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3 Vectors for Spread of Invasive Freshwater Vascular Plants with a North American Analysis

3.1 Introduction

Freshwater plants, or macrophytes, are important to the structure and function of lentic and lotic systems. They influence chemical and physical attributes of the aquatic environment while also providing habitat for invertebrates and fish as well as forage for waterfowl (Butcher, 1933; Spence, 1967; Westlake, 1982; Carpenter & Lodge, 1986; Sand-Jensen *et al.*, 1989). Growth form and characteristics of individual species are important determinants of aquatic plant function in aquatic ecosystems. Changes in community composition caused by introduction of alien invasive species of macrophytes can have cascading effects throughout aquatic food webs and alter ecosystem services provided by aquatic plants.

3.1.1 Growth Forms of Freshwater Plants

Growth form influences the relative importance of vectors of introduction and the type of system changes caused by invasive species. For example, emergent and floating-leaved plants with attractive foliage or flowers are popular ornamentals and are common in the horticultural trade, whereas submersed species with limp stems easily attach to boats. Invasive submersed plants can impede water flow and alter habitat structure for fish and invertebrates (Vermaat *et al.*, 2000; Toft *et al.*, 2003; Colon-Gaud *et al.*, 2004), whereas floating species can impede light penetration and gas exchange with the atmosphere (Frodge *et al.*, 1990; Goodwin *et al.*, 2008).

3.1.1.1 Reproduction and Dispersal in Aquatic Plants

The ability to reproduce vegetatively is ubiquitous among aquatic plants because it functions efficiently in aquatic environments (Philbrick & Les, 1996). Vegetative reproduction and clonal growth permits rapid expansion of favorable genotypes under conditions that are relatively favorable for plant growth, especially for submersed species, e.g., risk of desiccation is low and temperatures are moderate. Some highly invasive aquatic plants are dioecious (staminate and pistillate flowers borne on different individuals) and only one sex is invasive, illustrating the efficiency of vegetative reproduction. For example, in northern Europe, *Elodea canadensis* is widespread and nearly all the plants are female (Hutchinson, 1975). Similarly, in the western United States of America, *Egeria densa* are all male (Carter & Sytsma, 2001) and in New Zealand, South Africa, and North America all *Myriophyllum aquaticum* are female (Guillarmod, 1979; Orchard, 1979; Aiken, 1981).

Aquatic plants produce a variety of vegetative propagules (Grace, 1993). In many submersed macrophytes, plant fragments as small as a single node are capable of establishing new plants, so every node of the plant stem is a potential propagule. Specialized vegetative propagules, however, may convey advantages in survival and establishment. In *Hydrilla verticillata*, larger propagules (tubers) produce more competitive plants than smaller propagules (turions) (Spencer & Rejmánek, 1989) and have increased survival (Bowes *et al.*, 1979). Continued production of turions by *H. verticillata* may be advantageous if turions and tubers represent different survival and dispersal strategies. Spencer *et al.* (1987) suggested that turions, which are formed on the stem of the plant, are better suited for dispersal and occupation of open space where they are less likely to face competition, and that tubers, which are formed in the sediment and are not as easily dispersed, are more efficient at maintaining established stands where intraspecific competition would be more intense.

Flowering, pollination, and seed germination are problematic for many species of aquatic plants, especially for submersed species (Bornette & Puijalon, 2009). Flowers of aquatic and terrestrial plants in the same family are morphologically similar. For submersed species, the differences are primarily in their mechanisms to achieve an aerial position for wind or insect pollination or, more rarely, in the production of completely submersed, hydrophilous flowers. Sculthorpe (1967) provides numerous examples of reduced fertility and poor seed viability in aquatic plants as well as examples of pseudovivipary where vegetative propagules replace flowers, particularly in submersed species. Nevertheless, production of numerous hybrids in the *Potamogeton* (Kaplan *et al.*, 2009) and *Myriophyllum* (Moody & Les, 2002) genera suggests that sexual reproduction is common in submersed aquatic plants. Moody & Les (2002) proposed that hybridization between introduced and native *Myriophyllum* species may be responsible for the invasiveness of the species outside their native range.

