North America but nonindigenous in New England			
Cabomba caroliniana	Native	1920 (Hatfield, MA)[b]	1998
Myriophyllum heterophyllum	Native	1932 (Bridgeport, CT)[c]	1998
Limnobium spongia	Native	1998 (Mansfield, CT)[d]	1998
Category III: Nonindigenous to North America			
Acorus calamus	<1762*	<1893*	1998
Nasturtium officinale	<1826[e,*]	1831 (New Haven, CT)[f]	1998
Potamogeton crispus	1859 (Wilmington, DE)[g]	1880 (Middlesex Co., MA)[g]	1998
Marsilea quadrifolia	1860 (Bantam Lake, CT)[h]	1860 (Bantam Lake, CT)[h]	1998
Callitriche stagnalis	1861 (New York)[i]	1911 (Barnstable Co., MA)[i]	1998
Veronica beccabunga	1876 (Hudson Co., NJ)[j]	1879 (King's Co., NY)[j]	1998
Trapa natans	<1879 (Middlesex Co., MA)[k]	<1879 (Middlesex Co., MA)[k]	1998
Nymphoides peltata	1882 (Winchester, MA)[l]	1882 (Winchester, MA)[l]	1961
Egeria densa	1893 (Long Island, NY)[m]	1893 (Long Island, NY)[m]	1998
Myriophyllum aquaticum	1890 (Haddonfield, NJ)[n]	1929 (SE New York)[n]	1996
Butomus umbellatus	1905 (St. Lawrence R., QUE)[o]	1943 (New Haven, CT)[p]	1994
Najas minor	1934 (Hudson R., NY)[q]	1974 (Berkshire Co., MA)[r]	1998
Myriophyllum spicatum	1942 (Washington, DC)[s]	1971 (Berkshire Co., MA)[t]	1998
Hydrilla verticillata	1960 (E. Florida)[u]	1989 (Mystic, CT)[v]	1998

[a]Bicknell 1908; [b]Manning 1937; [c]specimen (CONN); [d]specimen (CONN); [e]Torrey 1826; [f]Ives et al. 1831; [g]Stuckey 1979; [h]Gray 1860; [i]Philbrick et al. 1998; [j]Les and Stuckey 1985; [k]Davenport 1879; [l]Stuckey 1973; [m]Weatherby 1932; [n]Couch and Nelson 1985b; [o]Knowlton 1923; [p]Countryman 1970; [q]Clausen 1936; [r]Weatherbee 1996; [s]Couch and Nelson 1985a; [t]specimen (NASC); [u]Blackburn et al. 1969; [v]Les et al. 1997; *uncertain (see text).

aquatic plants has increased steadily in the region over the past 150 years, with no indication of abatement. The relative impacts of these species on natural communities is difficult to quantify. The pace at which species establish and spread throughout an area is one indication of invasiveness. Herbarium specimen data are the only useful source of information for this assessment. Although plant collections can be incomplete, biased, or episodic, collection patterns of nonindigenous aquatic plants can provide a relative estimate of their rate and direction of spread.

We compiled herbarium specimen data for seven nonindigenous species (Couch and Nelson 1985a, b; Les and Stuckey 1985; Philbrick et al. 1998; Stuckey 1973; Stuckey 1979, 1980) where we were able to determine the number of localities reported at ten year intervals since their first year of collection. All North American occurrences were considered. Although purple loosestrife is not discussed above, it is included as a reference frame because it is regarded universally as highly invasive in its nonindigenous range (Thompson et al. 1987). This feature facilitates comparisons with other species; i.e., whether the rate of spread is more or less extreme than that of purple loosestrife.

Results varied among the species considered (Figure 2). The curve for purple loosestrife was moderate compared to other species. *Myriophyllum spicatum* records accumulated more rapidly, showing a steep collection curve. The curve for *M. aquaticum* approximated that of purple loosestrife. The curve for *Potamogeton crispus* was similar to, but slightly steeper than purple loosestrife. Records of *Nymphoides peltata*, *Callitriche stagnalis* and *Veronica beccabunga* have appeared more slowly (Figure 2). These results generally agree with relative 'ranks' of these species as management concerns. North American aquatic plant managers reported the most problems for *M. spicatum*, with purple loosestrife and *P. crispus* respectively in descending order of concern (Bartodziej and Ludlow 1998). *Nymphoides peltata*, *C. stagnalis*

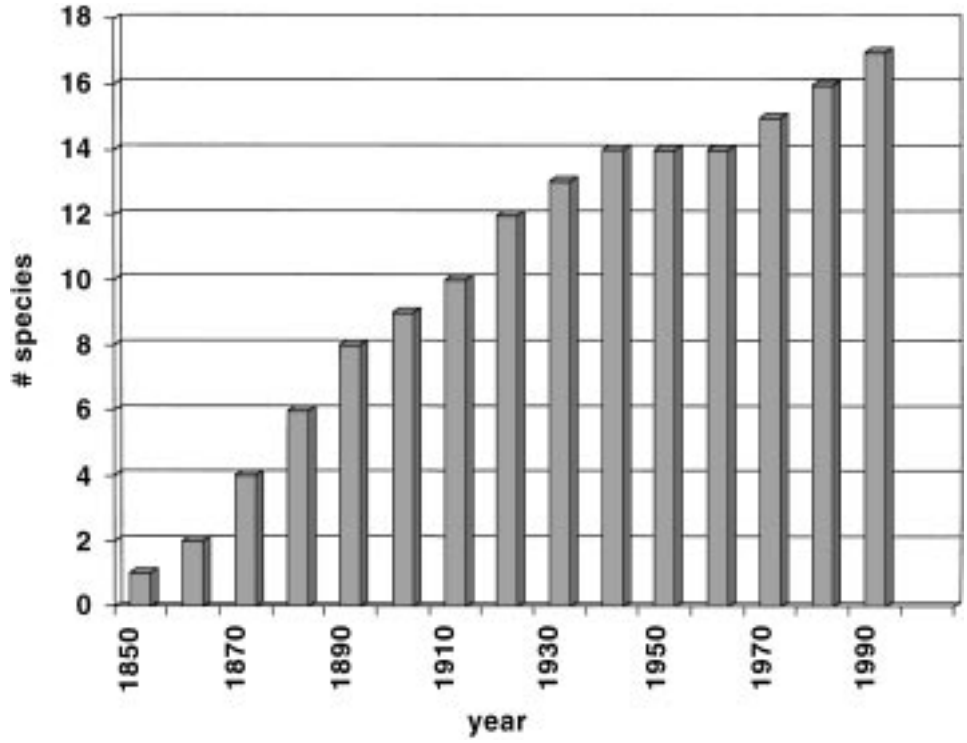

Figure 1. Increase in nonindigenous aquatic plant species in southern New England from the mid 19th century to present (data from Table 1). Nearly all species have persisted in the region and there is no indication that the introduction of other nonindigenous aquatics will diminish.

and *V. beccabunga* were not included among the 15 problem species reported in the USA.

Myriophyllum aquaticum is anomalous. It is not frequently reported as a problem (Bartodziej and Ludlow 1998), yet its specimen accumulation curve is steeper than that of purple loosestrife (Figure 2). *Myriophyllum aquaticum* has expanded its range mainly in the southern United States (Couch and Nelson 1985b) and may be relatively innocuous in the northeast due to a smaller number of occurrences. It is reportedly invasive in the south, but also provides refuge and habitat for fish and invertebrates (Hoyer et al. 1996). This species is hardy in southern New England and has caused serious local infestations.

Specimen collection curves provide a retrospective appraisal of nonindigenous species based solely on their distributional history. Although a correlation exists between steep collection curves and invasiveness, other factors must be considered when evaluating threats posed by a species. Some species with steep curves (e.g., *M. aquaticum*) may not be viewed as particularly threatening in some areas; however, they can cause serious problems elsewhere. In all cases where they are hardy, such species should be viewed as potentially invasive. Species with flatter collection curves may present lesser threats, but could be in an early phase of more explosive growth.

We similarly evaluated specimen records of *Cabomba* in southern New England. Considering only those records from southern New England, it was inappropriate to include *Cabomba* with the species analyzed in Figure 2. New *Cabomba* records have accumulated steadily in southern New England (Figure 3), indicating its continued spread in the region during the past 70 years since its first detection.

Nonindigenous aquatic plants and aquatic weeds

A distinction must be made between nonindigenous aquatic plants and aquatic weeds. Cook (1990) gives an excellent example of how difficult it is to characterize 'weedy' aquatic species, pointing out that *Heteranthera reniformis* is considered to be endangered

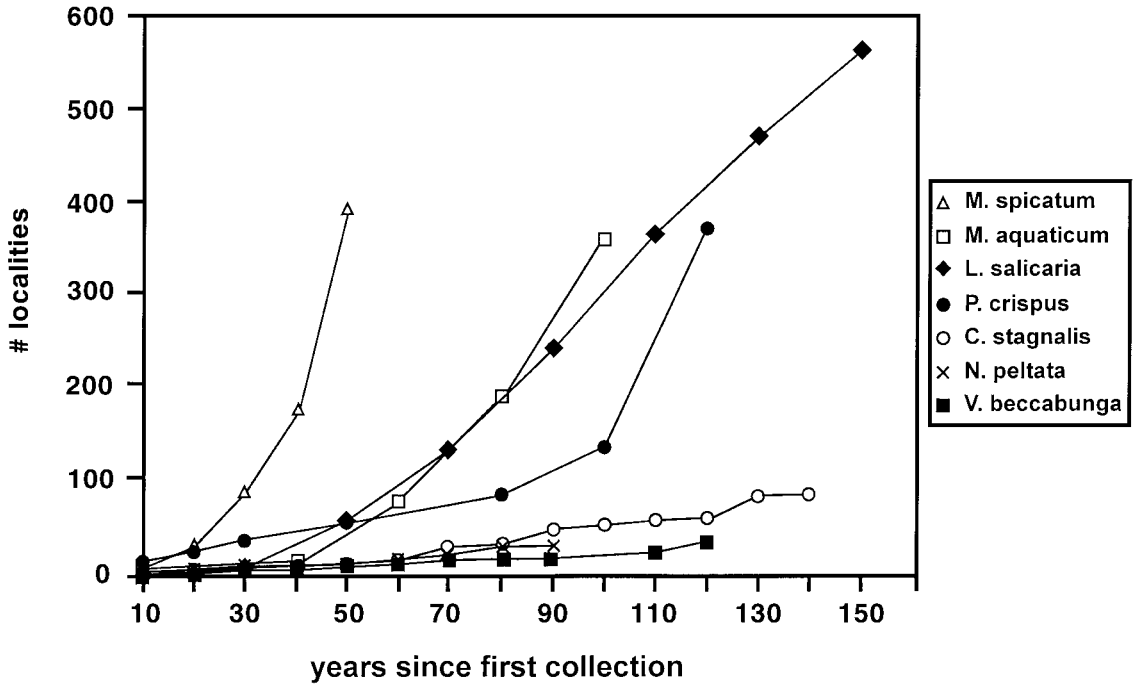

Figure 2. Collection curves for seven nonindigenous aquatic plants in southern New England. Curves were produced by plotting the number of specimen collections made in 10-year intervals relative to the time of first observance. Species characterized by steeply rising collection curves correlate with those species that are most often the focus of aquatic plant control programs; whereas, those with flatter collection curves are rarely reported as nuisance species (see text).

