

Hydrilla (*Hydrilla verticillata*)

Ecological Risk Screening Summary

U.S. Fish & Wildlife Service, November 2020
Revised, November 2020
Web Version, 9/9/2021

Organism Type: Plant (all biotypes)
Overall Risk Assessment Category: High



Photo: Sullivan J. Licensed under Flickr Creative Commons. Available: <https://www.flickr.com/photos/eddiesfisheriesfws/43003926565/>. (November 2020).

1 Native Range and Status in the United States

Native Range

From Jacono et al. (2020):

“The common dioecious type originates from the Indian subcontinent. Historical reports specify the island of Sri Lanka (Schmitz et al. 1991) while random amplified polymorphic DNA (RAPD) analysis points to India's southern mainland (Madeira et al. 1997). Korea appears the likely origin for the monoecious type (Madeira et al. 1997).”

From CABI (2020):

“In Asia, it is found from Iran and Afghanistan through Pakistan and India to South-East Asia, reaching northwards to Japan, Korea and Manchuria, China. It was first recorded on north Iraqi rivers by Al-Mandeeel (2013). It is thought to be native to Africa and south and southeast Asia (Zhuang and Beentje, 2017).”

“It also occurs in the Moluccas, Indonesia and Papua New Guinea. In the Indian Ocean it occurs on Mauritius, Réunion and Madagascar. In the Pacific Ocean it has been found on Fiji and Guam. It is a common plant in the northern and western parts of Australasia [*sic*] [...]”

“It is thought to be native but is relatively rare in Europe (Preston and Croft, 1997), sufficiently so that it is protected in Lithuania (Balevicius, 1998). It occurs in certain areas in Poland and Belarus, and has been found in solitary lakes in Ireland (Preston and Croft, 1997).”

From Department of Primary Industries, Parks, Water and Environment (Tasmania) (2020):

“Hydrilla is a native on mainland Australia and is not usually weedy.”

Status in the United States

Hydrilla verticillata is listed on the USDA (2020) Federal Noxious Weed List. It has the following State statuses:

- Alabama: Class A noxious weed
- Arizona: Prohibited noxious weed
- California: A list (noxious weeds); Noxious aquatic weed; Quarantine
- Colorado: A list (noxious weeds)
- Connecticut: Invasive, banned
- Florida: Prohibited aquatic plant, Class 1
- Maine: Invasive aquatic plant
- Massachusetts: Prohibited
- Mississippi: Noxious weed
- Nevada: Noxious weed
- New Mexico: Class A noxious weed
- North Carolina: Class A noxious weed
- Oregon: “A” designated weed; Quarantine
- South Carolina: Invasive aquatic plant; Plant pest
- Texas: Noxious plant
- Vermont: Class A noxious weed
- Washington: Class A noxious weed; Wetland and aquatic weed; Quarantine

H. verticillata is a prohibited species in New York (New York State Senate 2014).

H. verticillata is considered an invasive plant species in Ohio (Ohio Department of Agriculture 2018).

The United States Army Corps of Engineers treats established populations of *H. verticillata* in multiple districts of the United States, including the Erie Canal (New York) and Great Lakes Basin.

From Levenson (2020):

“The Corps of Engineers is authorized to treat Hydrilla (*Hydrilla verticillata*) under Section 104 of the River and Harbor Act of 1958, through the Aquatic Plant Control Research Program.”

From CABI (2020):

“In the USA it has been listed as a Federal Noxious Weed since 1976, and is regarded as one of the worst invasive aquatic weed problems in Florida and much of the country.”

From Jacono et al. (2020):

“The distribution of biotypes is changing rapidly, however, southern populations were predominantly dioecious female (plants having only female flowers) that overwinter as perennials (the monoecious biotype has spread south through Georgia, South Carolina, Tennessee, and Alabama). Populations north of South Carolina were often monoecious (having both male and female flowers on the same plant) (Cook and Lüönd 1982; Madeira et al. 2000).”

“Currently established in 28 states of the US (AL, AZ, AR, CA, CT, DE, FL, GA, ID, IN, LA, ME, MD, MA, MS, MO, NJ, NY, NC, OH, OK, PA, SC, TN, TX, VA, WV), as well as Guam and Puerto Rico; occurrences in Iowa, Kansas, Washington, and Wisconsin were removed or controlled in isolated ponds (Sample 1972; Kansas Department of Wildlife, Parks and Tourism 2009; Herrera 2011; Asplund 2007).”

From Harms et al. (2020):

“Both the monoecious and dioecious biotypes in the US belong to the B clade and were likely introduced from India (dioecious) and Korea (monoecious) (Madeira et al. 1997, 2000). In the US, the dioecious biotype occurs in southern regions, whereas the monoecious biotype has a more northern distribution (Madeira et al. 2000).”

“Tippery et al. (2020) recently reported a new introduction of hydrilla in the US Connecticut River. The new Connecticut River introduction belongs to clade C [...]”

A search for *H. verticillata* for sale online did not return results. However, according to the Center for Aquatic and Invasive Plants (2020), it can be found for sale online: “*Hydrilla verticillata* continues to be sold through aquarium supply dealers and over the Internet, even though the plant is on the U.S. Federal Noxious Weed List.”

Means of Introductions in the United States

From Jacono et al. (2020):

“The dioecious strain was imported to the United States in the early 1950s for use in aquariums. It entered Florida's inland water system after plants were discarded or planted into canals in Tampa and Miami (Schmitz et al 1991). The monoecious strain was a separate introduction, first found decades later in Delaware and the Potomac Basin (Environmental Laboratory 1985; Miller 1988; Madeira et al 2000).

Hydrilla is mainly introduced to new waters as fragments on recreational boats, their motors and trailers and in live wells. Stem pieces root in the substrate and develop into new colonies, commonly beginning near boat ramps. Once established, boat traffic continues to break and spread hydrilla throughout the waterbody. Both biotypes propagate primarily by stem fragmentation, although axillary buds (turions) and subterranean tubers are also important. Tubers are resistant to most control techniques (Schardt 1994) and may be viable as a source of reintroduction for years (Van and Steward 1990).

Hydrilla may be unknowingly transplanted into private ponds as a contaminant in water garden plants. It was found spreading after extensive 2,4-D use in Tennessee Valley Authority reservoirs and Lake Seminole, Georgia, once heavily populated with Eurasian water-milfoil (*Myriophyllum spicatum*) (Bates and Smith 1994). This has not yet been observed in northern lakes (M. Netherland, USACE pers. comm. 2015).”

Remarks

This ERSS was previously published in two versions in September 2017: one including information for the dioecious biotype, and one for the monoecious biotype. Since that publication, a third biotype has been discovered within the United States, in the Connecticut River. This screening includes information for all three known biotypes. Revisions were completed to incorporate new information and conform to updated standards.

According to ITIS (2020), this species is also commonly referred to as Florida Elodea and Water Thyme (other spellings: Water-Thyme and Waterthyme).

2 Biology and Ecology

Taxonomic Hierarchy and Taxonomic Standing

According to WFO (2021), *Hydrilla verticillata* is the accepted name for this species.

From ITIS (2020):

Kingdom Plantae
Subkingdom Viridiplantae
Infrakingdom Streptophyta
Superdivision Embryophyta
Division Tracheophyta

Subdivision Spermatophytina
Class Magnoliopsida
Superorder Lillanae
Order Alismatales
Family Hydrocharitaceae
Genus *Hydrilla*
Species *Hydrilla verticillata* (L. f.) Royle

Size, Weight, and Age Range

From Jacono et al. (2020):

“Stems grow up to 9 m in length; leaves are 6-20 mm long and 2-4 mm wide.”

From Zhuang and Beentje (2017):

“Hydrilla stems are [...] up to 25 feet long.”

From CABI (2020):

“Tubers can remain viable for several days out of water or for over 4 years in undisturbed sediment.”

Environment

From CABI (2020):

“*H. verticillata* can be found in freshwater [...] but it can tolerate salinities of up to 7%. This species can grow in springs, lakes, marshes, ditches, rivers, and tidal zones. It is also adapted to grow in relatively low light and CO₂ conditions. In areas where this species behaves as an invasive, it can be found infesting freshwater lakes, ponds, rivers, and impoundment canals.”