Sexual reproduction is more common in emergent species than in submersed and floating-leaved species (Philbrick & Les, 1996), and is important to long-term survival of aquatic plant species in systems subject to fluctuating water levels (Van der Valk & Davis, 1978; Westcott *et al.*, 1997; Combroux & Bornette, 2004). Seeds of aquatic plants survive longer than vegetative propagules and may permit escape from adverse conditions for decades to centuries. *Nelumbo nucifera* seeds as old as 1,300 years have been germinated (Shen-Miller *et al.*, 1995). Vegetative propagules are shorter-lived (Van & Steward, 1990; Kunii, 1993) and function primarily in perennation and dispersal.

Vectors

Vectors for dispersal of invasive freshwater plants can be coarsely classified as primary (vectors for initial introduction to a new habitat) and secondary (natural processes for spread following establishment). Primary vectors are human-mediated and may function over intercontinental, inter-watershed, or intra-watershed scales. Secondary vectors can also result in long-distance dispersal, but typically function more locally within a watershed.

Primary Vectors

Primary vectors for freshwater plants include shipping, trailered boats, and intentional importation. Intentional importation can result in invasion of natural systems by escape from cultivation, contaminated shipments, or by direct introduction. Association of any individual species introduction with a specific vector is often impossible because the lag in population growth following introduction provides a temporal discontinuity (e.g., *Eichhornia crassipes* was first introduced into Italy in the first half of the 19th century, but became invasive in late 20th century (Brundu *et al.*, 2013)) and because multiple vectors may be acting simultaneously.

Intentional Importation

Freshwater plants are intentionally introduced for a variety of beneficial uses. Often the biological characteristics that make the plants attractive for their intended use, e.g., rapid growth, wide environmental tolerances, and few pests, also make them invasive if they escape from cultivation or are intentionally introduced into natural systems.

Aquarium and Water Gardening

Water gardening is a growing hobby and a major source of invasive freshwater plants. Invasive plants in the USA are introduced primarily through the ornamental plant trade (Lehan *et al.*, 2013). In 2003, there were 16 million households in the USA with water gardening retail sales totaling $1.56 billion (Crosson, n.d.). Les & Mehrhoff (1999) found that up to 88% of the invasive aquatic plants in the USA entered as cultivated plants. In Europe, about 7 million aquatic plants are imported each year, primarily for aquarium use, but only 10 of the 247 species are considered potentially invasive (Brunel, 2009). Champion (1998, cited in Champion & Clayton, 2000) reported that 75% of the naturalized aquatic plants in New Zealand were introduced as ornamentals. There is seasonality in the aquatic plant trade, with sales peaking in July in the Pacific northwest of the USA (Strecker *et al.*, 2011). Strecker *et al.* (2011) found that propagule pressure of plants and fish released by aquarists was the same (< 1 released per aquarist per year), but released aquarium plants had a higher probability of establishment. In a detailed study of aquatic plant propagule pressure from aquaria releases in Montreal, Cohen *et al.* (2007) estimated that 3,015 plant propagules are released each year into the St Lawrence Seaway, and found that *Cabomba caroliniana* and *Egeria densa*, two known invasive species, were among the top seven species released.

Invasive freshwater plants may be introduced as hitchhikers with otherwise innocuous plants or products. Maki and Galatowitsch (2004) found that 93% of the orders received from aquatic plant vendors in the USA included plant and animal species that were not ordered, and that 10% of the orders included federal noxious weeds or other nonindigenous species. They reported that the frequency of hitchhiking species varied with growth form of plants ordered. Orders of submersed and floating species included hitchhiking plants 100% of the time; emergent plant orders included hitchhiking plants 62% of the time. *Hydrilla verticillata*, *Potamogeton crispus*, and *Salvinia molesta*, all highly invasive species, were among the plants that Maki and Galatowitsch (2004) received as unordered hitchhikers. The *Hydrilla verticillata* invasion in the northeastern (Les, 1996 cited in Kay & Hoyle, 2001) and western USA (Boersma *et al.*, 2006; Akers, 2011) were the result of contamination of water lily shipments. The first known invasive submerged plant in New Zealand, *Elodea canadensis*, was introduced as a contaminant in a shipment of fish eggs, and *Hydrodictyon reticulatum* was introduced into New Zealand with a shipment of ornamental fish (Champion & Clayton, 2000).