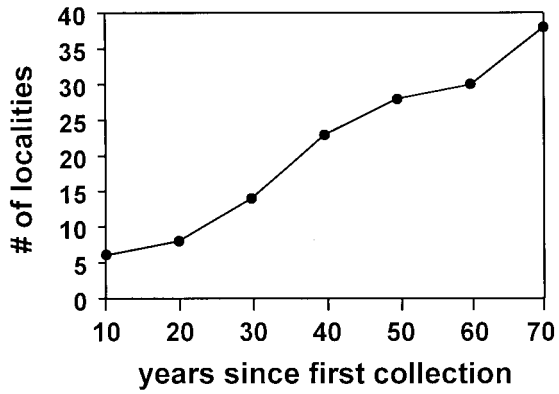

Figure 3. Collection curve for *Cabomba caroliniana* in southern New England (data from Figure 4) indicates continued spread in the region with no sign of abatement. *Cabomba* is indigenous to the southeastern United States and was first found in southern New England in 1920.

in Connecticut, yet is 'the worst weed today' in the northern Italian rice fields. He also emphasized that *Trapa natans*, a noxious aquatic weed in North America, is extirpated or endangered in much of Europe. We note that the native North American water lotus (*Nelumbo lutea*), is protected in the northern portion of its range (e.g., Michigan), relatively unobtrusive in the central portion of the United States, but actively managed by herbicides in the southeastern United States, where it is considered to be weedy.

Steward (1990) listed 10 major aquatic New England weeds including *Myriophyllum* spp., *Ceratophyllum demersum*, *Nuphar*, *Utricularia*, *Potamogeton* spp., *Cabomba caroliniana*, *Trapa natans*, *Elodea canadensis*, *Nymphaea* spp. and *Brasenia schreberi*. Six genera (*Brasenia*, *Ceratophyllum*, *Elodea*, *Nymphaea*, *Nuphar*, *Utricularia*) comprise species unequivocally native to the region and two genera contain species native to North America outside of New England (*Cabomba caroliniana*, *Myriophyllum heterophyllum*). Two genera (*Myriophyllum*, *Potamogeton*) have problematic taxa comprising both native and nonindigenous species. Two milfoils (*Myriophyllum aquaticum*, *M. spicatum*) and *Potamogeton crispus* are nonindigenous to North America; whereas, native

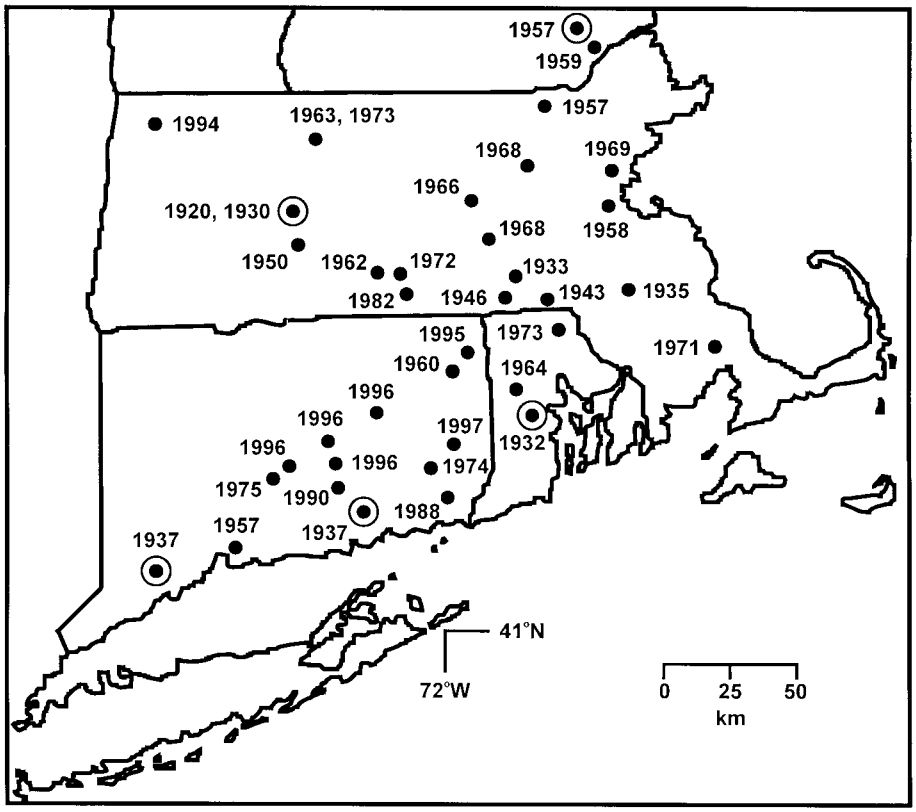

Figure 4. Distribution of *Cabomba caroliniana* in southern New England derived from specimens observed at regional herbaria (collection dates shown). Double circles indicate the oldest known specimen record(s) for that state. The distribution of *Cabomba* in Connecticut is similar to that of *Myriophyllum heterophyllum* (see Figure 5).

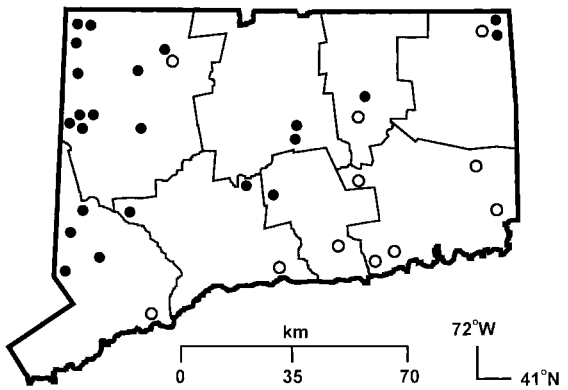

Figure 5. Distribution of *Myriophyllum spicatum* (solid circles) and *Myriophyllum heterophyllum* (open circles) in Connecticut from herbarium specimens and reliable reports. The Connecticut distributions of these species do not overlap significantly.

species such as *Potamogeton amplifolius*, *P. nodosus*, *P. robbinsii*, *P. richardsonii*, *P. pectinatus* are routinely controlled (Steward 1990). *Trapa* is the only genus on this list that is exclusively nonindigenous to North America.

It is noteworthy that more native species are targeted for control in New England than are nonindigenous species, although the most severe problems tend to be associated with nonindigenous species such as *Myriophyllum spicatum*. The native *Elodea canadensis* has long been a nuisance in Connecticut (Graves et al. 1910) and the native duckweed, *Lemna minor*, has been categorized as an 'aggressive weed' in portions of New England (Eaton 1947). However, many nonindigenous aquatic species such as *Acorus calamus*, *Butomus umbellatus*, *Callitriche stagnalis*, *Egeria densa*, *Myriophyllum aquaticum*, *Nasturtium officinale* and *Nymphoides peltata* are not considered to be problematic in southern New England. Furthermore, several of these species (*Callitriche stagnalis*, *Nymphoides*

peltata, *Myriophyllum aquaticum*) are not management problems in other parts of the country (Bartodziej and Ludlow 1998), and the former two species have not spread rapidly (see above).

This paradox illustrates several points. First, it confirms that not all nonindigenous species are destined to be weeds, which is consistent with results of aquatic plant management surveys (Bartodziej and Ludlow 1998). Secondly, criteria used to perceive weedy species varies considerably from the general public (e.g. lakeshore property owners) to biologists. Landowners tend to target high profile infestations such as overgrowth of vegetation in public recreational lakes, caring little whether the species are native or not. Biologists are more likely to characterize a species as 'weedy' if it is viewed as causing even a subtle disruption to the ecology of a natural community.

Aquatic plant cultivation: a major source of introduction

Escape from cultivation is responsible for most introductions of nonindigenous aquatic plants in southern New England (Table 2). Escapes are implicated in 76% of the cases, with only two species (*Limnobium*, *Veronica*; 12% of total) the result of natural dispersal or accidental introductions (e.g. ballast disposal). Two cases (*Najas minor*, *Callitriche stagnalis*; 12% of total) are uncertain, but may also be due to escapes from cultivation. As many as 88% of the invasive aquatic plants in southern New England probably first entered the country as cultivated plants.

Many nonindigenous New England aquatics (*Acorus calamus*, *Butomus umbellatus*, *Cabomba caroliniana*, *Callitriche*, *Egeria densa*, *Limnobium spongia*, *Myriophyllum aquaticum*, *M. heterophyllum*, *M. spicatum*, *Nymphoides peltata*, *Potamogeton crispus*, *Trapa natans*) have long been in cultivation (Bissett 1907; Samuel 1894; Tricker 1897). Although water hyacinth (*Eichhornia crassipes*) is not hardy in the north, a Pequonnock River record from Bridgeport, Connecticut in 1893 (Graves et al. 1910) demonstrates that escapes of cultivated, ornamental water plants had occurred prior to 1900. Many authors warned that *C. caroliniana*, *E. densa*, *E. crassipes*, *M. aquaticum*, *N. peltata*, *P. crispus* and *Trapa* could become invasive (Beal 1900; Bissett 1907; Bromley 1945; Brown 1879; Conard and Hus 1909; Eaton 1974; Knowlton 1940; Martin and Uhler 1939; Tricker 1897), but they were not heeded. Cleary, the best safeguard against new introductions is to eliminate potentially invasive species from cultivation.