“In the tropics, *H. verticillata* is described as tolerant of a wide variety of water conditions, from acidic and oligotrophic to eutrophic or brackish; it thrives on many kinds of pollution and tolerates a great deal of disturbance (Cook and Lüönd, 1982), although increasing salinity appears to limit its dispersal (Rout et al., 1998; Mataraza et al., 1999; Rout and Shaw, 2001). Due to its tolerance of low light conditions (White et al., 1996), it is capable of growing in water up to 7 m deep (Yeo et al., 1984). In the tropics, it forms dense monospecific stands (Valley and Bremigan, 2002). In temperate regions, it grows in alkaline, moderately calcareous, mesotrophic or slightly eutrophic waters (Preston and Croft, 1997), richer in SO₄, but generally poorer in Na, K and Cl than those of *Elodea canadensis* (Klosowski and Tomaszewicz, 1997). It also appears to occur more often as scattered stands within more diverse aquatic plant communities (Klosowski and Tomaszewicz, 1997; Balevicius, 1998). In the USA, *H. verticillata* grows optimally at 20-27°C. *H. verticillata* exhibits moderate salinity tolerance, persisting in a laboratory environment at 7 ppt when transitioned in one step from fresh water, and at up to 12 ppt when the transfer was gradual.”

From Zhuang and Beentje (2017):

“This species is hardy and tolerant to heavy metals. Many studies have investigated the ecological role of this species in polluted waters (i.e., Wang et al. 2007, Bao 2008, Huang et al. 2009).”

Climate

From CABI (2020):

“*H. verticillata* can be found in freshwater in tropical and temperate regions of the world [...]

From Harms et al. (2020):

“The specific cpDNA haplotype corresponding to the introduced US dioecious biotype [Clade B *H. verticillata*] is found at or below 30° latitude in the East African Great Lakes, Pakistan, India, Nepal, northern Vietnam, and China (Madeira et al. 2007; Williams et al. 2018; Zhu et al. 2015). The introduced US monoecious cpDNA haplotype has a very patchy distribution in eastern China and South Korea and is known to occur from 29° to 37° latitude (Williams et al. 2018; Zhu et al. 2015).”

“This haplotype [Clade C *H. verticillata*] occurs in north-eastern PRC between 38.9° and 45.0° latitude [...] which encompasses the latitude it was found in Connecticut (41.4°).”

Distribution Outside the United States

Native

From Jacono et al. (2020):

“The common dioecious type originates from the Indian subcontinent. Historical reports specify the island of Sri Lanka (Schmitz et al. 1991) while random amplified polymorphic DNA (RAPD) analysis points to India's southern mainland (Madeira et al. 1997). Korea appears the likely origin for the monoecious type (Madeira et al. 1997).”

From CABI (2020):

“In Asia, it is found from Iran and Afghanistan through Pakistan and India to South-East Asia, reaching northwards to Japan, Korea and Manchuria, China. It was first recorded on north Iraqi rivers by Al-Mandeel (2013). It is thought to be native to Africa and south and southeast Asia (Zhuang and Beentje, 2017).”

“It also occurs in the Moluccas, Indonesia and Papua New Guinea. In the Indian Ocean it occurs on Mauritius, Réunion and Madagascar. In the Pacific Ocean it has been found on Fiji and Guam. It is a common plant in the northern and western parts of Australasia [*sic*] [...]

“It is thought to be native but is relatively rare in Europe (Preston and Croft, 1997), sufficiently so that it is protected in Lithuania (Balevicius, 1998). It occurs in certain areas in Poland and Belarus, and has been found in solitary lakes in Ireland (Preston and Croft, 1997).”

From Department of Primary Industries, Parks, Water and Environment (Tasmania) (2020):

“Hydrilla is a native on mainland Australia and is not usually weedy.”

Introduced

From CABI (2020):

“On the African continent it occurs around Lake Victoria and Lake Tanganyika in the Rift Valley of East Africa, while it has also been reported from Mozambique and a few isolated places in West Africa and, in 2006, from South Africa.”

“At least three different strains of *H. verticillata* have spread to [...] the Panama Canal area.”

“There are recent reports from South America (Brazil) and Caribbean islands. It was locally introduced into the La Gamba valley of southern Costa Rica in 2005 (Haider et al., 2016).”

“Its import is prohibited in Western Australia and Tasmania, and it is on the EPPO alert list.”

“[...] and it also occurs in the North Island of New Zealand.”

According to CABI (2020), *H. verticillata* has also been introduced to the following countries outside of the United States: Côte d'Ivoire, Ghana, Iraq, Austria, Spain, Aruba, Barbados, Cuba, Dominica, Grenada, Guadeloupe, Guatemala, Honduras, Jamaica, Martinique, Mexico, Nicaragua, New Caledonia, Brazil, and Venezuela.

According to New Zealand Plant Conservation Network (2020), *H. verticillata* has been naturalized in New Zealand since 1963.

From Carniatto et al. (2014):

“This macrophyte was first recorded in the Paraná River [Brazil] in 2005, and it has rapidly invaded the main river and its lateral channels (Sousa 2011).”

From Coetzee et al. (2009):

“[...] this study has shown that there is considerable potential for hydrilla to spread from the only site in [South Africa] which it currently occurs to uninvaded systems around South Africa. Furthermore, should it spread from Pongolapoort Dam, its establishment is unlikely to be limited by climate according to the CLIMEX model.”

Means of Introduction Outside the United States

From CABI (2020):

“Worldwide shipments of aquatic herbs have been found contaminated with *H. verticulata* [sic] and this species is still sold as an aquarium plant. [...] As *H. verticillata* was introduced to the New World as an aquarium plant, legislative measures should be taken worldwide to restrain this trade.”

“It is readily dispersed by movement of plant fragments and can produce up to 6,000 tubers per m².”

From Coetzee et al. (2009):

“Hydrilla was introduced into the USA via the aquarium trade (Schmitz et al. 1991), and it is likely that this was the mode of introduction into South Africa too. Even though hydrilla has been present in central east Africa for considerable time (Mahler 1979), genetic analysis of South African hydrilla has shown that it is most closely related to hydrilla from Malaysia and Indonesia (Madeira et al. 2007), and interestingly, the majority of aquarium plants imported into South Africa come from Singapore, Malaysia (N. Stallard, personal communication).”

Short Description

From Zhuang and Beentje (2017):

“Hydrilla stems are slender, branched and up to 25 feet long. Hydrilla 's small leaves are strap-like and pointed. They grow in whorls or four to eight around the stem. The leaf margins are distinctly saw-toothed. It produces tiny white flowers on long stalks.”

From Jacono et al. (2020):

“Submersed perennial herb. Rooted, with long stems that branch at the surface where growth becomes horizontal and dense mats form. [...] Development of these features may vary with location, age, and water quality (Kay 1992).”

“Morphologically similar species include exotic Brazilian waterweed (*Egeria densa*), native western waterweed (*Elodea nuttallii*), and native (except Alaska and Puerto Rico) Canadian waterweed (*Elodea canadensis*). *E. densa*, *E. nuttallii*, and *E. canadensis* have 3-6 leaves per whorl, with inconspicuous leaf serration and no dentation on midrib, but *E. densa* leaves are 2-3 cm long, and both *E. nuttallii* and *E. canadensis* usually has 3 leaves per whorl near stem base (Langeland et al. 2008, Wunderlin and Hansen 2011, Rybicki et al. 2013).”

From CABI (2020):

“The sessile leaves are formed in whorls at the nodes; there are 3-8, sometimes up to 12 leaves in a whorl. The leaves are 7-40 mm long, linear to lanceolate, with a conspicuous midrib. They have sharply toothed margins and spines on the vein on the lower side of the leaves; a few teeth may also be formed on this vein.”

“The inflorescences are unisexual, arising from spathes situated in the leaf axils, each flower has three sepals and three petals. All six perianth parts are clear or translucent green (the sepals usually slightly reddish). The male spathe is about 1.5 mm long, solitary in the leaf axils, somewhat spiny. The female spathe is about 5 mm long, solitary in the leaf axils. There are three petals, three stamens and three styles. The ovary is cylindrical to narrowly conical and is enclosed in the base of a hypanthium; the style is as long as the hypanthium and there are three stigmas. For further information, see Cook et al. (1974) and Aston (1977).”

The fruit is cylindrical, about 7 mm long and 1.5 mm wide. It contains 2-7 oblong-elliptic seeds.”

Biology

From Jacono et al. (2020):

“Fertile seed production was reported in the monoecious type (Langeland and Smith 1984). Both biotypes depend on tubers for overwintering, although monoecious hydrilla exhibits a more annual habit than the dioecious type, with abundant tuber/turion production around September (Owens et al. 2012).”

“Recent research into molecular techniques for identifying hydrilla and its biotypes has proven successful (Verkleij 1983; Ryan et al. 1995; Madeira et al. 2004). An early method used isoenzyme patterns in hydrilla to distinguish origin and biotype (Verkleij 1983). A later method used a random amplified polymorphic DNA (RAPD) procedure to find DNA markers in hydrilla samples (Ryan et al. 1995; Les et al. 1997; Madeira et al. 1997, 2000). A relatively inexpensive alternative method used “universal primers” to sequence hydrilla DNA (Madeira et al 2004; Benoit and Les 2013; Rybicki et al. 2013).”