Food

There is a long history of human use of freshwater plant seeds, fruits, and perennating organs for food (Sculthorpe, 1967). Human transport and introduction of species used for food may relate to human migration and reluctance to sample unfamiliar food (Mack, 1999 cited in Mack & Lonsdale, 2001). Several aquatic plants used for food have become invasive when introduced outside their native range. Champion & Clayton (2000) reported that *Rorippa nasturtium-aquaticum* was introduced to New Zealand for culinary purposes and became a major weed problem, and that *Alternanthera philoxeroides* is cultivated in New Zealand as a food crop. *Ipomoea aquatica* has been cultivated for centuries in Asia and was introduced and is cultivated in the southern USA even though it is a federally listed noxious weed (Van & Madeira, 1998). *Trapa natans* was a significant food source for prehistoric Europeans (Karg, 2006), and has been shipped throughout the world (Sculthorpe, 1967). It is invasive in lakes in Kashmir, where it is an important food resource (Masoodi, 2013), and in the northeastern USA (Orth & Moore, 1984; Nieder *et al.*, 2004).

Medicine

Sculthorpe (1967) reviewed freshwater plants that have had historical medicinal uses, several of which are considered invasive outside their native range. *Acorus calamus* was introduced into Europe for medicinal purposes in 1574 (Weber and Brändle, 1996), where it forms monospecific stands and displaces native species (Dykyjová, 1980). *Monochoria vaginalis*, a common folk remedy for a variety of ailments (Latha & Latha, 2014), has been spread throughout Asia and the Pacific islands and is a common weed in rice fields from Japan (Shibayama, 2001) to California (Barrett & Seaman, 1980). Although they were most likely dispersed as ornamentals rather than for medical uses, several invasive *Nymphaea* species contain compounds with potential medical applications (Rajagopal & Sasikala, 2008; Bose *et al.*, 2012; Jesurun *et al.*, 2013)

Forage

Use of freshwater plants as forage for livestock has received extensive attention (see review by Little, 1979). Nearly all of the most invasive aquatic plant species have been considered as livestock feed. For most species it is unlikely that they were introduced with the intention of increasing forage. Rather, their use as forage appears to be a utilitarian exploitation of rampant growth resulting from introduction via a different vector. Introduction for forage, however, appears to have led to creation of invasive *Phalaris arundinacea* populations. Repeated introductions of *P. arundinacea* into North America from Europe for forage increased genetic diversity of the species in its North American native range and allowed development of a highly invasive phenotype (Lavergne & Molosfky, 2007). More generally, Roman & Darling (2007) concluded that high propagule pressure through repeated introductions can add genetic diversity, decrease founder effects, and increase success of a variety of introduced aquatic taxa.

Industrial Use

Because of their rapid growth rate, several invasive aquatic plant species have been proposed for treatment of industrial and domestic wastewater (Brix & Schierup, 1989). Floating species, such as *Pistia stratiotes, Eichhornia crassipes*, and *Salvinia* spp., provide tertiary treatment of wastewater and the nutrients the plants sequester can be easily removed from the system by harvesting the plants. *M. spicatum* was suggested as an efficient species for phytoremediation of industrial processes (Hughes *et al.*, 1997; Lesage *et al.*, 2007; Brundu *et al.*, 2013).

Shipping

The role of shipping in dispersal of aquatic invasive species is well documented (National Research Council, 1996). There are multiple sub-vectors associated with shipping, including hull fouling, ballast, sea chests, and dunnage. Solid ballast was used on ships until the 1880s when water-ballasting technology was developed. Water ballast can be pumped much more quickly than solid ballast can be loaded or offloaded, which shortened ship time in port and made shipping more profitable. The role of ballast water in dispersal of plant propagules is not well documented; however, the importance of solid ballast in introducing nonindigenous species to port areas has been documented for over 100 years (Mack, 2003). Nelson (1917) reported 92 species unique to a solid ballast disposal site near Portland, Oregon, USA, many of which were first reports in the USA. *Schoenoplectus californicus*, *Zizania latifolia*, and *Alterniflora philoxeroides* were likely solid ballast introductions into New Zealand (de Lange *et al.*, 1998). Solid ballast was a vector for *Veronica beccabunga* introduction into New England (Les & Mehrhoff, 1999) and for *Butomus umbellatus* introduction into the St. Lawrence River (Countryman, 1970).