Several aquatic plants were transplanted intentionally as waterfowl foods. McAtee (1917) reported 64 successful transplants of wild rice (*Zizania aquatica*) with six stations west of its native range; 20 successful transplants of wild celery (*Vallisneria americana*) were noted, with seven stations outside its native range. These reports document the intentional propagation

Table 2. Presumed means of original introduction and post-introduction dispersal for nonindegeous aquatic plants in southern New England (see text for explanation).

	Original means of introduction	Post-introduction dispersal
Acorus calamus	Escaped from cultivation	Intentional plantings; vegetative spread (rhizomes)
Butomus umbellatus	Escaped from cultivation	Intentional plantings; ballast; seeds and vegetative propagules
Cabomba caroliniana	Escaped from cultivation	Escaped from cultivation; seeds and vegetative propagules
Callitriche stagnalis	Uncertain (accidental/escaped)	Seeds
Egeria densa	Escaped from cultivation	Escaped from cultivation; vegetative propagules
Hydrilla verticillata	Escaped from cultivation	Escaped from cultivation; vegetative propagules
Limnobium spongia	Natural (indigenous)	Seeds
Marsilea quadrifolia	Escaped from cultivation	Escaped from cultivation; sporocarps
Myriophyllum aquaticum	Escaped from cultivation	Escaped from cultivation; vegetative propagules
M. heterophyllum	Escaped from cultivation	Vegetative propagules
M. spicatum	Escaped from cultivation	Vegetative propagules
Najas minor	Uncertain (accidental/escaped)	Seeds
Nasturtium officinale	Escaped from cultivation	Escaped from cultivation; seeds and vegetative propagules
Nymphoides peltata	Escaped from cultivation	Escaped from cultivation; seeds
Potamogeton crispus	Escaped from cultivation	Vegetative propagules
Trapa natans	Escaped from cultivation	Seeds
Veronica beccabunga	Accidental (ballast dispersal)	Escaped from cultivation; seeds and vegetative fragments

of aquatic species beyond their native ranges and demonstrate their relative ease of establishment in nonindigenous habitats.

Summary

The nonindigenous aquatic flora of southern New England consists of species that are perceived both as desirable cultivated ornamentals and as invasive. Four species are indigenous to North America, two species are native to South America, and the remaining 12 are native to Europe or Eurasia. Although dispersal in ship's ballast or other unintentional methods for their introduction to the region are often suggested in the literature, we find that most species were popular 19th century water garden or aquarium plants which arrived to this region by human intervention. However, once established, their dispersal has involved both natural and human agents.

Some nonindigenous aquatic species are widespread and well-established in southern New England, but others are known only from a few occurrences. All pose potential ecological threats because of their unpredictable spread and establishment in natural communities. Unless cultivation of invasive aquatic plants is curtailed, their introduction to southern New England (and elsewhere) will inevitably continue.

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Appendix I: historical overview of major nonindigenous aquatic plants in southern New England

Acorus calamus *(sweet flag)*

The oldest account of *Acorus* in New England was by Josselyn (1672) who described it from southeastern Maine in 1638–1663 as one 'Of such plants as are proper to the country.' American plants resembled the familiar sterile European hybrid, but were 'not barren' (Josselyn 1672). Originally, North America was believed to contain a single species, *A. calamus*, which is listed in some of the earliest floras of the United States (Gronovious 1762; Walter 1788; Torrey 1826; Eaton 1833) and New England (Bigelow 1840). *Acorus* was described as 'naturalized' in the southeastern United States (Elliot 1817) but as 'truly indigenous northward' (Gray 1857). Wood and Bache (1854) noted that American plants of *A. calamus* differed slightly from European plants and regarded them as indigenous.

American botanists assumed that sterile North American plants of *Acorus calamus* (a native of Asia) were introduced as they had been in Europe (Buell 1935). After finding fertile Minnesota populations and fruiting herbarium specimens from New England, Buell (1935) concluded that *A. calamus* was native to North America, although some sterile plants possibly represented introductions. Jervis and Buell (1964) later acknowledged that except for one New Jersey population, viable seed was unknown in any *Acorus* population 'east of the Appalachians' and that some sterile clones must have been introduced. *Acorus calamus* is assumed to have been introduced early in North America's settlement (Bogner and Mayo 1998; Merrill 1954). Its introduction was associated with many uses including flooring (Tuckerman 1865), food and medicine (Creevey 1897; Graves et al. 1910).

Discrepancies in early accounts likely reflect the existence of two *Acorus* species in North America (Packer and Ringius 1984). The native *A. americanus* (a fertile diploid) is probably the fertile taxon observed by Buell and Josselyn rather than *A. calamus*, a sterile triploid (Löve and Löve 1957). The difficult distinction of diploid *A. americanus* and triploid *A. calamus* from either herbarium material or published accounts, makes it difficult to approximate the latter's time of introduction into eastern North America, as infertile material could represent either species. The CONN herbarium contains a mature, flowering, but sterile specimen, collected from Rhode Island on July 30, 1893, that is likely to be *A. calamus*. However, many *Acorus* specimens are collected in May–June when it is too early to determine whether they are sterile or simply immature. Sterile *Acorus* is not readily discernable in the field from similar species such as *Iris pseudacorus* (hence its specific epithet) and *Typha* spp., and may go unnoticed for years following an introduction.

Pollen-sterile (presumably triploid) specimens of *Acorus calamus* from Canada date back to 1855 (Packer and Ringius 1984). Because the native range of *A. americanus* did not extend south of New Jersey (Jervis and Buell 1964), early reports of *A. calamus* from the southeastern United States (Walter 1788; Elliot 1817) are probably accurate, placing its introduction prior to the 19th century. The first edition of Flora Virginica (Gronovius 1739) did not mention *A. calamus*, whereas the second edition (Gronovius 1762) did. Its introduction to Virginia may have occurred during this 23-year period.

Acorus calamus is not often perceived as weedy, but it competes with more productive waterfowl food plants (Martin and Uhler 1939). A better assessment of its distribution and invasiveness awaits more sophisticated means of species identification.

Butomus umbellatus *(flowering rush)*

The introduction of *Butomus* in North America is estimated as 'circa 1897' (Countryman 1970). It was first discovered at Laprairie, Quebec in 1905 (Core 1941; Knowlton 1923; Nash 1909). By the 1950s, *Butomus* was so prevalent as to represent the dominant species

of a distinct community type in southern Quebec (Dansereau 1958; Knowlton 1930a). The first reports of *Butomus* in the United States were from plants found along the south shore of Lake Champlain in 1929 (Knowlton 1930b; Muenscher 1930). Countryman (1970) located a herbarium specimen from the same locality collected in 1928.

The first record of *Butomus* in southern New England is from flowering specimens collected in 1943 at the New Haven, CT airport (letter from J.J. Neale to E.H. Eames, CONN archives). Neale concluded that *Butomus* originated there from discarded bouquets or disposed packing materials, convinced that it was introduced to the site by people. Countryman (1970) assumed that the *Butomus* plants died out, because they had '. . . never again been reported or collected from Connecticut.' However, *Butomus* specimens later materialized at two different localities near Hartford, CT in 1978 (specimen at NEBC) and 1992 (K. Metzler and A. Damman, personal communication).

It is difficult to elucidate the earliest records of *Butomus*, because sterile material (which superficially resembles *Sparganium*) could easily be overlooked. The 1978 Connecticut record was discovered in a flowering population. The 1992 record was obtained from a vegetative population, when an intensive research investigation of the site was underway. At that time, plants were confined to an approximately 1 m^2 area (A. Damman, personal communication) which doubled in size within a year when the site was revisited (Mehrhoff, personal observation). Plants propagated from this population failed to flower (Mehrhoff, personal observation). *Butomus* has not yet been reported from Massachusetts, Rhode Island, or other parts of southern New England (Crow and Hellquist 1982).

We believe that *Butomus* originally escaped from water gardens where it is cultivated for its attractive flowers (Joyce 1990). *Butomus* was promoted for water gardening nearly a decade before it was first observed as an escape in the wild (Bissett 1907; Tricker 1897). Catling and Porebski (1995) described a pond near Ottawa, Canada that, by intentional introductions, contained 'well established populations of alien aquatics for many years' including *Nymphoides peltata* and *Butomus umbellatus* which was 'established there in 1906.' This record places cultivated *Butomus* plants only 190 km west of its first known occurrence in North America (Laprairie, Quebec) which was discovered a year earlier.

Ballast disposal may have facilitated the movement of *Butomus* along the St. Lawrence River (Countryman 1970), but sexual and vegetative propagules are dispersed naturally (Stuckey 1968). Seeds and corms make it 'well adapted' for the rapid spread observed after its initial introduction (Knowlton 1930a; Muenscher 1930). *Butomus* seeds retain 68% viability after five years of coldwater storage (Muenscher 1944). The corms are consumed in abundance by green-winged teal (Martin and Uhler 1939).

Introduction of *Butomus* into the Great Lakes region might have originated 'by seeds purchased from Toledo' (Gaiser 1949), demonstrating that nurseries were distributing *Butomus* at that time. *Butomus* plants introduced intentionally by W.C. Muenscher to Cayuga Lake, NY in 1930 and to Cortland Co., NY in 1940 spread by as much as 5 km within a decade (Gaiser 1949). *Butomus* was possibly distributed as an effort to propagate waterfowl food plants (Martin and Uhler 1939). Anderson et al. (1974) concluded that at least two separate introductions of *Butomus* have occurred in North America with plants in the St. Lawrence region more similar morphologically to Asian plants and those from the Great Lakes region resembling European plants.