“Hydrilla is found in freshwater lakes, ponds, rivers, impoundments, and canals. It mainly spreads vegetatively through dispersal of plant fragments, axillary turions, and tubers (Langeland and Sutton 1980). Tubers remain viable out of water for several days (Basiouny et al. 1978) and in undisturbed sediment for over 4 years (Van and Steward 1990). Viability remains after ingestion and regurgitation by waterfowl, although passage of vegetative propagules through [sic] the digestive tract likely renders them non-viable (Joyce et al. 1980). Sexual reproduction among and between monoecious and dioecious strains is possible (Steward 1993), but its importance is unknown (Langeland and Smith 1984). Sites such as Lake Guntersville, Alabama have large co-occurring stands of monoecious and dioecious hydrilla. Pollination occurs when pollen from free-floating male flowers disperses on the water surface (epihydrophyly) to female flowers (Tanaka 2000; Tanaka 2003).”

From CABI (2020):

“*H. verticillata* may be either monoecious or dioecious. The flowers are unisexual, arising from spathes situated in the leaf axils, each flower has three sepals and three petals. All six perianth parts are clear or translucent green (the sepals usually slightly reddish). The ovary is enclosed in the base of a hypanthium, the style is as long as the hypanthium and there are three stigmas. Due to an elongation of the hypanthium, the female flower ascends to the surface of the water. The

perianth segments remain closed over the stigmas during this movement and retain a bubble of air above them. The perianth segments open to form a wide funnel which floats with its rim just at the water surface, its walls holding back the water and preventing wetting of the stigmas. The male flower becomes detached from the plant and subsequently rises to the surface of the water where the perianth segments uncurl. The anthers dehisce explosively and spread pollen for some 20 cm around the open flower. Pollination occurs via the air.

This species also reproduce [sic] vegetatively through the formation of large clones. In California and the Gulf States of the USA, and in Europe, there is no seed formation because only female flowers are produced.”

“*H. verticillata* exhibits a degree of phenotypic plasticity in response to age, habitat conditions, and water quality. The family is notable for the unique pollination mechanism of some genera (e.g., *Elodea*, *Enhalus*, *Hydrilla*, and *Vallisneria*). The male flowers become detached and float about until they encounter and transfer pollen to a female flower, which has reached the surface of the water by means of an elongated stalk. After pollination, the developing fruit is drawn under the water to finish ripening.”

“*H. verticillata* is an herbaceous perennial that experiences seasonal winter dieback. In order to survive unfavourable growth conditions, this species produces two types of special hibernating organs. These structures are respectively formed in the axil of a leaf (generally described as axillary turions, turions or green turions) and at the tip of branches which grow into the hydrosol (generally described as subterranean turions, brown turions or tubers).”

From Harms et al. (2020):

“The new Connecticut River introduction belongs to clade C [genetically distinct from the known monocious and dioecious biotypes already known in the United States] which has an extensive geographic range, and has been found in China, South Korea, Japan, and Europe (Tippary et al.2020).The sexual strategy of the Connecticut River introduction is unknown. However, clade C individuals in the native range all appear to be dioecious (Williams et al. 2018).”

Human Uses

From Zhuang and Beentje (2017):

“A dried powder from the plant has been used as detergent in the treatment of abscesses, burns and wounds. The plant is also often used to furnish aquaria.”

Diseases

From Smither-Kopperl et al. (1999):

“*Plectosporium tabacinum*, the anamorph of *Plectosphaerella cucumerina*, was isolated in 1996 from *Hydrilla verticillata* (hydrilla), an invasive aquatic weed in Florida. *P. tabacinum*, applied as a suspension of conidia, was pathogenic to hydrilla shoots maintained in aqueous solutions in test tubes. [...] The disease developed over a range of temperatures from 15 to 30°C. At 25°C,

symptoms were most severe in 5% Hoagland's solution, followed by river water, deionized water, 0.5% Hoagland's, tap water, and spring water. Disease severity increased as inoculum concentration was increased from 105 to 107 conidia ml⁻¹. This is the first report of *P. tabacinum* as a pathogen of hydrilla, a fully submerged aquatic plant species.”

Threat to Humans

No direct threats to humans were reported in the literature. The following section refers to economic and social impacts to humans.

From CABI (2020):

“Harmful effects of *H. verticillata* include: impeding the movement of irrigation and drainage water; hindering navigation and recreational use of the water; physical interference with hydro-electric schemes and fisheries; competition with native plants; impacts on native fauna; reductions in size and weight of sport fish (Colle and Shireman, 1980 in Jacono et al., 2011); and the creation of favourable habitats for organisms which cause or transmit disease.

Although it is increasingly troublesome in its original habitat in South-East Asia and Australia, particularly in man-made lakes and irrigation canals, its impact is most significant where it is introduced. This applies, in particular, to the USA, where it was introduced in Florida in the early 1950s (Schardt, 1995). The costs of controlling *H. verticillata* in Florida were reported to be \$200 per ha per year (Haller, 1995) when an area of more than 12,000 ha were heavily infested in the state. Useful summaries of economic and ecological costs due to *H. verticillata* are provided by the Northeast Aquatic Nuisance Species Panel (for the USA) and by Hofstra and Champion (2006) for New Zealand. On one Florida lake (Orange Lake, north-central FL), in years when *H. verticillata* completely covered the lake, recreational activities [*sic*] worth 11 million dollars were lost. In 1994-95, the state of Florida spent ~ 14.5 million dollars on *H. verticillata* control (Langeland, 1996).”

“As *H. verticillata* rapidly forms such dense mats, it becomes impossible to use outboard motors and to pursue fishing, swimming and other recreational activities. It can also result in reduced water flow and stagnant pools which become habitats for mosquito larvae.”

3 Impacts of Introductions

From Jacono et al. (2020):

“It is commonly reported that once established, hydrilla results in an array of ecosystem disruptions. Hydrilla grows aggressively and competitively, spreading through shallower areas and forming thick mats in surface waters that block sunlight penetration to native plants below (van Dijk 1985). In the southeast, hydrilla effectively displaces beneficial native vegetation (Bates and Smith 1994) such as wild-celery (*Vallisneria americana*) and coontail (*Ceratophyllum demersum*) (van Dijk 1985; Rizzo et al. 1996). However, others reported that in a community of submerged aquatic vegetation including monoecious hydrilla, other exotic and native species responded to fluctuations in weather and water quality in the fresh tidal Potomac River (Carter et al. 1994) and the Upper James River in the Chesapeake Bay watershed (Shields

et al. 2012). Hydrilla does not necessarily displace native species and may be beneficial to wildlife (Rybicki and Carter 2002; Rybicki and Landwehr 2007).

Hydrilla has been shown to alter the physical and chemical characteristics of lakes. Colle and Shireman (1980) found reduced weight and size in sportfish when hydrilla occupied the majority of the water column, suggesting that foraging efficiency was reduced as open water and natural vegetation gradients were lost. Stratification of the water column (Schmitz et al. 1993; Rizzo et al. 1996), decreased oxygen levels (Pesacreta 1988), and fish kills (Rizzo et al. 1996) have been documented in waters with hydrilla. Changes in water chemistry due to hydrilla may also be implicated in zooplankton and phytoplankton declines (Schmitz and Osborne 1984; Schmitz et al. 1993). However, other studies find a lack of negative effects of hydrilla on other biota, such as plants, fish, and aquatic bird communities (Killgore et al 1989; Hoyer et al 2008).

Dense beds of hydrilla affects water flow (Rybicki et al 1997) and water use. Beds in the Mobile Delta are reducing flow in small tidal streams and creating a backwater habitat (J. Zolcynski pers. comm. 1998). Its heavy growth may obstruct boating, swimming and fishing in lakes and rivers and may block the withdrawal of water used for power generation and agricultural irrigation. However, because of the resilience of hydrilla to control efforts and its competitive success and comparative vigor in stressed systems and capacity to provide at least some beneficial services combine to suggest it may have a useful role in some systems (Herschner and Havens 2008).”

From CABI (2020):

“*H. verticillata* is a submerged fast-growing aquatic herb. It has a highly effective survival strategy that makes it one of the most troublesome aquatic weeds of water bodies in the world. It has the potential to alter fishery populations, cause shifts in zooplankton communities and affect water chemistry. It forms dense masses, outcompeting native plants and interfering with many uses of waterways.”

“Impact on Habitats

H. verticillata forms dense masses, which may completely fill the volume of waterbodies. Invasion often begins in deep dark waters where most plants cannot grow. Hydrilla grows aggressively and competitively, spreading through shallower areas and forming thick mats in surface waters that may become so deep that sunlight is blocked out (Jacono et al., 2011).”