The importance of shipping as a vector for plants dropped substantially with the abandonment of solid ballast and the adoption of water-ballast technology (Mills *et al.*, 1996; Riccardi, 2006; Keller *et al.*, 2009). Furthermore, shipping and ballasting occurs primarily in marine and estuarine systems, and current ballast management strategies include mid-ocean ballast water exchange with movement toward ballast water treatment, all of which reduce the importance of shipping as a vector for freshwater macrophytes.

Boats and Trailers

Multiple environmental impacts of boating on freshwater systems have been long recognized (Liddle & Scorgie, 1980; Mosisch & Arthington, 1998). Given the speed and long distance that they travel over land, trailered boats have been a major focus of study as vectors for aquatic invasive species. Much of the research on recreational boats as vectors for invasive species has focused on *Dreissena polymorpha* and *D. rostriformis bugensis* (Rothlisberger *et al.*, 2011; Choi *et al.*, 2013; Dalton & Cottrell, 2013). Many models of mussel dispersal by boat vectors that were stimulated by the mussel invasion of North America (Buchan & Padilla, 1999; Bossenbroek *et al.*, 2001; Johnson *et al.*, 2001; Leung *et al.*, 2006) are equally useful for understanding dispersal of aquatic plants. Few models have been developed specifically for aquatic plant dispersal by boats (Jacobs & MacIsaac, 2009).

The importance of boats as dispersal vectors seems intuitively obvious; however, definitive documentation of its importance is not available. Biological characteristics of the invader and the source water body, environmental conditions in the receiving water body, and transit time interact to determine the effectiveness of the boat vector in dispersal of aquatic plants. Johnstone *et al.* (1985) found that the distribution of five invasive submerged plant species in New Zealand was associated with boating activity, and that boats leaving lakes carried plant fragments only when the haul-out area was near an invasive plant bed. They also reported that biotic factors, such as lateral bud frequency, internode length, and resistance to desiccation may influence the effectiveness of boats as vectors for aquatic plants. The length of *M. spicatum* fragments and whether they originated from the plant apex or near the bottom of the stem influenced desiccation rate and survival (Mcalarnen *et al.*, 2012) and by inference distance that a viable fragment could be transported between lakes. Jerde *et al.* (2012) and Barnes *et al.* (2013) also described differences in the desiccation rate of invasive freshwater plant species and related it to probability of survival during interlake transport by boats. In Minnesota, USA, distance to the nearest invaded lake, and by inference the importance of boats as vectors, was a predictor of presence of *M. spicatum*; however, lake size, alkalinity, Secchi depth, and lake depth were also significant predictors (Roley & Newman, 2008). Factors associated with boating activity, such as the number of boat ramps and proximity to roads, were less important than water quality factors, especially inorganic carbon concentration, in predicting *M. spicatum* presence in lakes in Wisconsin, USA (Buchan & Padilla, 2000). In addition to physically moving plant propagules, boat wakes and propeller-wash uproot plants and propellers produce plant fragments that can be dispersed via multiple secondary vectors (Mumma *et al.*, 1996; Owens *et al.*, 2001).

Secondary vectors

Secondary vectors are processes that can facilitate dispersal following introduction by primary vectors (Ridley, 1930 cited by Mack & Lonsdale, 2001). Secondary vectors for freshwater plants are not mediated by humans and typically function at a watershed scale, but can result in rapid, long-distance dispersal of established populations of invasive species.

Hydrochory (Water Currents)

Hydrochory is the dispersal of plant propagules by water and is the primary mode of dispersal for many aquatic plants (Sculthorpe, 1967; Sarneel, 2012). Much of the research on the importance of hydrochory has focused on dispersal in lotic systems and riparian plant species (Johansson *et al.*, 1996; Mills *et al.*, 1996; Nilsson *et al.*, 2010). The importance of hydrochory in lentic systems is less studied; however, Nilsson *et al.* (2010) hypothesized that zoochory or anemochory may be more important for lentic species than hydrochory.