Cabomba caroliniana *(fanwort)*

Cabomba caroliniana is native to North America, but its presettlement distribution along the east coast did not extend northward of Virginia (Chapman 1887; Fassett 1953). In New England, *Cabomba caroliniana* was first observed at Hatfield, MA (Manning 1937). The earliest specimens from this site were collected in 1930, but plants were observed there since 1920 (Manning 1937). One specimen from this locality (*A.S. Pease*, 26 September, 1930; MASS) was originally misidentified as *Ranunculus aquatilis*. *Cabomba* and *Ranunculus* are often confused, and searches of *Ranunculus* collections may disclose other *Cabomba* records. *Cabomba* has occurred in eastern Massachusetts (Uxbridge) since at least 1933 and in northeastern Massachusetts (Andover) and southeastern New Hampshire (Derry) before 1956 (Harris 1958; Hodgdon 1959). The Andover site was botanized thoroughly in 1903 by A. Pease who did not observe *Cabomba*; thus its introduction must have occurred there between 1903 and 1957 (Harris 1958). *Cabomba* was discovered recently in northern Berkshire Co., MA (Hellquist 1997). It has been collected in Connecticut since 1937 (Gates 1958) and is now common throughout the southern and eastern part of the state (Figure 4). *Cabomba* was first collected from the Hudson River basin (Woodstock, Ulster Co., NY) in 1955 (Mills et al. 1997), and subsequently at other sites in southeastern New York and eastern Long Island (Ogden 1974).

Cabomba has been invasive in southern New England since its early introduction. It was 'very abundant' at Hatfield, MA, with stems 'over five feet long' (Manning 1937). It also grew profusely in central/eastern Massachusetts (Blackstone River, Worcester Co.; Uxbridge; Fosters Pond, Andover; Muddy River, Boston; Uxbridge), with some stems exceeding 2 m in length (Gates 1958; Harris 1958). *Cabomba* was described as 'very abundant' in Rodgers Pond, Middlesex Co., CT (Gates 1958). Its 'explosive' growth in New Hampshire was said to be 'frightening' and prompted a State Legislative bill directed at its control (Hodgdon 1959).

Cabomba plants overwinter vegetatively in Massachusetts where viable green shoots have been collected beneath the ice in January (Burk et al. 1976). *Cabomba* flowers and fruits infrequently and irregularly (Gates 1958; Burk et al. 1976) and the dispersal role of its seeds is uncertain. It is not among food items preferred by waterfowl (Martin and Uhler 1939), but its foliage and seeds are eaten by wood, mallard and ruddy ducks (McAtee 1939). Although transport of seeds or fragments by waterfowl cannot be ruled out, the low level and irregularity of flowering, together with its limited use by waterfowl, indicate more effective means of dispersal.

Humans surely are the major agents of introduction and dispersal for *Cabomba* in southern New England. *Cabomba* has been marketed since the early days of the aquarium plant trade and has been widely scattered by discarded plants (Weldon et al. 1973). Within 60 years of its discovery, *Cabomba caroliniana* was recommended for use in aquaria and water gardens (Samuel 1894; Tricker 1897; Martin and Uhler 1939). Beal (1900) purchased and planted specimens of *Cabomba* in a Michigan pond around 1890. Bissett (1907) described *Cabomba* as a 'desirable water plant' but believed that it was not hardy north of New Jersey. Innes (1917) remarked that 'Enormous quantities (of *Cabomba*) are gathered from ponds, some of them purposely planted, from Maryland to North Carolina.' Samuel (1894) noted that *Cabomba* had been 'transplanted to the District of Columbia.' Apparently, *Cabomba* was associated with fish culture in the Washington, DC area (Fowler 1936; McAtee 1939). Despite its invasiveness, *C. caroliniana* remains available from major water

plant distributors (e.g., Carolina Biological Supply Co. 1998, Tricker 1998). Repeated, multiple introductions in southern New England are indicated by the haphazard collection pattern observed in the region (Figure 4).

The spread of *Cabomba* in New Hampshire was facilitated by stem fragments cut by motor boats (Hodgdon 1959). We observe that *Cabomba* fragments abound in lakes used heavily by motor boats in Massachusetts and Connecticut. Typically, *Cabomba* is widely dispersed within such lakes. Its long, trailing stems easily become entwined on boat trailers which facilitates its dispersal between lakes.

Cabomba ideally illustrates problems with species that become invasive peripheral to their native range. First, there must be criteria to determine whether a species should be considered indigenous or non-indigenous to a given region. Herbarium records may approximate dates of first occurrence in an area, but often do not provide insight into their means of introduction. Dispersal by natural agents (e.g. waterfowl) may indicate the continuation of post-glacial migration. In such cases, it would be difficult to argue that a species was not naturally expanding its 'native' range. However, documentation of human mediated dispersal (e.g., aquarium disposal) would indicate that such populations were nonindigenous. Yet, in many instances, the means of dispersal can only be inferred and not documented conclusively. The use of a specific reference date to determine whether a species is indigenous avoids this complication.

Callitriche stagnalis *(water starwort)*

Philbrick et al. (1998) discovered New York specimens of *Callitriche stagnalis* dating back to 1861. The first New England occurrence is from Barnstable Co., MA in 1911 (Philbrick et al. 1998). Svenson (1932) reported other records of *C. stagnalis* from Cape Cod collected in 1914 and 1928. The species spread to New Jersey before 1891, to Maryland by 1915 and to Pennsylvania by the early 1920s (Fassett 1951; Svenson 1932). Several early records of *C. stagnalis* are from localities as distant as Oregon (in 1871) and Montana (in 1898) (Fassett 1951; Philbrick et al. 1998).

The means of introduction for *Callitriche stagnalis* remains uncertain. Because many early records occurred in port cities, Philbrick et al. (1998) attributed its introduction to shipping and considered ballast disposal as a possible factor. However, 'landlocked' localities such as those in Montana, Georgia and Wisconsin are difficult to explain via shipping patterns. The burgeoning aquarium plant industry may have played a role in its introduction. *Callitriche* had become a popular aquarium plant before the turn of the century (Samuel 1894; Tricker 1897). Although the species sold in the aquarium trade was usually listed as *C. verna*, a confident distinction between *C. verna* and *C. stagnalis* would have been difficult due to the poor taxonomic understanding of the genus in the 19th century (C.T. Philbrick, personal communication). Disposal of aquarium plants would account for the sporadic distribution pattern observed in the early history of this species in North America.

Callitriche species are mainly annuals with abundant seed (Fernald 1932). Shoots of *C. stagnalis* are cold tolerant and overwinter on Long Island and in southwestern Connecticut (Philbrick et al. 1998, Svenson 1932). Locally, *C. stagnalis* probably disperses by seeds and vegetative fragments (Philbrick et al. 1998). *Callitriche stagnalis* grows luxuriantly in lotic waters, but does not fruit in such conditions (Cook 1973; Svenson 1932). Fruiting is restricted to plants growing in quiet waters or on mudflats (Svenson 1932). Yet, seed production is prolific in *C. stagnalis* (nearly 100%) and its flowering period extends from April to November (Philbrick et al. 1998).

Callitriche is not mentioned in any major waterfowl food plant references. The lack of an effective seed dispersal agent may explain why the distribution of *C. stagnalis* is concentrated around sites of introduction. *Callitriche stagnalis* is widely distributed in North America, but its spread has been slow-paced (Figure 2). Most specimens have been collected along the central east coast or Pacific Northwest regions of North America where, in the latter region, the species exhibited its most rapid dispersion (Philbrick et al. 1998). *Callitriche stagnalis* is scattered throughout the remainder of the continent. Philbrick et al. (1998) suggested that seed transport in mud attached to motor vehicles might have hastened the spread of *C. stagnalis* along the west coast.

In northern Italian rice fields, *Callitriche stagnalis* occurs with other 'ecological specialists' that must withstand successive draining and plowing of the fields to persist (Cook 1973). Although *Callitriche* species are not usually thought of as weedy, the dense clonal growth of *C. stagnalis* can impact native species (Philbrick et al. 1998).

Egeria densa *(Egeria)*

Egeria densa was first collected in North America (and southern New England as considered here) in 1893 from Long Island, NY, where it was not expected to persist (Weatherby 1932). However, Clausen later reported *Egeria* as naturalized in the Peconic River in eastern Long Island (Knowlton 1940). Knowlton (1940) discovered an invasive population of *Egeria* in Abington, MA which persisted even after the pond was drained. The pond was again drained to control *Egeria* in 1968 (Countryman 1970). Stations were later discovered in Essex and Norfolk counties, MA and in Windham Co., VT (Crow and Hellquist 1982; Seymour 1969). *Egeria* was mistakenly reported from Connecticut in 1989, due to a misidentified specimen of *Hydrilla* (see below). The first authentic Connecticut collection of *Egeria* was made in 1992 at Westport, where it was 'Introduced by a Mr. Frank Boylan' (*Aarrastad 92-008*, CONN). Subsequent Connecticut collections were made at Darien in 1996 and East Haddam in 1998 (specimens at CONN). The persistence of *Egeria* in Massachusetts for more than 30 years, its resistance to control measures, and its continued spread in New England duly warn of the threat posed by this invasive species.

By all indications, *Egeria densa* was introduced to North America as an escape from aquaria and water gardens where it was cultivated for decades (Bissett 1907; Muenscher 1944). Its widespread distribution is probably due to the fact that it is a 'favorite aquarium plant and as such is sold everywhere' (Weldon et al. 1973). Only staminate plants occur in North America where reproduction is strictly by vegetative fragments (Weldon et al. 1973). *Egeria* may have spread slowly in southern New England due to its lack of seed production. However, recreational use of infested lakes could accelerate its dispersal by inadvertent transport of fragments on boating equipment. *Egeria* is the 'elodea' typically used in biology teaching labs. Plants should be destroyed after use in experiments, and never cultivated outdoors.

In the northeast, *Egeria* remains a popular submersed species, available from aquarium and water garden suppliers under an assortment of names including '*Anacharis canadensis gigantea*' (Bissett 1907; McAtee 1939), *Elodea canadensis gigantea* (Weatherby 1932), and even *Elodea canadensis* (Tricker 1998). The nomenclatural disguise of *Egeria* can mislead consumers who may think they

have purchased a native species for their pond or aquarium rather than an invasive, nonindigenous species. *Egeria* definitely is hardy in southern New England and cannot be cultivated without risk of escape.

It is inevitable that additional *Egeria* infestations will appear in New England. Because we have seen *Egeria* for sale in pet stores and water garden shops throughout the region, it is surprising that so few populations of *Egeria* occur in the northeast (Crow and Hellquist 1982). Perhaps, many *Egeria* populations remain undetected because of its superficial similarity to the native *Elodea*.