“Infestation has been shown to alter the physical and chemical characteristics of lakes: affecting stratification of the water column (Schmitz et al., 1993; Rizzo et al., 1996), decreasing oxygen levels (Pesacreta, 1988; Miranda and Hodges, 2000), and impeding the movement of irrigation and drainage water (Jacono et al., 2011). Dense stands also alter water quality by increasing pH and water temperature.”

“Impact on Biodiversity

H. verticillata outcompetes native aquatic plants. In southeast USA, it displaces native vegetation such as wild celery (*Vallisneria americana*) and coontail (*Ceratophyllum demersum*) (van Dijk, 1985; Rizzo et al., 1996 in Jacono et al., 2011).”

“It affects zooplankton and phytoplankton densities (Schmitz and Osbourne, 1984; Schmitz et al., 1993 in Jacono et al., 2011) and supports reduced invertebrate species diversity (Thorp et al., 1997). It has been implicated in reduced fish numbers, size and in fish kills (Rizzo et al., 1996 in Jacono et al., 2011). In a heavy infestation, predatory fish cannot hunt effectively; however ISSG (2011) notes a benefit to prey fish at <30% hydrilla cover.”

“Epiphytic cyanobacteria found on hydrilla are thought to be the agents producing a toxin that causes avian vacuolar myelinopathy (AVM) a disease that has killed at least 100 bald eagles (*Haliaeetus leucocephalus*) and thousands of American coots (*Fulica americana*) since 1994 in locations from Texas to North Carolina, USA (Wilde et al., 2005). The incidence of AVM is likely to increase as *H. verticillata* spreads. Fouts et al. (2017) report 90 bald eagle and hundreds of waterfowl deaths attributed to AVM on a reservoir on the border of Georgia and South Carolina infested with hydrilla.”

From Carniatto et al. (2014):

“In addition to its negative effects on native macrophytes, the spread of *H. verticillata* may have complex implications. For example, although it is morphologically similar to *E. najas*, *H. verticillata* may differ in terms of its associated organisms (e.g., microalgae and ostracods; Theel et al. 2008; Mormul et al. 2010a, b), which may serve as food resources for small sized-fish (Casatti et al. 2003; Pelicice & Agostinho 2006). Thus, since macroinvertebrates may be considered the primary link between plants and fish (Schultz & Dibble 2012), alterations of invertebrate assemblages following invasions by plants may produce cascade effects on fish assemblages.”

“[...] our results indicate that *H. verticillata* did not influence the foraging activity of small-sized fish, but it affected their diet composition. We suggest that these differences are results of the availability of food items, such as invertebrates and microalgae, which most likely tend to colonize each species of macrophyte in different ways.”

Hydrilla verticillata is regulated in multiple States, see section 1.

4 History of Invasiveness

Hydrilla verticillata has a long history of introduction through aquarium use and natural dispersion, starting new colonies through viable fragments. Peer-reviewed studies demonstrate that *H. verticillata* can impact zooplankton communities, block sunlight penetration, reduce dissolved oxygen availability, and outcompete native plant communities in areas where it is introduced. It can also host a cyanobacteria that produces toxins harmful to avian wildlife. Negative impacts of introduction have been shown in numerous peer-reviewed literature for this species, therefore the history of invasiveness is classified as High.

5 Global Distribution

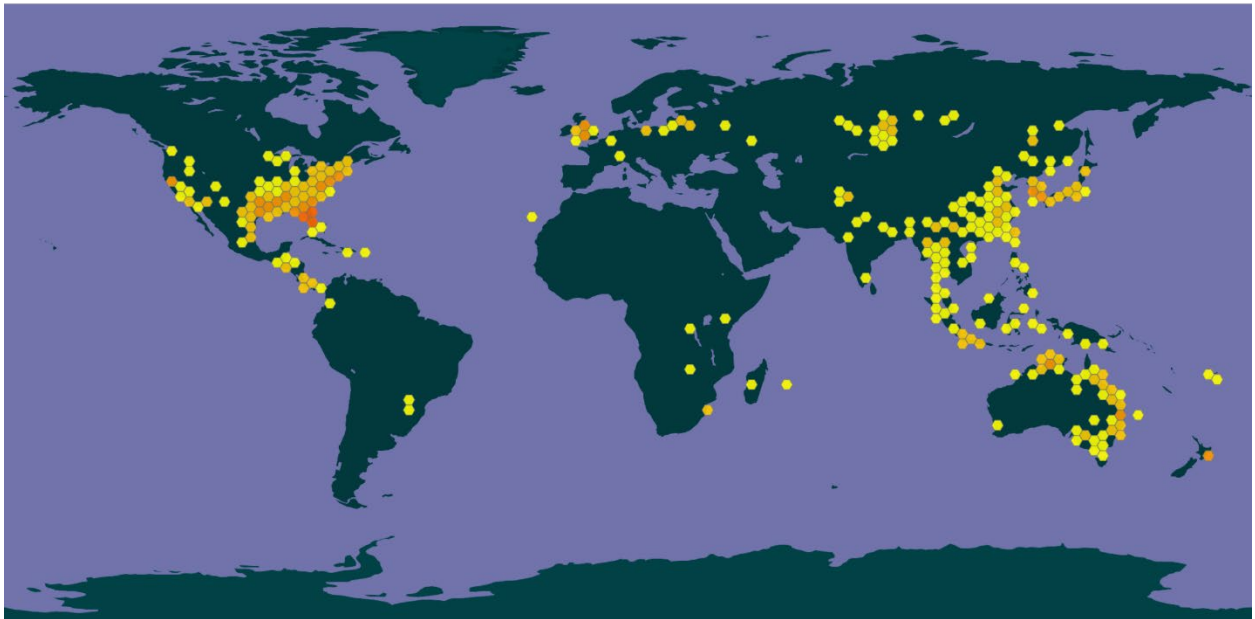


Figure 1. Known global distribution of *Hydrilla verticillata*. Locations are on every continent except Antarctica. Map from GBIF Secretariat (2020). Global distribution represents all biotypes.

6 Distribution Within the United States

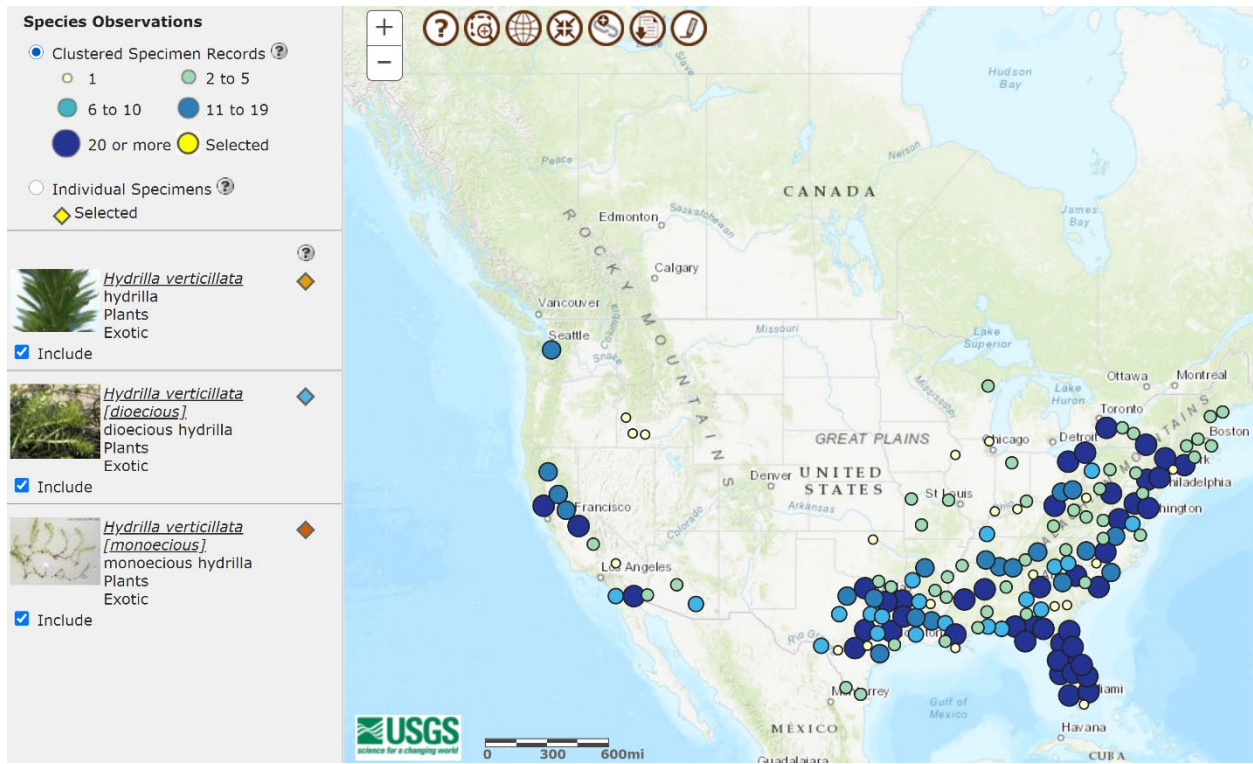


Figure 2. Known distribution of *Hydrilla verticillata* in the United States. Map from BISON (2020). Although according to Jacano et al. (2020), occurrences in Iowa, Kansas, Washington, and Wisconsin were removed or controlled, those records were not removed from climate match analysis because it is known that the plant can establish in the environmental conditions present at those locations.