The importance of hydrochory in dispersal of freshwater plants is a function of plant growth form, propagule buoyancy and type (vegetative versus generative), and the timing of hydrology and plant phenology. Boedeltje *et al.* (2003) found that that 100% of the propagules from free-floating plants, 98.9% of the propagules from submerged plants, and 23.7% of the propagules from emergent plants were vegetative in a lowland stream in The Netherlands. Seeds and vegetative propagules function differently in hydrochory. Vegetative propagules are usually larger than seeds and more buoyant, which allows them to disperse longer distances, but also makes them more likely to become trapped by obstacles. Vegetative propagules have a greater probability to establish but are more short-lived than seeds (Johansson & Nilsson, 1993). Buoyancy is an important determinant of dispersal distance and fate of dispersing propagules in flowing systems. Highly buoyant stem fragments tend to be deposited in shallow water or trapped in riparian vegetation, whereas less buoyant fragments that float beneath the water surface are more likely to be retained in deeper water with established submerged vegetation and obstacles in the streambed (Riis & Sand-Jensen, 2006). High flow and turbulence can overcome buoyancy effects (Andersson *et al.*, 2000) and non-buoyant seeds can be transported in the bed load of more turbulent, fast moving rivers (Markwith & Leigh, 2008); however, seed production must be timed to seasonal hydrology to ensure long-distance dispersal (Truscott *et al.*, 2006).

Dams and reservoirs can impede hydrochory by altering hydrology (timing, magnitude, and duration of high and low flows and the rate of change in flow), the timing of exposure of shorelines, and act as a sink for downstream movement of seeds (Nilsson *et al.*, 2010). Rood *et al.* (2010) found that dams impeded the downstream movement of riparian weeds in the Snake River, USA, which they attributed to repeated reservoir drawdown and refilling for hydropower production. These activities result in alternating periods of flood and drought that impede riparian plant establishment. The high disturbance regime may also facilitate establishment of other invaders. Non-indigenous species, including *M. spicatum*, are more likely to occur in reservoirs than in natural lakes in the Laurentian Great Lakes region (Johnson *et al.*, 2008). Johnson *et al.* (2008) attributed this to the young age of reservoirs, increased niche availability, and disturbance in most impoundments. They further argued that reservoirs may act as invasive "hubs" *sensu* (Muirhead & MacIsaac, 2005) that serve as a source of propagules for invasion of nearby natural water bodies.

Anemochory (Wind)

Although wind dispersal of free-floating plants is commonly observed, there are few published studies documenting its importance. Wind has moved even large mats of *Eichhornia crassipes* in Lake Victoria and resulted in markedly different daily and seasonal differences in distribution (Albright *et al.*, 2004). Wind was also cited as a vector for dispersal of water hyacinth in Bahia, Brazil (Fidelman, 2005), and of *Salvinia molesta* on Lake Kariba, Africa (Mitchell, 1973) and the Sepik River, Papua New Guinea (Mitchell *et al.*, 1980). The effectiveness of anemochory in dispersal of free-floating plants is a function of the "sail area" that the leaves provide, which is a plastic phenotypic trait in some plants. The morphology of free-floating plants is often density dependent: crowded stands of *E. crassipes* and *S. molesta* tend to form upright leaves (Agami & Reddy, 1990; Jacono *et al.*, 2001) that facilitate anemochory.

Fruits and seeds of aquatic plants lack structures known to facilitate aerial transport and aerial dispersal is typically limited to a few meters (Sculthorpe, 1967; Cook, 1985). Champion and Clayton (2000) suggested, however, that *Typha* species were introduced to New Zealand from Australia by windblown seeds. Sarneel *et al.* (2014) found that wind had an important role in dispersal of floating seeds in lentic systems. They reported that increasing wind speed increased dispersal speed but decreased dispersal distance.

Zoochory (Animals)

Over 150 years ago in the *Origin of Species*, Charles Darwin (1859) proposed that the wide range of some freshwater plant species was a result of dispersal on the plumage and muddy feet of waterfowl. Zoochory has been suggested as an important mechanism for maintaining plant population genetic diversity in rivers in the face of continuous downstream movement of propagules (Honnay *et al.*, 2010; Chen *et al.*, 2009). Waterfowl are perhaps the most-studied zoochorous vector for aquatic plants (Figuerola & Green, 2002; Charalambidou & Santamaría, 2002). Dispersal by fish (Agami & Waisel, 1988; Pollux *et al.*, 2007) and beavers (Medwecka-Kornaś & Hawro, 1993) has also been documented. Dispersal by waterfowl is thought to likely facilitate longer distance dispersal than mammals or fish and has been implicated in maintenance of continent-scale biodiversity and as an important vector for adjustment of aquatic plant communities in response to climate change (Raulings *et al.*, 2011; Viana *et al.*, 2013).