Egeria seriously threatens native aquatic plant communities. The senior author has observed invasive *Egeria* populations in Oregon where, in one instance, it infested portions of Siltcoos Lake (*Les 420*, CONN) where a rare species (*Ceratophyllum echinatum*) occurred. The scarcity of *C. echinatum* at that site is due, at least in part, to the spread of *Egeria*. *Egeria* was introduced to Japan about 1940 as an escape from plant physiology experiments (Kadono et al. 1997). Its growth in Japan is described as 'explosive' and the species now dominates many aquatic communities.

Hydrilla verticillata *(Hydrilla)*

Hydrilla verticillata was first discovered in North America near Miami, Florida in 1960 (Blackburn et al. 1969). It was introduced to the United States aquarium trade in the 1950s under the names 'star vine' and 'oxygen plants' (Sutton 1991). Escaping from cultivation, *Hydrilla* spread rapidly throughout Florida, eventually occupying 16 states, the District of Columbia and Mexico. Two 'biotypes' have been identified in the USA; a female strain and a monoecious strain (Steward et al. 1984). Plants originally introduced to Florida comprised entirely the female strain and reproduce vegetatively.

In 1982, monoecious *Hydrilla* plants were discovered at Kenilworth Aquatic Gardens, Washington, DC (Steward et al. 1984). Monoecious *Hydrilla* was also found at Lilypons aquatic nursery in nearby Maryland (Steward et al. 1984) which exchanged material with Kenilworth (Kenilworth staff, personal communication). The monoecious plants indicate at least a second *Hydrilla* introduction into North America and they may have occurred at Kenilworth for decades. *Hydrilla* plants were spread inadvertently throughout the Washington, DC area when they were mistaken for *Elodea* and used in experimental plantings in the Potomac River in 1980 (Steward et al. 1984).

Hydrilla was first documented in New England from a 1989 collection made in Mystic, CT, originally misidentified as *Egeria* (Les et al. 1997). Although the Mystic locality is within several hundred kilometers of monoecious *Hydrilla* localities in Delaware, DNA 'fingerprinting' indicated that the Connecticut plants were dioecious (Les et al. 1997). Because the Mystic *Hydrilla* site was a small, artificial pond along a heavily visited tourist thoroughfare, it was suspected that the plants had been carelessly discarded there. In 1997, *Hydrilla* was verified on nearby Mason's Island where herbicide applicators had formerly mistaken it as *Elodea canadensis*. Discovery of *Hydrilla* at two relatively close sites indicates that some natural dispersal may have occurred in Connecticut. Awareness of *Hydrilla* introductions is complicated by the taxonomic confusion of this species.

Growth of *Hydrilla* in southern Connecticut is prolific and it apparently thrives on a variety of substrates in the region (Les et al. 1997). Both sites formed dense populations that grew to the surface in virtual exclusion of native species. Connecticut *Hydrilla* plants overwinter by stem tubers, and nearly all traces of the foliage disappear in the fall (personal observations). *Hydrilla* grows rapidly from the nearly barren condition of the ponds in the spring, to thorough infestations by mid-summer.

Vegetative parts of *Hydrilla* are eaten by waterfowl (Sutton 1991), but it is not clear whether birds disperse it widely. Transport on boating trailers is a more effective means of dispersal. Although only two *Hydrilla* sites are currently known in southern New England, we believe that this species presents the most serious threat to natural aquatic communities in the region. In Chesapeake Bay, *Hydrilla* spread along 500 ha of Potomac River shoreline within eight years (Hurley 1990).

Limnobium spongia *(North American frog-bit)*

The indigenous range of *Limnobium spongia* in North American extended south of New Jersey and southern Illinois (Muenscher 1944). Three disjunct populations are known from Monroe and Yates Counties, NY and Lake Co., IN (Catling and Dore 1982; Cook and Urmi König 1983; Lowden 1992). The Indiana record has no voucher, but specimens were first collected from Monroe Co., NY in 1828. The population disappeared from this site by 1895 (House 1924). Mitchell and Tucker (1997) categorized the species as an introduction that did not persist in New York. *Limnobium* has long been recommended as an aquarium and water garden plant (Tricker 1897; Bissett 1907); however, the Monroe Co., NY record substantially predates the popularity of water plant cultivation in North America and it is doubtful that it would have escaped from cultivation.

Limnobium has been collected only once in New England, when a few small plants were observed at a Mansfield, CT pond in 1998 (*Les s.n.*, CONN). It was probably dispersed to this site by waterfowl. *Limnobium* overwinters as green plants where winter temperatures remain above 0 °C, but in northern localities like New York, it overwinters by small buds or seed (Cook and Urmi König 1983). Connecticut plants appeared to be seedlings which, according to McAtee (1939), float or eventually establish on the shore.

Waterfowl consume *Limnobium* seeds, though they are utilized mostly in the Mississippi embayment area (Martin and Uhler 1939). The seeds are consumed by goldeneye, green wing teal, mallard, old squaw, pintail, ringneck, and wood ducks (Cottam 1939; Mabbott 1920; McAtee 1918, 1939). It is not a major waterfowl food, but its occasional use provides an avenue for seed dispersal. Because of natural dispersal (Lowden 1992), disjunct sites in New York and Connecticut probably originated from waterfowl. Martin and Uhler (1939) recommended propagation of *Limnobium* as a waterfowl food. Frogbit may fail to thrive in the northeast because of its tropical affinities (Lowden 1992), or the scarcity of alkaline, hardwater, nutrient-rich lakes where it tends to occur (Hoyer et al. 1996).

Limnobium spongia is included with 'nonindigenous aquatic monocots' because it has been introduced outside of its former range (http://nas.er.usgs.gov/monocots/monocotslist.htm). Although native to North America, frog-bit is capable of weedy growth. Steward (1990) listed *L. spongia* among problematic aquatic plants in the eastern USA, but not as a major weed. Knight (1985) indicated that *Limnobium* was as troublesome as nonindigenous species. It is difficult to control and can assume 'water hyacinth-like growth' in some Florida localities (Knight 1985; Bodle 1986).

It hinders navigation in the St. John's River, Florida where it is targeted for control more often than water hyacinth (Knight 1985).

It is difficult to evaluate the threat of *Limnobium* introductions to New England. *Limnobium* is not well established in the northeast, possibly because of the cool climate and widespread occurrence of acidic, softwater habitats. However, its ability to reproduce both vegetatively and by seed is worrisome. Its availability as a water garden and aquarium plant is generally limited, so introductions of this species beyond its native range would likely occur by waterfowl seed dispersal. Minimally, *Limnobium* occurrences in the northeast should be monitored carefully.

Marsilea quadrifolia *(water clover; water shamrock)*

The first report of *Marsilea quadrifolia* in North America was from Bantam Lake, Litchfield Co., CT in August, 1860. Timothy Allen sent a specimen to D.C. Eaton at Yale College, who made further collections at the site and gave live material to Asa Gray. Gray (1860) considered *Marsilea* to be either a 'recent and casual introduction' or a once widespread species nearing extinction. Conard and Hus (1909) described *M. quadrifolia* as native, but Graves et al. (1910) considered it native only to Bantam Lake, and introduced elsewhere. No record exists of its introduction to Bantam lake, but it was not recorded by Brace (1822) who collected other aquatic plants there. We conclude that *Marsilea* was introduced to North America sometime between 1820 and 1860.

Marsilea quadrifolia from Bantam Lake, CT was introduced to the Harvard Botanical Garden (Cambridge, MA) prior to 1868 (Johnson 1986). Before 1872, it was introduced from the Botanical Garden by its gardener, L. Gauerineau, into Fresh Pond in Cambridge (Gray 1872). According to Eaton (1974), it was introduced by M. Pratt from the Botanical Garden 'where fully established' into the Concord River (Concord MA) in 1879 (*E.S. Hoar, s.n.*, 1879, GH). By 1900, there were additional collections from the Charles River in Needham and Dedham (Norfolk Co.), 'Glacialis' (near Cambridge, Middlesex Co.), and Jamaica Plain (Suffolk Co.) in eastern Massachusetts.

Marsilea quadrifolia was introduced intentionally elsewhere in New England by 1900. Daniel C. Eaton introduced it into Lake Whitney (New Haven Co., CT) by 1882 ('planted by Professor Eaton', *J.A. Allen, s.n.*, 1882, GH). John Russell introduced it to his garden in Salem, MA from Bantam Lake and probably also planted it nearby (Willey 1881). A Seabrook, NH (Rockingham Co.) specimen (NEBC) collected by A. Eaton notes: 'Raised at Seabrook from plants collected at Bantam Lake.' A Skowhegan, ME (Somerset Co.) record may have been introduced intentionally to a town park which was well known to the collector, L.H. Coburn.

At least four 20th century reports document intentional introductions. A 1985 specimen collected from Mill River, Northampton, MA (Hampshire Co.) originated at Smith College 'where it escaped from the greenhouse pond ca. 10 years ago' (see also Burk et al. 1976). Specimens collected in 1908 from Cromwell, CT (Middlesex Co.), indicate the intentional introduction of *Marsilea*. A 1946 specimen (CONN) from Haystack Pond in Norfolk, CT (Litchfield Co.) carries the notation: 'apparently first introduced.' A cursory survey in 1984 failed to relocate populations of *Marsilea quadrifolia* at either of these sites (L.J. Mehrhoff, personal observation). A 1991 Fairfield, CT (Fairfield Co.) record is from an artificial pond whose owner admits to having introduced *Marsilea* from Lake Whitney in New Haven (see above). In 1991 it had spread into the adjacent Saugatuck River where it appeared to be established (L.J. Mehrhoff, personal observation).

Although people probably first introduced *Marsilea quadrifolia* into Bantam Lake, Meehan (1882) speculated that plants might have arrived there by Siberian water birds. Aquatic birds may have facilitated its post-introduction dispersal, because waterfowl do consume the sporocarps (Martin and Uhler 1939). We are unaware of intentional plantings of *Marsilea* as a waterfowl food in New England.