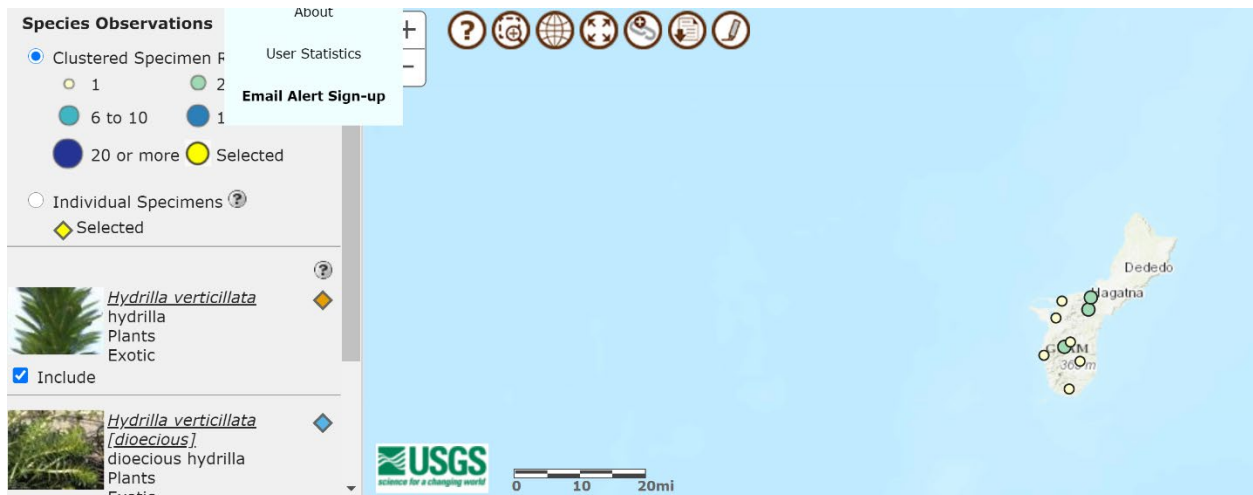


Figure 3. Known distribution of *Hydrilla verticillata* in Guam. Map from BISON (2020).

7 Climate Matching

Summary of Climate Matching Analysis

The climate match for *Hydrilla verticillata* was generally high for the contiguous United States. Match was universally high across the eastern portion of the United States, northern Midwest, and much of the western coast and desert southwest. The overall Climate 6 score (Sanders et al. 2018; 16 climate variables; Euclidean distance) was 0.939, high (scores of 0.103 and greater are classified as high). All States within the contiguous United States received high individual Climate 6 scores.

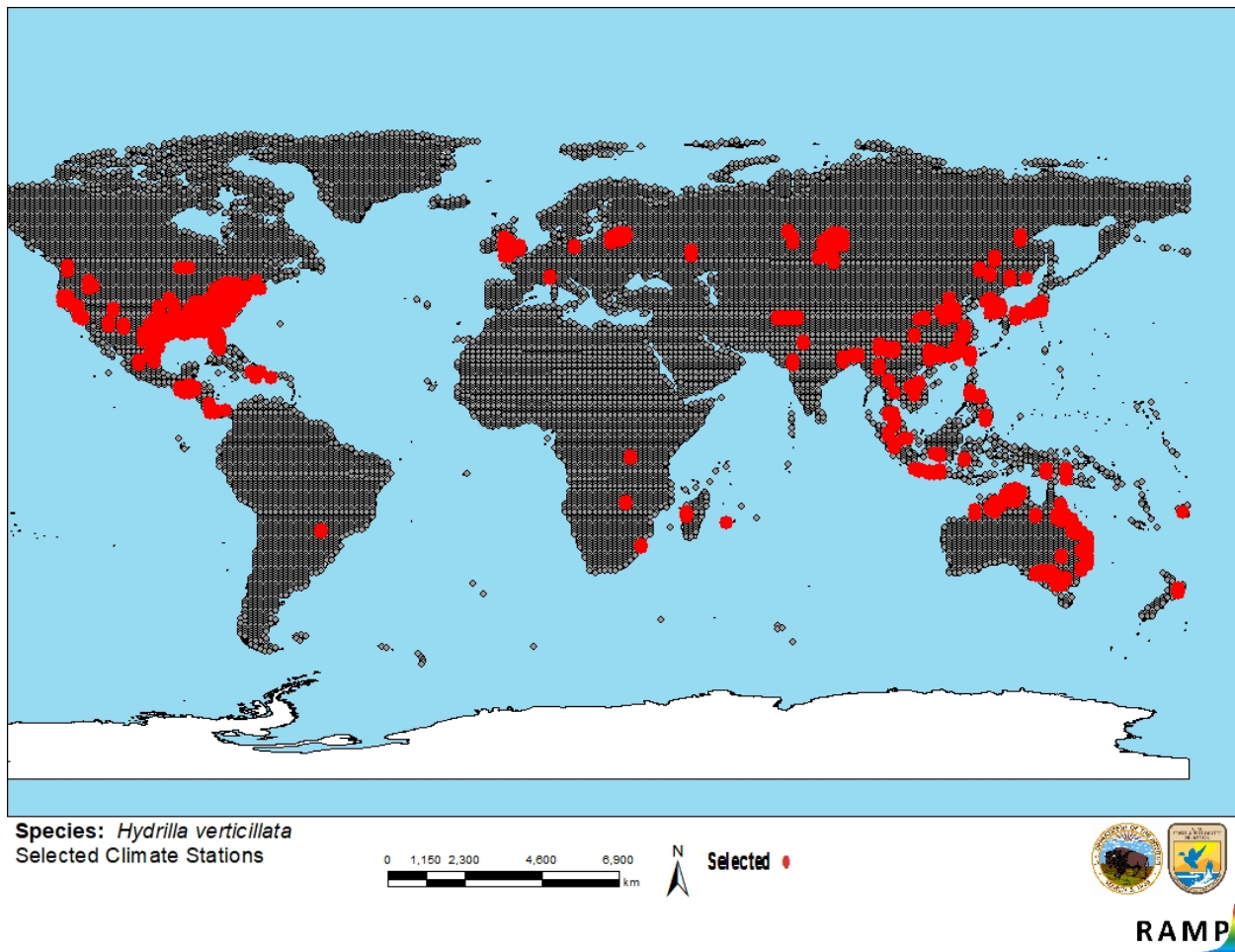


Figure 4. RAMP (Sanders et al. 2018) source map showing weather stations widely distributed across a global map selected as source locations (red) and non-source locations (gray) for *Hydrilla verticillata* climate matching. Source locations from BISON (2020) and GBIF Secretariat (2020). Selected source locations are within 100 km of one or more species occurrences, and do not necessarily represent the locations of occurrences themselves.