Zoochory can occur through transport of plant propagules internally in the digestive tract (endozoochory) or externally on the animal's body (exozoochory). It is clear that waterbirds and some fish consume aquatic plant propagules, but the importance of endozoochory as a dispersal agent for aquatic plants is unclear. Plant propagules differ in their tolerance to gut passage and waterfowl species differ in their gut metabolism and migratory patterns (Figuerola & Green, 2002). Clausen *et al.* (2002) suggested that long-distance endozoochory by waterfowl is likely to be rare because: 1) most long-distance movements of waterfowl are out of phase with the reproductive efforts of the plants, and if birds arrive at sites when plants still bear seeds then the birds are likely to leave well after the seed stock has been depleted; 2) most long-distance seed transport by birds is likely to be uni-directional, from north to south during autumn migration; 3) most gut contents are likely to be discharged within 300 km of departure; and 4) in many cases birds will arrive in habitats much different from the ones they left, reducing the probability of environmental match and establishment in the receiving environment. Although the possibility of an individual waterfowl transporting aquatic plant seeds may be rare, the large numbers of migrating waterfowl may, collectively, make them effective dispersal agents (Mueller & van der Valk, 2002). Endozoochory in fish and mammals is less well studied than in waterfowl. Agami & Waisel (1988) and Pollux *et al.* (2007) found that fish species and plant species were both important considerations in fish dispersal of aquatic plant seeds. Gottsberger (1978) documented fish dispersal of allochthonous seeds and fruits by fish in Amazonia.

Exozoochory is more difficult to quantify than endozoochory. There are surprisingly few rigorous studies of plant propagules transported attached to birds and mammals. Sculthorpe (1967, p. 357) cited "innumerable" reports of waterfowl carrying fragments of submersed aquatic plants and suggested that even the larger flying aquatic insects could transport small plant fragments. Johnstone *et al.* (1985) found that several highly invasive submerged plants were absent from lakes that were near lakes colonized by these species and concluded that waterfowl were ineffective vectors for plants, even over short distances. Cook (1990) examined transport of *Nymphoides peltata* seeds on ducks. He found that the marginal trichomes on the *N. peltata* seeds allowed the seeds to adhere to duck feathers even in a dry atmosphere. When the trichomes were removed, the seeds did not adhere after they dried. Brochet *et al.* (2010) found that endozoochory was much more important than exozoochory in dispersal of aquatic plant propagules by teal (*Anas crecca*) in the Carmargue in southern France. They found 21 plant taxa were transported internally and 10 were transported externally on the birds. Up to 171 endochorous propagules were found per bird, but no bird had carried more than one propagule externally. Exozoochory by mammals is poorly documented although aquatic mammals may be expected to be effective vectors for small floating plants such as *Lemna*, *Salvinia*, *Spirodela*, and *Wolffia* species. Manatees and turtles have been suggested as vectors for seagrass dispersal (Kendrick *et al.*, 2012), but we could find no published reports of these species as vectors for freshwater aquatic plants. MedweckaKornaś & Hawro (1993) reported that beavers transported plant propagules on the food, branches, stones, and mud used in construction of dams.

3.2 Relative Importance of Aquatic Plant Vectors

Keller *et al.* (2009) reported that 71% (22 of 31) of the nonindigenous freshwater plants in Great Britain were introduced as ornamentals, six percent were agricultural imports, 10% were introduced as contaminants, and the vector for 13% of the species could not be discerned. The relative importance of vectors of introduction of invasive freshwater plants in the USA was assessed using the United States Geological Survey Nuisance Aquatic Species (USGS NAS) database. This database includes 34,150 records of invasive freshwater plants (including plants that can survive in fresh-brackish water) in the USA. The database was populated through online reports and literature surveys. Twenty-one species account for 80% of the freshwater plant records in the database (Table 3.1). Approximately half of the database records are for emergent species (Figure 3.1). Free-floating and submersed plants each account for about one-quarter of the database entries. Rooted, floating-leaf plants comprise only 1% of the database records.