Myriophyllum aquaticum *(parrot's feather)*

The earliest known specimen of *Myriophyllum aquaticum* in North America was collected in 1890 at 'Haddonville' (sic), NJ (i.e. Haddonfield) (Couch and Nelson 1985b). A Missouri collection in 1897 (Couch and Nelson 1985b), was probably a separate introduction rather than originating from localities on the east coast. This species was clearly introduced as an ornamental which escaped from aquarium and water garden cultivation during the late 19th century, with several specimens from the 1890s bearing notations of 'cultivated' (Couch and Nelson 1985b). The luxuriant, pendulous habit of *M. aquaticum* (formerly known as *M. proserpinacoides*) was recommended for aquatic 'hanging baskets', fountains and aquaria (Bissett 1907; Tricker 1897). Couch and Nelson (1985a,b) found annotated specimens indicating the cultivation of *M. aquaticum* in Washington, DC and its escape from cultivation in that area. An old photograph from Washington, DC shows *M. aquaticum* hanging from a fountain basin in festoons several feet long (Bissett 1907). It was routinely available from Kenilworth Aquatic Gardens in Washington, DC (Fowler 1936). Innes (1917) indicated that *M. aquaticum* flourished and became very robust along partially shaded lake margins.

Myriophyllum aquaticum was first reported in the southern New England region (southeastern New York) in 1929 (Couch and Nelson 1985b). By 1940, it was well established in southeastern New York and on Long Island (Couch and Nelson 1985b; Muenscher 1944; Ogden 1974). A specimen of *M. aquaticum* (originally misidentified as *Proserpinaca*) was collected in southern Connecticut (West Lake, Guilford, New Haven Co.) in 1946, but a survey of that lake by the authors in 1993 failed to detect the species. According to Hellquist (1997), *M. aquaticum* is winter hardy in western Massachusetts but has not yet escaped to natural waters in the state. It survives relatively severe, freezing winters in northern California and persists through mild winters in the Pacific Northwest, but can be killed by extended periods of frost (Aiken 1981; O. Ceska and A. Ceska 1985).

Couch and Nelson (1985b) concluded that *Myriophyllum aquaticum* was introduced successfully to North America and was slowly expanding its range. Collection data indicate that *M. aquaticum* has rapidly expanded its range, at a rate similar to that of purple loosestrife (Figure 2). Its rapid spread is surprising, given that only pistillate plants have been introduced into North America, making seed production impossible (Aiken 1981). Reproduction and dispersal occurs by vegetative fragmentation, which may be efficient locally, but in this species, is not effective over long distances. The rapid spread of *M. aquaticum* is apparently related to its cultivation. Without vagile dispersal agents like waterfowl, the threat of its escape and establishment depends much on the number of localities where it is grown. Unfortunately, *M. aquaticum* remains widely available from sources of cultivated water plants (e.g., Tricker 1998) and

dealers occasionally plant it intentionally as stock (Aiken 1981). Careful cultivation of this species in artificial, managed ponds can probably be conducted without danger of escape, but under no circumstances should it be introduced to natural water bodies or to sites in their proximity.

With an affinity for alkaline, hardwater, eutrophic lakes (Hoyer et al. 1996), *Myriophyllum aquaticum* may not pose as serious a threat in New England where such habitats are limited. However, a severe infestation of *M. aquaticum* has occurred recently in Westchester Co., NY, where it has spread rampantly in several ponds (Bladen 1997). Like other perennial, vegetatively reproducing aquatics, this species is dispersed among recreational lakes by fragments transported inadvertently on boat trailers.

Myriophyllum heterophyllum *(variable water milfoil)*

The indigenous range of *Myriophyllum heterophyllum* in North American extended northward along the East Coast to Virginia (Aiken 1981). Early distribution maps show *M. heterophyllum* absent from southern New England except for Long Island, NY (Martin and Uhler 1939). We have not searched herbaria exhaustively for this species, but have seen an early specimen from Delaware (*Tatnall, 1896*, CONN). This 'Delaware and Chesapeake canal' locality indicates the northward spread of the species along artificial waterways. *Myriophyllum heterophyllum* was reported from southern New England (Connecticut) in 1936 (Trudeau 1982); however, we have seen an earlier specimen collected from Bridgeport, CT by Eames in 1932 (CONN) which bears the annotation: 'escaped and becoming established in Burrell's pond.' We are unaware of the rational for Eames' annotation, but assume the intentional introduction of plants at this site. Consequently, the introduction of *M. heterophyllum* into southern New England is likely to have occurred as an escape from cultivation. Muenscher (1944) showed *M. heterophyllum* to be distributed throughout New England and the United States. It was first collected in the Hudson River basin (Orange Co., NY) in 1953 and was subsequently found at several nearby sites (Mills et al. 1997). By 1974, *M. heterophyllum* occurred throughout New York state, extending its distribution north of the 44th parallel (Ogden 1974). Herbarium records show *M. heterophyllum* currently distributed all through southern New England, including Connecticut, Massachusetts, New Hampshire, and Rhode Island. The recency of many records (after 1980) indicates its continued spread through the region. Crow and Hellquist (1983) reported *M. heterophyllum* from New Hampshire and Maine, but it is not in a later Maine checklist (Campbell et al. 1995). In Rhode Island, it is considered a native by Gould et al. (1998), but a naturalized and 'aggressive pest' by George (1998).

Myriophyllum species are confusing taxonomically (O. Ceska and A. Ceska 1985) and it is difficult to determine the species discussed in early literature accounts. We have seen a number of herbarium specimens of *M. heterophyllum* misidentified as *M. verticillatum*, and additional records may be sought in collections of the latter. Samuel (1894) illustrated '*Proserpinaca palustris'* which was surely drawn from a specimen of *Myriophyllum* strongly resembling the habit of *M. heterophyllum*. Specimens of *M. heterophyllum* were probably distributed in the aquarium plant trade under a variety of names. However, Tricker (1897) and Bissett (1907) specifically recommended *M. heterophyllum* as a species for aquarium and water garden culture. Brochure photographs still show *M. heterophyllum* promoted as an aquarium plant (e.g., James 1984), but it is typically identified simply as '*Myriophyllum* sp.' (e.g., Tricker 1998).

We know little about the reproductive biology of *Myriophyllum heterophyllum*, but many fertile specimens appear to contain viable seeds. Its stems serve as efficient organs for vegetative reproduction, and their draping habit facilitates transport on boat trailers. Winter buds enable *M. heterophyllum* to overwinter in northern New Hampshire (Aiken 1981). Water milfoil foliage is rarely consumed by waterfowl, but seeds (including those of *M. heterophyllum*) are eaten by 21 species of ducks (Martin and Uhler 1939; McAtee 1939). All native North American milfoils are productive waterfowl food plants (McAtee 1939). Thus, seed dispersal by waterfowl likely accounts in part for the spread of this species throughout southern New England.

Myriophyllum heterophyllum is distributed mostly in the southeastern half of Connecticut, to the virtual exclusion of *Myriophyllum spicatum* (Figure 5). This same distribution pattern is noted for *Cabomba caroliniana*, another invasive aquatic in the state (Figure 4). The restricted distribution pattern of these species may relate to water chemistry, recreational boating or competition.

Myriophyllum spicatum *(Eurasian water milfoil)*

The first reliable record of *Myriophyllum spicatum* in North America is a specimen collected in 1942 from Washington, DC (Couch and Nelson 1985a; cf. Reed 1977; Holm et al. 1969). Soon thereafter, specimens of the species were collected in such widely scattered localities as Arizona (1944), California (1948) and Ohio (1949) (Couch and Nelson 1985a). The pattern of multiple, widely separated occurrences indicates independent escapes from cultivation (Couch and Nelson 1985a). Eurasian water milfoil reached New Jersey during the 1950s (Trudeau 1982), and by 1960, it was rampant in the Chesapeake Bay area where possibly introduced as an aquarium plant (Hirzel 1962). Ballast disposal has also been suggested as the means of introduction (Trudeau 1982), but neither hypothesis is substantiated.

Myriophyllum spicatum has occurred in New England since at least 1965 (Crow and Hellquist 1983), and in southern New England (Stockbridge Bowl, Berkshire Co., MA) since 1971 (specimens at NASC). It was first collected in northeastern Connecticut (East Thompson) in 1979 (specimen at NASC); however, it probably occurred in the state earlier, given that most collections are in western Connecticut, adjacent to older New York populations (Ogden 1974). There is a western Connecticut (Twin Lakes, Salisbury) specimen from 1985 (CONN).

Myriophyllum exalbescens was not distinguished from *M. spicatum* by early wildlife biologists who considered it the best milfoil species for waterfowl (Martin and Uhler 1939). Because the similar *M. spicatum* was first verified from the Washington, DC area (where other aquatics were cultured by wildlife biologists), it is possible that *M. spicatum* was distributed for planting in managed marshes.The spread of *M. spicatum* throughout the United States has been astonishingly rapid (Figure 2) and it is arguably one of the most highly invasive aquatic species ever introduced to North America. It grows aggressively in alkaline lakes of southern New England. During the past six years, the species has not spread materially in Coventry Lake, CT (an acidic oligotrophic, lake), but has increased dramatically in East Twin Lake (an alkaline, marl lake) in northwest Connecticut

(personal observations). We observed a concomitant decline in native aquatic species diversity in East Twin Lake, particularly those of *Potamogeton*. Schloesser and Manny (1984) reported a coincident displacement of native *Potamogeton* species with the invasion of *M. spicatum* in Michigan.

Myriophyllum spicatum occurs throughout western Connecticut where there are many alkaline lakes. Its Connecticut distribution (roughly the northwest half of the state) essentially does not overlap with the distribution of *M. heterophyllum*, which primarily occupies the southeastern half of the state (Figure 5). Hellquist (1997) observed that *M. spicatum* was 'extremely abundant in the alkaline waters of Berkshire County' (MA), but was also 'becoming aggressive' in eastern Massachusetts.

Myriophyllum spicatum was recommended for aquaria and water gardens since at least the early 20th century (Bissett 1907). Specific accounts of separate introductions (Couch and Nelson 1985a) evidence its dispersal by careless disposal of cultivated specimens. Natural seed set in *M. spicatum* is low and it is propagated primarily by vegetative fragments (Aiken 1981; Madsen and Boylen 1989). Boat trailers that become draped in long stem fragments are likely agents of transport. Viable shoots of *M. spicatum* have also been used as a packing material for fishing bait which was inevitably dumped into lakes (Couch and Nelson 1985a). Migratory waterfowl evidently disperse *M. spicatum* (Couch and Nelson 1985a), but probably do not transport the heavy fragments over long distances.