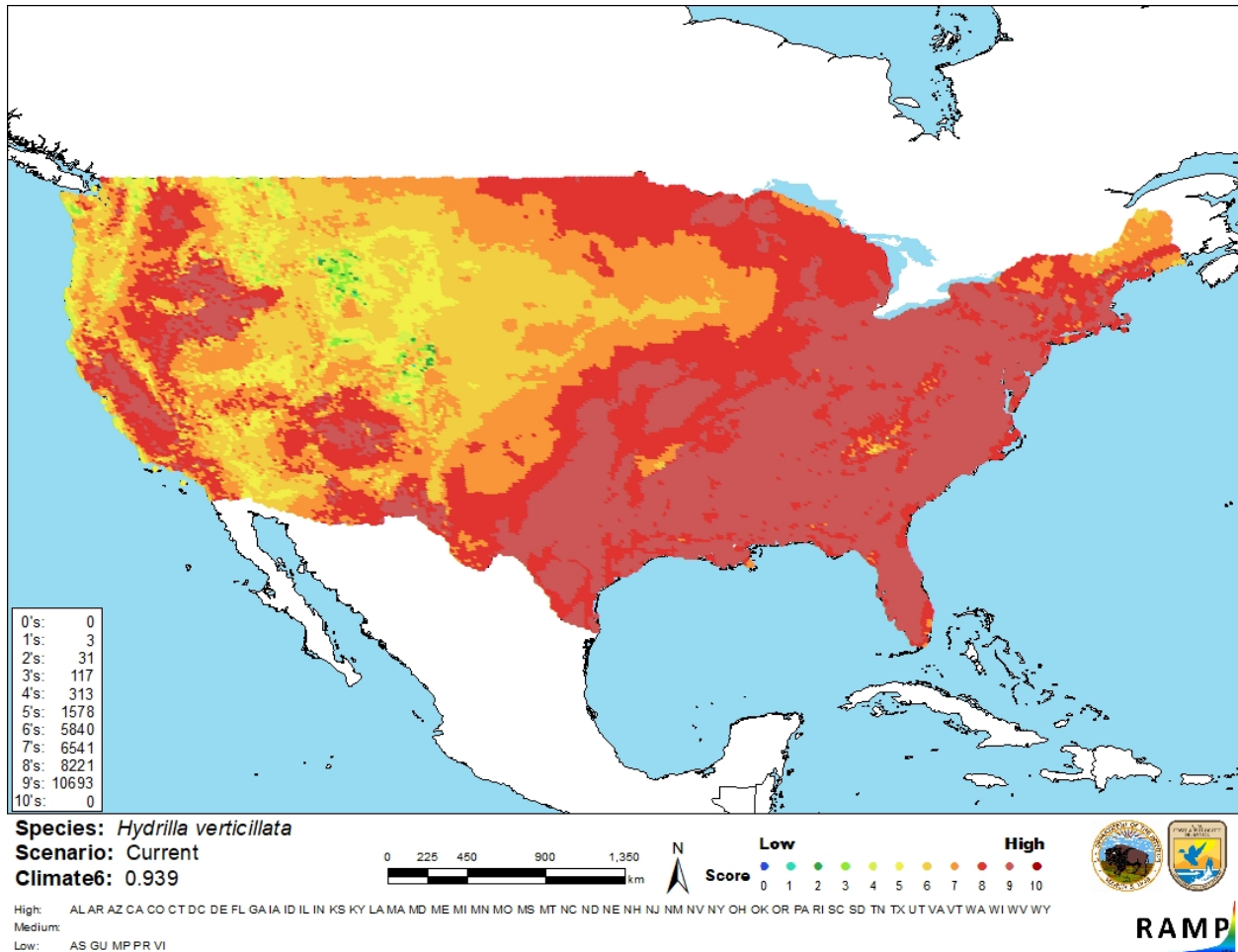


Figure 5. Map of RAMP (Sanders et al. 2020) climate matches for *Hydrilla verticillata* in the contiguous United States based on source locations reported by BISON (2020) and GBIF Secretariat (2020). Counts of climate match scores are tabulated on the left. 0/Blue = Lowest match, 10/Red = Highest match.

The High, Medium, and Low Climate match Categories are based on the following table:

Climate 6: (Count of target points with climate scores 6-10)/ (Count of all target points)	Overall Climate Match Category
$0.000 \leq X \leq 0.005$	Low
$0.005 < X < 0.103$	Medium
≥ 0.103	High

8 Certainty of Assessment

The certainty of assessment is High. There is quality information available about the biology and ecology of *Hydrilla verticillata*. Records of introduction resulting in established populations

were found on a worldwide level. Information on impacts and history of invasiveness were from peer-reviewed and reliable government agency sources.

9 Risk Assessment

Summary of Risk to the Contiguous United States

Hydrilla (*Hydrilla verticillata*) is a freshwater plant native to Asia, Australia and parts of Africa. The species has three separate biotypes, two of which have documented reproductive strategies, and a third biotype discovered in 2020 with little information known regarding reproduction. Hydrilla is a common aquarium plant. The history of invasiveness is classified as High. There is a long history of accidental introductions through contaminated aquarium plant shipments, and natural dispersion when plant fragments break off and re-establish. Boaters and anglers often incidentally transfer the plant from contaminated waterways into unestablished ones. It has been listed as a noxious weed in the United States since 1976 and is regulated at the state level by multiple States. Almost all introductions have resulted in established populations, and the plant is established on every continent except Antarctica. There are documented negative impacts of introductions, including outcompeting native plants, altering zooplankton communities and thereby affecting fish prey availability, and decreasing dissolved oxygen content of waterways when thick vegetative mats that block sunlight decompose. The overall climate match was High throughout the contiguous United States. The certainty of assessment is High. The overall risk assessment category is High.

Assessment Elements

- **History of Invasiveness (Sec. 4): High**
- **Overall Climate Match Category (Sec. 7): High**
- **Certainty of Assessment (Sec. 8): High**
- **Remarks/Important additional information:** *Hydrilla verticillata* is a Federal Noxious Weed. There are three known biotypes within the United States.
- **Overall Risk Assessment Category: High**

10 Literature Cited

Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 11.

BISON. 2020. Biodiversity Information Serving Our Nation. U.S. Geological Survey. Available: <https://bison.usgs.gov> (November 2020).

[CABI] CABI International. 2020. *Hydrilla verticillata* (Hydrilla). [original text by Rojas-Sandoval J]. CABI Invasive Species Compendium. Wallingford, United Kingdom: CAB International. Available: <https://www.cabi.org/isc/datasheet/28170> (November 2020).

Carniatio N, Fugi R, Thomaz SM, Cunha ER. 2014. The invasive submerged macrophyte *Hydrilla verticillata* as a foraging habitat for small-sized fish. *Natureza and Conservação* 12:30–35.

- Center for Aquatic and Invasive Plants. 2020. *Hydrilla verticillata*. Plant Directory. University of Florida. Available: <https://plants.ifas.ufl.edu/plant-directory/hydrilla-verticillata/> (November 2020).
- Coetzee JA, Hill MP, Schlange D. 2009. Potential spread of the invasive plant *Hydrilla verticillata* in South Africa based on anthropogenic spread and climate suitability. *Biological Invasions* 11(4):801–812.
- Department of Primary Industries, Parks, Water and Environment (Tasmania). 2020. *Hydrilla (Hydrilla verticillata)*. Available: <https://dipwe.tas.gov.au/invasive-species/weeds/weeds-index/declared-weeds-index/hydrilla#:~:text=Hydrilla%20is%20a%20native%20on,is%20artificially%20enriched%20with%20nutrients> (November 2020).
- GBIF Secretariat. 2020. GBIF backbone taxonomy: *Hydrilla verticillata* (L.f.) Royle. Copenhagen: Global Biodiversity Information Facility. Available: <https://www.gbif.org/species/5329570> (November 2020).
- Harms NE, Williams DA, Purcell MF. 2020. The role of overseas genetic surveys to potentially accelerate biological control development for a new *Hydrilla verticillata* introduction in the USA. *BioControl*:1–10.
- [ITIS] Integrated Taxonomic Information System. 2020. *Hydrilla verticillata* (L. f.) Royle. Reston, Virginia: Integrated Taxonomic Information System. Available: https://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=38974#null (November 2020).
- Jacono CC, Richerson MM, Howard Morgan V, Pfingsten IA. 2020. *Hydrilla verticillata* (L. f) Royle. Gainesville, Florida: U.S. Geological Survey, Nonindigenous Aquatic Species Database. Available: <https://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID=6> (November 2020).
- Levenson J, U.S. Army Corps of Engineers. 2020. Buffalo District fights invasive hydrilla on the Great Lakes. Available: <https://www.usace.army.mil/Media/News-Archive/Story-Article-View/Article/2054009/buffalo-district-fights-invasive-hydrilla-on-the-great-lakes/> (November 2020).
- New York State Senate. 2014. Prohibited and regulated invasive species. Codes, Rules and Regulations of the State of New York, Title 6, Chapter 5, Subchapter C, Part 575.
- New Zealand Plant Conservation Network. 2020. *Hydrilla verticillata*. Available: <https://www.nzpcn.org.nz/flora/species/hydrilla-verticillata/> (November 2020).

- Ohio Department of Agriculture. 2018. Invasive plants. Available:
https://www.oipc.info/uploads/5/8/6/5/58652481/invasive_plants_of_ohio.pdf
(November 2020).
- Sanders S, Castiglione C, Hoff M. 2020. Risk Assessment Mapping Program: RAMP. Version 3.1. U.S. Fish and Wildlife Service.
- Smither-Kopperl ML, Charudattan R, Berger RD. 1999. *Plectosporium tabacinum*, a pathogen of the invasive aquatic weed *Hydrilla verticillata* in Florida. *Plant Disease* 83:24–8.
- USDA, NRCS. 2020. *Hydrilla verticillata*. The PLANTS database. Greensboro, North Carolina: National Plant Data Team. Available:
<https://plants.usda.gov/core/profile?symbol=HYVE3> (November 2020).
- World Flora Online. 2021. *Hydrilla verticillata* (L.f) Royle. World Flora Online – a project of the World Flora Online Consortium. Available:
<http://www.worldfloraonline.org/taxon/wfo-0000769366> (September 2021).
- Zhuang X, Beentje HJ. 2017. *Hydrilla verticillata*. The IUCN Red List of Threatened Species 2017: e.T167871A65905991. Available:
<https://www.iucnredlist.org/species/167871/65905991> (November 2020).