Tab. 3.1: Species of freshwater invasive plants recorded in the USGS NAS database that comprise 80% of the database records.

Growth Form	Species	% of Database Records
Emergent	*Eichhornia crassipes*	11.00
Submersed	*Myriophyllum spicatum*	8.14
Submersed	*Hydrilla verticillata*	8.11
Emergent	*Panicum repens*	5.58
Emergent	*Alternanthera philoxeroides*	5.53
Emergent	*Lythrum salicaria*	4.94
Floating	*Salvinia minima*	4.88
Floating	*Pistia stratiotes*	4.61
Submersed	*Potamogeton crispus*	4.00
Emergent	*Urochloa mutica*	3.48
Emergent	*Colocasia esculenta*	3.36
Emergent	*Nasturtium officinale*	2.46
Emergent	*Iris pseudacorus*	1.84
Emergent	*Myriophyllum aquaticum*	1.78
Submersed	*Egeria densa*	1.78
Emergent	*Agrostis gigantea*	1.77
Emergent	*Persicaria maculosa*	1.63

continued **Tab. 3.1:** Species of freshwater invasive plants recorded in the USGS NAS database that comprise 80% of the database records.

Growth Form	Species	% of Database Records
Emergent	*Lysimachia nummularia*	1.29
Emergent	*Echinochloa crus-galli*	1.25
Submersed	*Najas minor*	1.22
Emergent	*Typha angustifolia*	1.05

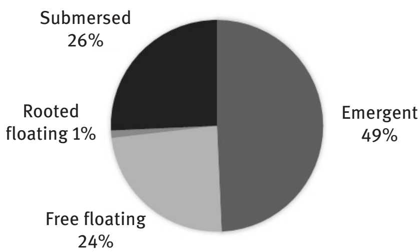

Fig. 3.1: Proportion of freshwater plant growth forms represented in the USGS NAS database.

The database contains records on 136 different species of freshwater aquatic plants that include assignment of a primary vector of introduction, although the vector descriptions differed from those described above (Table 3.2). Some plants that were entered into the database from multiple sites have more than one primary vector assigned to them. For example, *E. crassipes* has 3,657 records in the database, which include four different primary vector assignments (dispersed, hitchhiker, planted/escaped, and released). A total of 182 individual records had a primary vector assignment. Natural dispersal, hitchhiking, planted/escaped, and released vectors were each associated with 21 to 27% of the records. Shipping was associated with nine percent of the records (Figure 3.2).

Tab. 3.2: Categories of dispersal of freshwater aquatic plants in the USGS NAS database.

Dispersed	**Natural dispersal by water, animals, etc.**
Hitchhiker	Introduction via fishing/boating, aquaculture, or on other introduced plants
Planted/Escaped	Intentionally planted for wildlife habitat, erosion control, or as an ornamental or escaped from cultivation
Released	Aquarium or other unspecified release into the environment
Shipping	Solid or water ballast

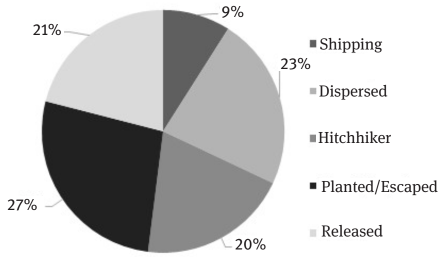

Fig. 3.2: Primary vector associated with freshwater plant records in the USGS NAS database.

The database included 3,573 records that included both growth form and vector fields. The relative importance of vectors differed with growth form. Natural dispersal was the most important vector for emergent plants, free-floating and submersed plants were primarily dispersed by hitchhiking, and planting was the dominant vector for rooted-floating plants (Figure 3.3). Emergent plants often produce abundant rhizomes, stems, or other specialized vegetative organs that are adapted to natural dispersal by hydrochory (Sarneel, 2013). Free-floating plants are located at the surface and submersed plants are typically flaccid, characteristics that facilitate attachment to boats and hitchhiking. Rooted, floating-leaved plants are popular ornamentals and are intentionally planted in water gardens (Nash & Thorpe, 1998).