Najas guadalupensis *(southern naiad)*

It is difficult to evaluate whether this species is native or nonindigenous in New England. Upon the discovery of *Najas guadalupensis* in southern New York, Fernald (1908) predicted its eventual collection in southeastern Massachusetts and Rhode Island. Bicknell (1908) recorded the first New England record of *N. guadalupensis* that same year, from specimens collected in Miacomet Pond (1904) and Long Pond (1907) on Nantucket Island. Bicknell thought *N. guadalupensis* to be long established at these stations. He considered bird dispersal and even introduction from a shipwrecked tropical vessel as possible explanations for its occurrence there. Subsequently, Harger et al. (1922) discovered a specimen in the Gray herbarium of *N. guadalupensis* from Connecticut, but without date or specific locality. Fernald (1923) remarked that *N. guadalupensis* was 'of much wider range northward than has been supposed.' By then, collections had materialized from Block Island, Long Island, Martha's Vineyard, Nantucket and the undetermined Connecticut locality. Furthermore, the species was known to occur from the St. Lawrence basin (Fernald and Wiegand 1923) to the upper Great Lakes and as far west as Oregon (Fernald 1923). From the characteristic lack of fruits in northern specimens, Fernald assumed that *N. guadalupensis* was a 'tropical' species which was 'too far north for successful fruiting' and believed that it was disseminated by shoot fragments. Svenson (1928) discovered two populations of *N. guadalupensis* on the Massachusetts mainland (Cape Cod). Clausen (1936) considered that *N. guadalupensis* was native to Massachusetts and New York southward, but had been overlooked in northern populations because of its infrequent fruiting.

Hellquist (1997) described *Najas guadalupensis* as an aggressive 'native species' that was becoming locally abundant in Massachusetts. Paradoxically, the scarcity of historical records for *N. guadalupensis* has resulted in its consideration as an imperiled species in Connecticut (Brumback and Mehrhoff 1996); yet, it is reportedly a nuisance in at least one southwestern Connecticut lake (Ball Pond) where measures have been taken to eradicate it. Muenscher (1935a) listed *N. guadalupensis* as one of 'the most abundant species, covering large areas' of the Mohawk River mouth. Although *N. guadalupensis* is probably native to New England, it exhibits aggressive growth in parts of its range and should be monitored. It is an early colonizing species of artificial lakes in Missouri (Moyle et al. 1946) and is regarded as an aquatic weed in the southwestern United States (Anderson 1990).

Najas minor *(minor naiad)*

Najas minor was discovered in the United States in 1934 in the Hudson River at the mouth of the Mohawk (Clausen 1936, 1937). In 1935, W. Muenscher intentionally introduced *N. minor* into Cayuga Lake, NY (Clausen 1936). By 1974, it had spread southward along the Hudson River with new localities also appearing in the 'finger lakes' region of New York where it was introduced intentionally (Ogden 1974). Meriläinen (1968) had not yet recorded *N. minor* from New England. Hellquist and Crow's (1980) report for western Massachusetts is the earliest published record for southern New England, although the oldest of these localities (Berkshire Co., MA) was discovered in 1974 (Weatherbee 1996). Western Massachusetts stations were less than 80 km from the site where *N. minor* was first seen in New York. Hellquist and Crow (1980) observed that *N. minor* was more abundant in New York and had not made much eastward movement into New England. Connecticut specimens (Fairfield Co.) were first collected in 1995 within 80 km of westward New York stations. Within two years, specimens were collected in two additional Connecticut counties at sites in northwestern and south central portions of the state (specimens at CONN).

Clausen (1936) suspected that *Najas minor* was 'brought here on shipping from Europe' or possibly introduced by disposed aquarium plants. It may have been introduced accidentally from waterfowl plant propagation programs. Intentional propagation of *Najas* species for waterfowl food was widely advocated in the 1930s (Cottam 1939; Martin and Uhler 1939), but species are difficult to identify. If *N. minor* had been introduced to ponds where waterfowl food plants were raised, then it could easily have been distributed along with them. In any case, *N. minor* appears to have escaped from cultivation because it was first detected in the same watershed (Hudson/Mohawk River) where other cultivated, nonindigenous aquatic species (e.g., *Nymphoides peltata*, *Trapa natans*) were first observed.

The spread of *Najas minor* in southern New England has probably occurred by waterfowl, its primary dispersal agent (Meriläinen 1968). *Najas* is a choice waterfowl food (Martin and Uhler 1939), and fruits are consumed by 20 American duck species at quantities that can exceed 4000 per bird (McAtee 1939). Most *Najas* species are annual and typically produce prodigious quantities of seed. Experimental germination is poor (1–2%), but this rate may be based on immature fruits (Muenscher 1936).

The confined distribution of *Najas minor* in western Massachusetts could indicate a slow spread in that region, but it may have beeen overlooked at other sites. Intensive collecting efforts in Connecticut account for many recent records throughout the state (N. Murray, personal communication).

Nasturtium officinale *(watercress)*

Settlers of Plymouth, MA and the Massachusetts Bay colony made references to 'water-cresses' as early as 1620 (Young 1841, 1846). Parish (1901) assumed that the plants were *Nasturtium officinale* and contemplated its dispersal to the 'virgin soil' of the Pilgrims. Yet, the identity of the Plymouth watercresses is questionable. Josselyn (1672) observed 'watercresses' in Maine during the 1630s as '. . . such plants as are common with us in England'. However, Tuckerman (1865) believed that Josselyn probably saw *Rorippa palustris*. Lewis and Clark gathered 'Creases' [cresses] as 'Greens for our Dinner' from Missouri's Osage River in 1804 (DeVoto 1953). Whether the plants noticed in these early accounts were actually European watercress (*Nasturtium*) or a native species of *Rorippa* or *Cardamine* cannot be determined with certainty. One of the first specific reports of *N. officinale* from North America was by Torrey (1826), although Rollins (1978) indicated its introduction occurred 'at least by the early 1800s and most likely . . . much earlier'. Green (1962) believed that watercress was introduced during the mid 18th century. Ives et al. (1831) is the earliest citation that we could locate for *N. officinale* in southern New England. It was recognized as an 'exotic' species by the early 19th century (Eaton 1833) and was familiar enough to be included among regional medicinal plants (Wood and Bache 1854).

Despite presumed multiple introductions to North America (Green 1962), the paucity of early specimens and indications of its rarity by botanists, indicate that watercress did not establish well until the mid 19th century. The earliest North American specimen was collected in 1847 from Niagara, NY (Green 1962). Gray (1857) characterized it as a 'rare' escape from cultivation. Graves et al. (1910) remarked that water cress was introduced for salad and was 'rare eastward and frequent westward' in Connecticut. Rollins (1981) concluded it had 'Escaped from deliberate plantings in streams.'

Watercress was widespread by the end of the 19th century when its distribution extended to the Pacific coast (Creevey 1897). Cook (1899) described *Nasturtium officinale* as so abundant near Concord and Lexington (MA) that it had '. . . to be removed in cartloads from a brook in Lexington to prevent its blocking the stream and so flooding the meadows.' By 1900, specimens of *N. officinale* had been collected in 17 states including Connecticut, Massachusetts, New York and Vermont (Green 1962). Connecticut specimens of watercress (YU) confirm its introduction to the state prior to 1851; however, it is mentioned in an earlier catalog of plants from New Haven (Ives et al. 1831).

Nasturtium officinale is infrequently perceived as weedy because of its restriction to coldwater brooks where it is generally innocuous (but see above). The popularity of watercress for salads may account for its relative acceptance as a naturalized species. However, it grows quickly when cultivated under satisfactory conditions, and can be harvested in as little as 30 days (National Academy of Sciences 1976). Watercress seeds retain 68% viability after five years of coldwater storage (Muenscher 1944), and exhibit up to 97% germination after 5–7 months of dry storage (Muenscher 1936). Watercress is not eaten by waterfowl, but seeds probably facilitate short distance dispersal among introduced sites. Local dispersal by vegetative fragments is also possible.

Two cytotypes (diploid, tetraploid) of *Nasturtium* were introduced to North America, each recognized at the species level (diploid = *N. officinale*; tetraploid = *N. microphyllum*) (Green 1962). We have considered records of these taxa together because both are nonindigenous, invasive and presumably introduced intentionally as a food source (Green 1962). The diploid *N. officinale* has become far more extensive in North America than the tetraploid which occurs mainly in the northeast (Green 1962).

Nymphoides peltata *(floating heart)*

Countryman (1970) concluded that *Nymphoides peltata* was introduced to New England before 1963 when it was first collected at West Haven, Vermont. However, *N. peltata* has occurred in southern New England since at least 1882 when it was collected at Winchester, MA (Stuckey 1973). Specimens of *N. peltata* were grown in New York's Central Park Terrace Pond in 1886 (Hollick 1887). Trade catalogs in 1891 advertised the sale of *N. peltata* (Countryman 1970) and it was among the plants recommended in the earliest water gardening books (Tricker 1897; Bissett 1907). There is little question that this species was introduced as an escape from cultivation (Stuckey 1973).

Several records of *Nymphoides peltata* are known from the Washington, DC area in the 1890s (Stuckey 1973). Specimen labels described the plants as 'abundantly naturalized' in ornamental ponds and fish ponds managed by the U.S. Fish Commission (Stuckey 1973).

An 'abundant' and 'well-established' population of *Nymphoides peltata* was discovered in the Hudson River drainage in 1929 by W. Barker (Mills et al. 1997). It later formed 'dense beds' in shallow parts of the river (Muenscher 1935a). Other records of *N. peltata* from southeastern New York include Rensselaer Co. (in 1932), Columbia Co. (in 1936), and Ulster Co. (in 1961) (Stuckey 1973).

Nymphoides peltata is 'extremely hardy' but currently uncommon in Massachusetts (Hellquist 1997). It is recorded only from three Massachusetts counties: Middlesex, Norfolk and Worcester (P. Somers, personal communication). *Nymphoides peltata* has not yet been found in southern New Hampshire or Rhode Island. The only known Connecticut record was collected in 1939 from a pond on the University of Connecticut campus where it was reportedly 'naturalized' (Stuckey 1973). The species no longer occurs there (personal observations) and we have no information on its history in that pond.