11 Literature Cited in Quoted Material

Note: The following references are cited within quoted text within this ERSS, but were not accessed for its preparation. They are included here to provide the reader with more information.

- Al-Mandeel FA. 2013. A new record of the invasive species *Hydrilla verticillata* (Linn. F.) royal on the Iraqi rivers. *Advances in Environmental Biology* 7(2):384–390.
- Asplund T. 2007. *Hydrilla* in Wisconsin. Gainesville, Florida: Aquatic Plant Management Society 86:6.
- Aston HI. 1977. *Aquatic plants of Australia*. Melbourne, Australia: Melbourne University Press.
- Balevicius A. 1998. The vegetation of lakes in Veisiejai Regional Park. *Botanica Lithuanica* 4(3):267–284.
- Bao X. 2008. Effects with Growing of *Hydrilla verticillata* on the nutrient level of nitrogen and phosphorus in interstitial water of eutrophic lake. *Journal of Huaibei Coal Industry Teachers College (Natural Science Edition)* 29(4):44–47.
- Basiouny FM, Haller WT, Garrard LA. 1978. Survival of hydrilla (*Hydrilla verticillata*) plants and propagules after removal from the aquatic habitat. *Weed Science* 26:502–504.

- Bates AL, Smith CS. 1994. Submersed plant invasions and declines in the southeastern United States. *Journal of Lake and Reservoir Management* 10:53–55.
- Benoit LK, Les D. 2013. Rapid identification and molecular characterization of phytoene desaturase mutations in fluridone-resistant hydrilla (*Hydrilla verticillata*). *Weed Science* 61:32–40.
- Carter V, Rybicki NB. 1994. Invasions and declines of submersed macrophytes in the tidal Potomac River and estuary, the Currituck Sound-Back Bay system, and the Pamlico River Estuary. *Journal of Lake and Reservoir Management* 10:39–48.
- Casatti L, Mendes HF, Ferreira KM. 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana reservoir, Paranapanema River, Southeastern Brazil. *Brazilian Journal of Biology* 63:213–222.
- Colle DE, Shireman JV. 1980. Coefficients of condition for largemouth bass, bluegill, and redear sunfish in Hydrilla-infested lakes. *Transactions of the American Fisheries Society* 109:521–531.
- Cook CDK, Gut BJ, Rix EM, Schneller J, Seitz M. 1974. *Water plants of the world: A manual for the identification of the genera of freshwater macrophytes*. The Hague, The Netherlands: Dr W Junk.
- Cook CDK, Lüönd R. 1982. A revision of the genus *Hydrilla* (Hydrocharitaceae). *Aquatic Botany* 13:485–504.
- Environmental Laboratory. 1985. Monoecious Hydrilla in the Potomac River. Vicksburg, Mississippi: US Army Engineer Waterways Experiment Station. Miscellaneous Paper MP A-85-5.
- Fouts KL, Poudyal NC, Moore R, Herrin J, Wilde SB. 2017. Informed stakeholder support for managing invasive *Hydrilla verticillata* linked to wildlife deaths in a Southeastern reservoir. 33(3):260–269. [Source material did not give full citation for this reference.]
- Haider JA, Höbart R, Kovacs N, Milchram M, Dullinger S, Huber W, Essl F. 2016. The role of habitat, landscape structure and residence time on plant species invasions in a neotropical landscape. 32(3):240–249. [Source material did not give full citation for this reference.]
- Haller WT. 1995. Hydrilla control – past, present and future. *Aquatics* 17:6–8.
- Herrera Environmental Consultants. 2011. Pipe and Lucerne lakes – hydrilla and aquatic vegetation surveys 2010: final report. Olympia, Washington: King County Department of Natural Resources and Parks.
- Herschner C, Havens KJ. 2008. Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. *Conservation Biology* 22(3):544–550.

- Hofstra DE, Champion PD. 2006. Organism consequence assessment: *Hydrilla verticillata*. Hamilton, New Zealand: National Institute for Water and Atmospheric Research.
- Hoyer MV, Jackson MW, Allen MS, Canfield II DE. 2008. Lack of exotic hydrilla infestation effects on plant, fish and aquatic bird community measures. *Lake and Reservoir Management* 24:331–338.
- Huang L, Zeng G, Huang D, Li L, Zhang L. 2009. Adsorption of Zn-(2+) in wastewater containing heavy metal ions by *Hydrilla verticillata*. *Materials Protection* 42(3):81–83.
- ISSG. 2011. Global Invasive Species Database (GISD). Invasive Species Specialist Group of the IUCN Species Survival Commission. Available: <http://www.issg.org/database>.
- Jacono CC, Richerson MM, Howard Morgan V. 2011. *Hydrilla verticillata* fact sheet. Gainesville, Florida: USGS Nonindigenous Aquatic Species Database. Available: <http://nas.er.usgs.gov/queries/factsheet.aspx?speciesid=6>.
- Joyce JC, Haller WT, Colle DE. 1980. Investigation of the presence and survivability of hydrilla propagules in waterfowl. *Aquatics* 2:10–14.
- Kansas Department of Wildlife, Parks and Tourism. 2009. Hydrilla eradication project underway at Olathe Pond. Topeka: Kansas Department of Wildlife, Parks and Tourism. Available: <http://ksoutdoors.com/KDWPT-Info/News/News-Archive/2009-Weekly-News-Archive/7-15-09/HYDRILLA-ERADICATION-PROJECT-UNDERWAY-AT-OLATHE-POND>.
- Kay SH. 1992. Hydrilla: A rapidly spreading aquatic weed in North Carolina. North Carolina State University, North Carolina Cooperative Extension Service. Publication AG-449.
- Killgore et al. 1989. [Source material did not give full citation for this reference.]
- Kłosowski S, Tomaszewicz H. 1997. Sociology and ecology of *Hydrilletum verticillatae* Tomaszewicz 1979 and *Elodeetum canadensis* (Pign. 1953) Pass. 1964 in north-eastern Poland. (Zur Soziologie und Ökologie des *Hydrilletum verticillatae* Tomaszewicz 1979 und des *Elodeetum canadensis* (Pign. 1953) Pass. 1964 in Nordost-Polen.). *Tuexenia*: 125–136.
- Langeland KA. 1996. Hydrilla tuber formation in response to single and sequential bensulfuron methyl exposures at different times. Pages 247–251 in Caffrey JM, Barrett PRF, Murphy KJ, Wade PM, editors. *Hydrobiologia* 340(1/3). [Source material did not give full citation for this reference.]
- Langeland KA, Cherry HM, McCormick CM, Craddock Burks KA. 2008. Identification and biology of nonnative plants in Florida's natural areas. 2nd edition. Gainesville, Florida: UF IFAS Communication Services.

- Langeland KA, Smith CB. 1984. Hydrilla produces viable seed in North Carolina lakes. *Aquatics* 6:20–22.
- Langeland KA, Sutton DL. 1980. Regrowth of Hydrilla from axillary buds. *Journal of Aquatic Plant Management* 18:27–29.
- Les DH, Merhoff LJ, Cleland MA, Gabel JD. 1997. *Hydrilla verticillata* (Hydrocharitaceae) in Connecticut. *Journal of Aquatic Plant Management* 35:10–14.
- Madeira PT, Coetzee JA, Center TD, White EE, Tipping PW. 2007. The origin of *Hydrilla verticillata* recently discovered at a South African dam. *Aquatic Botany* 87:176–180.
- Madeira PT, Jacono CC, Van TK. 2000. Monitoring hydrilla using two RAPD procedures and the Nonindigenous Aquatic Species Database. *Journal of Aquatic Plant Management* 38:33–40.
- Madeira PT, Van TK, Center TD. 2004. An improved molecular tool for distinguishing monoecious and dioecious Hydrilla. *Journal of Aquatic Plant Management* 42:28–32.
- Madeira PT, Van T, Steward D, Schnell R. 1997. Random amplified polymorphic DNA analysis of the phenetic relationships among world-wide accessions of *Hydrilla verticillata*. *Aquatic Botany* 59:217–236.
- Mahler MJ. 1979. Hydrilla the number one problem. *Aquatics* 1:56.
- Mataraza LK, Terrell JB, Munson AB, Canfield DE Jr. 1999. Changes in submersed macrophytes in relation to tidal storm surges. *Journal of Aquatic Plant Management* 37:3–12.
- Miller RW. 1988. The First State's experiences controlling the northern monoecious form of hydrilla. *Aquatics* 10(2):16–23.
- Miranda LE, Hodges KB. 2000. Role of aquatic vegetation coverage on hypoxia and sunfish abundance in bays of a eutrophic reservoir. *Hydrobiologia* 427(1/3):51–57.
- Mormul RP, et al. 2010a. Ostracod (Crustacea) colonization of a native and a non-native macrophyte species of Hydrocharitaceae in the Upper Paraná floodplain (Brazil): an experimental evaluation. *Hydrobiologia* 644:185–193. [Source material did not give full citation for this reference.]
- Mormul RP, et al. 2010b. Epiphyton or macrophyte: Which primary producer attracts the snail *Hebetancylus moricandi*? *American Malacological Bulletin* 28:127–133. [Source material did not give full citation for this reference.]