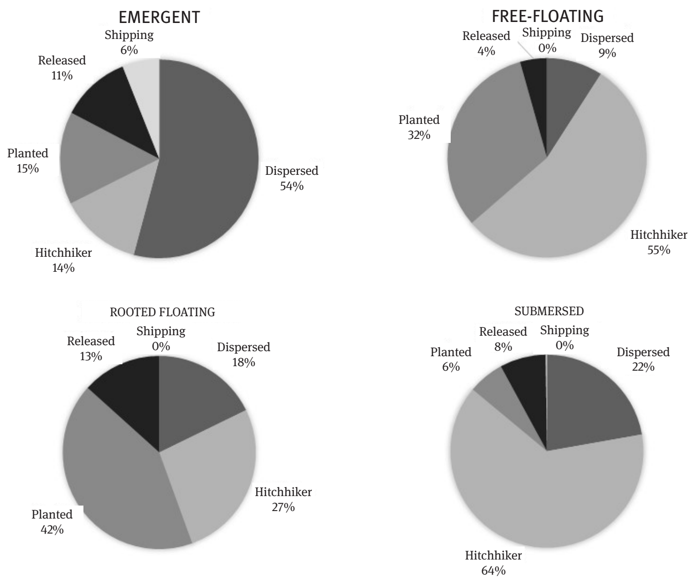

Fig. 3.3: Relative importance of vector by growth form of invasive freshwater aquatic plants in the USGS NAS database.

3.2.1 Conclusions

Vector management is the key to successful and economical management of alien invasive species. Development of the predictive models of alien invasive species dispersal that are required for effective management of aquatic plant invasions will require combining understanding of organism biology, probability of introduction, and site suitability (Buchan & Padilla, 2000; Vander Zanden & Olden, 2008; Jacobs & MacIsaac, 2009; Tamayo & Olden, 2013). Our understanding of all three of these key elements is inadequate for aquatic plants. In addition, several environmental and social factors can be expected to alter each of them to some degree, which will further complicate our ability to make useful predictions. For example, climate change that results in alteration of seasonal precipitation patterns or the timing of significant hydrological events could have multiple, interacting influences on aquatic plant vectors. Water scarcity could reduce popularity of water gardening, the most important primary vector, and increase the number of reservoirs, which would alter hydrology and hydrochory, the most important secondary vector. Other factors could also influence the relative importance of aquatic plant vectors. Increases in fuel cost could lead to a decrease in the number recreational boats and a reduction in the boating vector strength (National Marine Manufacturers Association Canada, 2012). Increased border security in response to terrorism will have the ancillary benefit of increasing inspections and strengthening of biosecurity enforcement, which will reduce instances of intentional introduction.

More detailed and in-depth analysis of primary vectors for aquatic plant introduction is required for cost-effective suppression of vector strength. Recent assessment of vectors for marine alien invasive species introduction into California provides an excellent model (California Ocean Science Trust, 2014) that could be applied to freshwater invasions in general and freshwater plants specifically. Better understanding of the underlying sociological factors that influence individual interest in aquatic plant culture would aid in development of effective outreach and education programs to minimize escape or release from cultivation. Finally, research on factors that control propagule establishment success, and how those factors interact in time and space with vectors, is needed for development of early detection programs that are necessary for cost-effective eradication of pioneering populations of invasive aquatic plants.

3.3 Acknowledgements

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In a nutshell

- Invasive freshwater aquatic plants degrade fish and wildlife habitat and other ecosystem services provided by aquatic systems.
- A vector is the physical means or agent by which species are transported (see Chapter 1).
- Primary vectors of introduction, such as intentional introduction for ornamental use or accidental introduction on boats, are human-mediated and are subject to interdiction with appropriate vector management.
- Secondary vectors are natural dispersal mechanisms, such as waterfowl and water currents, which can function in local and long-distance dispersal of established species.
- Factors that determine success of propagule establishment and how it interacts with vector strength are poorly understood.
- Climate change may alter the importance of vectors in unpredictable ways and complicate development of the predictive models that are necessary for cost-effective early detection and rapid response to new introductions..

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