Nymphoides peltata has not spread as rapidly as other nonindigenous aquatics (Figure 2), but its potential invasiveness should not be underestimated. Pollard (1896) reported that *N. peltata* had not only covered the surface of Washington Fish Commission ponds, but also spread to nearby ponds. It persisted in Central Park for at least 60 years as evidenced by a 1946 specimen label describing it as 'a pest in ponds' (Stuckey 1973). *Nymphoides peltata* is a serious weed in parts of Europe (Murphy et al. 1990) and plants 'show strong, weedy tendencies' in parts of southern New England (Stuckey 1973).

Historical data indicate that *N. peltata* is dispersed mainly by people, i.e., by intentional plantings or escapes from cultivation. Early escapes of *N. peltata* occurred near New York and Washington (Innes 1917). Natural agents are less important in its dispersal. *Nymphoides peltata* flowers and fruits 'freely' in New York (Countryman 1970) where it has spread by seeds and rhizomes (Muenscher 1933). However, plants or seeds of *Nymphoides* species are 'only sparingly used by waterfowl' (McAtee 1939) and they are not among the waterfowl food plants considered by Martin and Uhler (1939). Although

seeds and fragments of *Nymphoides* will facilitate local dispersal (especially along watercourses), the paucity of more vagile dispersal agents (e.g. waterfowl) is probably responsible for its slow movement to new, remote localities. The best defense against continued infestations of *N. peltata* would be to limit or restrict its use as a cultivated water garden plant.

Potamogeton crispus *(curly pondweed)*

The oldest verified record of *Potamogeton crispus* in North America is from a herbarium specimen collected at Wilmington, DE in 1860; however, Asa Gray reported seeing a specimen from the same locality in 1859 (Stuckey 1979). Earlier records (ca. 1840) putatively exist in European herbaria, but have not been verified (Stuckey 1979). The earliest record for southern New England is 1880, from a specimen collected at Spy Pond near Arlington, MA (Stuckey 1979). By 1900, it was collected in southeastern New York State and Long Island, and was found in Vermont in 1911 (Stuckey 1979). Moore (1913) remarked that *P. crispus* had become '. . . the most abundant Potamogeton in the vicinity of Ithaca . . . ' (NY). *Potamogeton crispus* reached Connecticut and Rhode Island by 1932 (specimens at CONN) and now occurs throughout southern New England (Stuckey 1979; Hellquist and Crow 1980). Collections from 1932 to 1938 document *P. crispus* in at least 11 Connecticut localities (specimens at CONN) and it was probably in the state much earlier than these first collections would indicate.

Stuckey (1979) concluded that *P. crispus* first spread in North America as an escape from contaminated fish hatchery stocks. He cited 24 collections of *P. crispus* associated with fish hatcheries in the eastern United States. Wildlife biologists regarded *P. crispus* as a resource, and it was intentionally planted in waterfowl marshes from as early as 1918 (Stuckey 1979; McAtee 1939; Moore 1913).

Although Stuckey (1979) presented compelling evidence to implicate fish hatcheries in the spread of *Potamogeton crispus*, it may originally have been introduced as an aquarium plant. Some localities (e.g. Santa Barbara, California) are thought to have originated from intentional plantings (Stuckey 1979). Hull (1913) described an isolated population of *P. crispus* from an Illinois park, but did not explain its origin. With its bright coloration and attractive foliage, *P. crispus* has been recognized as a 'useful' aquarium plant since the early days of aquatic plant cultivation (Samuel 1894; Bissett 1907).

Potamogeton crispus propagates mainly by vegetative turions that form in late spring. This coldwater species is dormant during summer when water temperatures are high (Wehrmeister and Stuckey 1992). Turions germinate in the fall and develop into plants that remain green throughout winter. Flowers and fruits occur in North America, but fruit germination is yet undetected (Wehrmeister and Stuckey 1992). Because of its life history, *P. crispus* is usually perceived as weedy early in the spring when populations can grow to impressive levels. It disappears by mid-summer when in the dormant turion phase.

Trapa natans *(water chestnut)*

Trapa natans was introduced as an escape from cultivation. Its floating habit and edible fruits made it an interesting specimen for water garden cultivation (Bissett 1907). *Trapa* must have been widely available from cultivated sources in the late 19th century. Aquarium plant dealers regularly sold *Trapa* plants in the United States (Innes 1917; Muenscher 1935a, b).

Trapa natans first became established in North America in eastern Massachusetts. Louis Gauerineau, a gardener at the Cambridge Botanical Garden, intentionally planted *Trapa* in Fresh Pond, Cambridge, MA, and 'other ponds' in the area sometime before 1879 (Davenport 1879). Davenport (1879) distributed plants and seeds of *Trapa* to M. Pratt of Concord, MA, and they planted it in a pond near the Sudbury River. Pratt probably distributed the plant to other sites including a pond near Concord, MA (Davenport 1879). Davenport (1879) did not consider *Trapa* to be aggressive, but Sargent reported it as a nuisance near Cambridge (Brown 1879). By 1899, it became so invasive in the Concord and Sudbury Rivers, that it had to be 'weeded out' (Cook 1899).

Eaton (1947) cited a water chestnut specimen from Concord, MA dating 1859; however, notes on the specimen and in the New England Botanical Club archives indicate that the date was in error and probably intended as 1879 (R. Angelo, personal communication).

Trapa 'remained relatively unaggressive' on the Sudbury River in Massachusetts through the 1930s, but by 1946, had colonized vast stretches of the river (Eaton 1947). Eaton (1947) conveyed remarks by H. Bigelow who described the 'spectacular explosion of the water chestnut' in the summer of 1944 when 'the thing ran wild.' These reports emphasize the ability of some nonindigenous species to remain dormant for prolonged periods, but then to suddenly spread rapidly.

Trapa reached western Massachusetts by 1920 (Burk et al. 1976) and continues to spread in that region (Hellquist 1997). In the summer of 1999, it was discovered for the first time in Connecticut (N. Murray, personal communication). *Trapa* was planted intentionally on the University of Massachusetts, Amherst campus in the 1950s (Burk et al. 1976) where the plants grew so aggressively that the pond had to be drained to eradicate them.

Trapa was introduced in the Hudson River basin at Collins Lake, Scotia, NY in 1884 (Muenscher 1935a; Wibbe 1886) and quickly spread into the Mohawk River (Mills et al. 1997). Photographs from Collins Lake in 1934 (Muenscher 1935a) show a severe water chestnut infestation that had persisted at the site for 50 years. Muenscher (1935a, b) estimated that water chestnut covered 400–500 ha within the Hudson River basin by 1934.

Trapa natans is annual and sets abundant seed; var. *japonica* is known to be self-compatible and apomictic (Kadono and Schneider 1986). The spiny *Trapa* fruits can wound swimmers (Muenscher 1935a). High seed production makes it difficult to eradicate from infested areas. A two-week drying period (at room temperature) is sufficient to kill the embryos (Martin and Uhler 1939).

Hellquist (1997) believed that *Trapa* is dispersed mainly by ducks and geese, but waterfowl carriage over long distances is unlikely. Ducks and geese reject the foliage and fruits of water chestnut (Jäggi 1883) and the size and spinature of the latter make it 'impossible for birds or fish to consume them' (Muenscher 1935a). Although Hellquist (1997) observed Canada geese with *Trapa* fruits attached to their feathers, the size and weight (6 g) of the propagules (see Muenscher 1935a) make it unlikely they would remain attached to feathers during prolonged flight. Because ripe *Trapa* fruits 'drop to the bottom like sinkers' (Muenscher 1935a), their chance of entanglement in plumage is minimal. Like Muenscher (1935a), we have collected floating *Trapa* fruits that were devoid of seeds (none weighed over 1.7 g). Fruits observed on waterfowl plumage may actually be these lighter husks which remain after germination (W. Countryman, personal communication). Viability of fruits

obtained directly from waterfowl should be determined. Muskrats eat *Trapa* fruits (Muenscher 1935a) and may facilitate their dispersal.

People have dispersed *Trapa* since ancient times (Jäggi 1883). Fragment transport on boating equipment and planting of the 'attractive' specimens have contributed to its spread (Anon 1994). *Trapa* is believed to have 'hitchhiked' from the Hudson River to Lake Champlain on boats (the spiny fruits clinging to ropes and nets) using the barge canal (Countryman 1970). Wind and wave action disperse fragments and fruits locally (Anon 1994). *Trapa* fruits have long been used as a food (Cook 1899) and were sold by street vendors in western New York state from about 1925 to 1935 (Muenscher 1935a, b). Canned *Trapa* fruits are sold in gourmet food shops and plants may still be cultivated for the edible nuts.

The floating life-form of *Trapa* presents a serious threat to natural aquatic communities. Plants produce 'dense shade' which 'prevents nearly all other aquatic plants from growing among them' (Muenscher 1935a). Martin and Uhler (1939) characterized *Trapa natans* as a 'dangerous competitor' that interfered with the propagation of 'useful' waterfowl food species.

Veronica beccabunga *(European brooklime)*

New Jersey collections from 1876 first confirmed the presence of *Veronica beccabunga* in North America (Les and Stuckey 1985). A number of observations clearly document its spread from disposed shipping ballast (Les and Stuckey 1985). However, multiple introductions may have occurred as escapes from aquaria and fish hatcheries (Les and Stuckey 1985). Specimens were first observed in New York City in 1879 (Brown 1879) and were collected in Quebec in 1905 and in Maine in 1937 (Les and Stuckey 1985). Two populations are known from Connecticut, the earliest from 1980 in Litchfield Co. (*Mehrhoff 3417*, CONN) and another observed in 1993 in northwest Connecticut (D. H. Les, personal observation). *Veronica beccabunga* occurs in Hampshire Co., MA (P. Somers, personal communication) but is not reported from Maine, New Hampshire, Rhode Island or Vermont.

The spread of *Veronica beccabunga* in North America has not been rapid (Figure 2), an indication that it is not a seriously invasive species. However, it can be aggressive locally (Dore and Gillett 1950). This species often occurs along naturally disturbed habitats of watercourse margins where it is not likely to be perceived as a weed. Competition with *V. americana*, a closely related, native species, may explain the poor ability of *V. beccabunga* to invade native habitats (Les and Stuckey 1985). The Connecticut populations are unimpressive, and at one locality, *V. beccabunga* grows along with *Nasturtium officinale*, another nonindigenous aquatic (see above).

Veronica beccabunga is dispersed locally by stem fragments and over greater distances by seeds (Les and Stuckey 1985). Its potential to colonize new localities should be of concern near areas where the species presently occurs.

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