- Owens CS, Smart RM, Dick GO. 2012. Tuber and turion dynamics in monoecious and dioecious hydrilla (*Hydrilla verticillata*). *Journal of Aquatic Plant Management* 50:58–62.
- Pelicice FM, Agostinho AA. 2006. Feeding ecology of fishes associated with *Egeria* spp. patches in a tropical reservoir, Brazil. *Ecology of Freshwater Fish* 15:10–19.
- Pesacreta G. 1988. Water chemistry from North Carolina piedmont impoundments with hydrilla (*Hydrilla verticillata* (L.f.)Royle). Doctoral Dissertation. Raleigh: North Carolina State University.
- Preston CD, Croft JM. 1997. *Aquatic plants in Britain and Ireland*. Colchester, UK: Harley.
- Rizzo WM, Boustany RG, Meaux DR. 1996. Ecosystem changes in a subtropical Louisiana lake due to invasion by Hydrilla. Abstract in: *From small streams to big rivers*. Kansas City, Missouri: Society of Wetland Scientists 17th Annual Meeting, June 9–14, 1996.
- Rout NP, Shaw BP. 2001. Salt tolerance in aquatic macrophytes: possible involvement of the antioxidative enzymes. *Plant Science* 160(3):415–423.
- Rout NP, Tripathi SB, Shaw BP. 1998. Effect of salinity on chlorophyll and proline contents in three aquatic macrophytes. *Biologia Plantarum* 40(3):453–458.
- Ryan FJ, Cooley CR, Kay SH. 1995. Coexistence of monoecious and dioecious hydrilla in Lake Gaston, North Carolina and Virginia. *Journal of Aquatic Plant Management* 33:8–12.
- Rybicki NB, Carter V. 2002. Light and temperature effects on the growth of wild celery and hydrilla. *Journal of Aquatic Plant Management* 40(2):92–99.
- Rybicki NB, Jenter HL, Carter V, Baltzer RA. 1997. Observations of tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. *Limnology and Oceanography* 42(2):307–317.
- Rybicki N, Kirshtein JD, Voytek MA. 2013. Molecular techniques to distinguish morphologically similar *Hydrilla verticillata*, *Egeria densa*, *Elodea nuttallii*, and *Elodea canadensis*. *Journal of Aquatic Plant Management* 51:94–102.
- Rybicki NB, Landwehr JM. 2007. Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. *Limnology and Oceanography* 52(3):1195–1207.
- Sample J. 1972. Hydrilla in Iowa. Ohio: Weed Trees and Turf Cleveland. October 1972:2.
- Schardt J. 1994. 1994 Florida Aquatic Plant Survey Report. Tallahassee: Florida Department of Environmental Protection, Bureau of Aquatic Plant Management.
- Schardt J. 1995. Hydrilla reaches crisis levels in Florida waters. *Aquatics* 17:10–12.

- Schmitz DC, Nelson BV, Nall LE, Schardt JD. 1991. Exotic aquatic plants in Florida: a historical perspective and review of the present aquatic plant regulation program. Pages 303–326 in Center TC, Doren RF, Hofstetter RL, Myers RL, Whiteaker LD, editors. Proceedings of a Symposium on Exotic Pest Plants. Denver, Colorado: National Park Service. Technical Report NPS/NREVER/NRTR–91/06.
- Schmitz DC, Osborne JA. 1984. Zooplankton densities in a Hydrilla infested lake. *Hydrobiologia* 111:127–132.
- Schmitz DJ, Schardt JD, Leslie AJ, Dray FA Jr, Osborne JA, Nelson BV. 1993. The ecological impact and management history of three invasive alien aquatic plant species in Florida. Pages 173–194 in McKnight BN, editor. *Biological pollution: The control and impact of invasive exotic species*. Indianapolis: Indiana Academy of Science.
- Schultz R, Dibble E. 2012. Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: the role of invasive plant traits. *Hydrobiologia* 684:1–14.
- Shields EC, Moore KA, Parrish DB. 2012. Influences of salinity and light availability on abundance and distribution of tidal freshwater and oligohaline submersed aquatic vegetation. *Estuaries and Coasts* 35:515–526.
- Sousa WTZ. 2011. *Hydrilla verticillata* (Hydrocharitaceae), a recent invader threatening Brazil's freshwater environments: a review of the extent of the problem. *Hydrobiologia* 669:1–20.
- Steward KK. 1993. Seed production in monoecious and dioecious populations of hydrilla. *Aquatic Botany* 46:169–183.
- Tanaka N. 2000. Pollination of the genus *Hydrilla* (Hydrocharitaceae) by waterborne pollen grains. *Annals of the Tsukuba Botanical Garden* 19:7–12.
- Tanaka N. 2003. Pollination of the genus *Hydrilla* (Hydrocharitaceae) by waterborne pollen grains: II. Air bubbles cause the male flower to surface. *Annals of the Tsukuba Botanical Garden* 22:143–145.
- Theel HJ, Dibble ED, Madsen JD. 2008. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. *Hydrobiologia* 600:77–87.
- Thorp AG, Jones RC, Kelso DP. 1997. A comparison of water-column macroinvertebrate communities in beds of differing submersed aquatic vegetation in the tidal freshwater Potomac River. *Estuaries* 20:86–95.

- Tippery NP, Bugbee GJ, Stebbins SE. 2020. Evidence for a genetically distinct strain of introduced *Hydrilla verticillata* (Hydrocharitaceae) in North America. *Journal of Aquatic Plant Management* 58:1–6.
- Valley RD, Bremigan MT. 2002. Effects of macrophyte bed architecture on largemouth bass foraging: implications of exotic macrophyte invasions. *Transactions of the American Fisheries Society* 131(2):234–244.
- Van T, Steward K. 1990. Longevity of monoecious hydrilla propagules. *Journal of Aquatic Plant Management* 28:74–76.
- van Dijk G. 1985. *Vallisneria* and its interactions with other species. *Aquatics* 7(3):6–10.
- Verkleij JAC. 1983. A comparative study of the morphology and isoenzyme patterns of *Hydrilla verticillata* (L.f.) Royle. *Aquatic Botany* 17:43–59.
- Wang J, Wang S, Jin X, Zhang Y, Zhu S. 2007. Effect of submerged aquatic plant *Hydrilla verticilla* on the sorption/release characteristic of ammonia nitrogen on sediment. *Ecological Environment* 16(2):336–341.
- White A, Reiskind JB, Bowes G. 1996. Dissolved inorganic carbon influences the photosynthetic responses of hydrilla to photoinhibitory conditions. *Aquatic Botany* 53(1/2):3–13.
- Wilde SB, Murphy TM, Hope CP, Habrun SK, Kempton J, Birrenkott A, Wiley F, Bowerman WW, Lewitus AJ. 2005. Avian vacuolar myelinopathy linked to exotic aquatic plants and a novel cyanobacterial species. *Environmental Toxicology* 20(3):348–353.
- Williams DA, Harms NE, Grodowitz MJ, Purcell M. 2018. Genetic structure of *Hydrilla verticillata* L.f. Royle in eastern China and the Republic of Korea: implications for surveys of biological control agents for the invasive monoecious biotype. *Aquatic Botany* 149:17–27.
- Wunderlin RP, Hansen BF. 2011. *Guide to the vascular plants of Florida*. 3rd edition. Gainesville: University Press of Florida.
- Yeo RR, Falk RH, Thurston JR. 1984. The morphology of hydrilla (*Hydrilla verticillata*) (L.f.) Royle). *Journal of Aquatic Plant Management* 22:1–17.
- Zhu J, Yu D, Xu X. 2015. The phylogeographic structure of *Hydrilla verticillata* (Hydrocharitaceae) in China and its implications for the biogeographic history of this worldwide-distributed submerged macrophyte. *BMC Evolutionary Biology* 15:95.