

# *Najas guadalupensis* var. *guadalupensis*

Southern Water-nymph

Hydrocharitaceae



*Najas guadalupensis* var. *guadalupensis* by Jordan Collins, 2022

## *Najas guadalupensis* var. *guadalupensis* Rare Plant Profile

New Jersey Department of Environmental Protection  
State Parks, Forests & Historic Sites  
Forests & Natural Lands  
Office of Natural Lands Management  
New Jersey Natural Heritage Program

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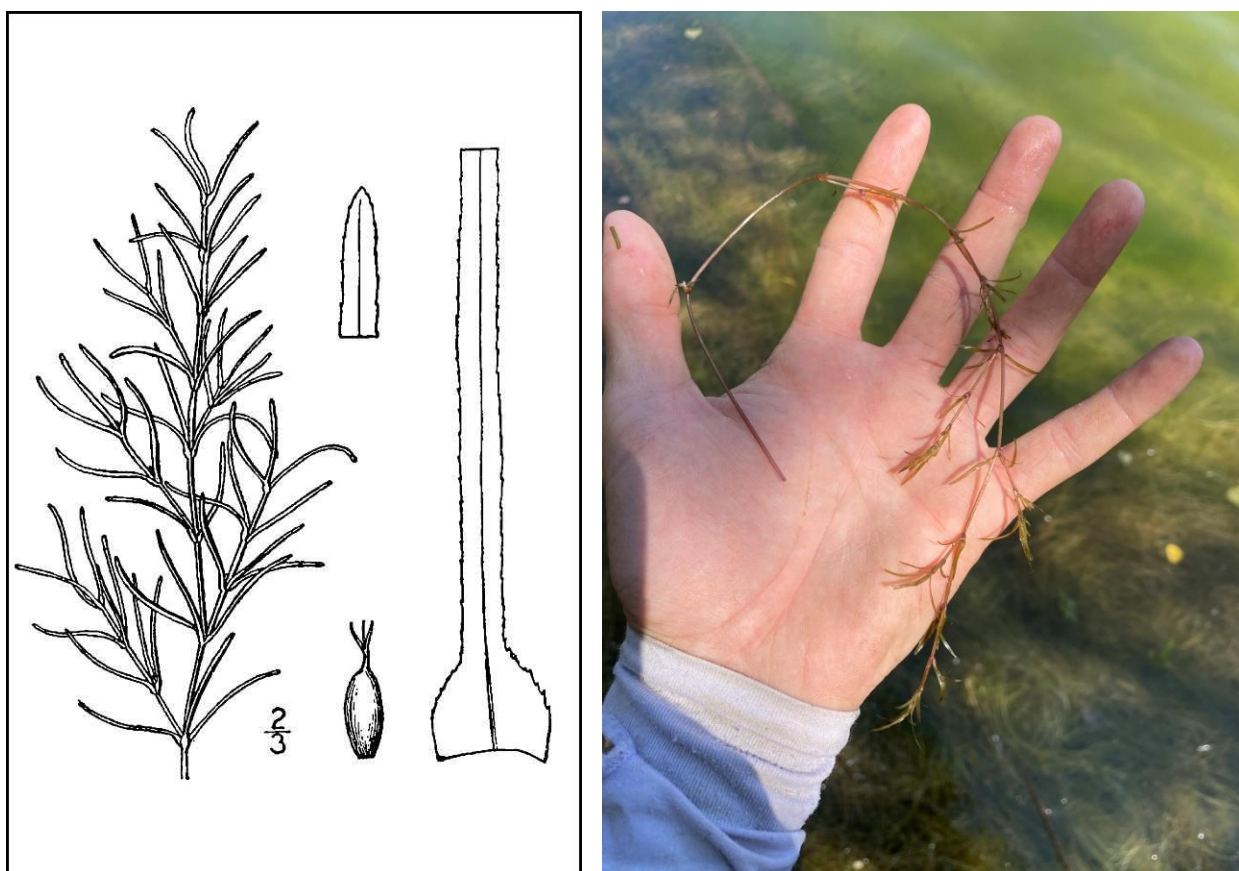
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## **Life History**

*Najas guadalupensis* var. *guadalupensis* (Southern Water-nymph) is a rooted, submergent aquatic plant. *Najas* was traditionally placed in the Najadaceae, which has alternately included an assortment of primarily aquatic genera or been reduced to a single-genus family (Morong 1893, Haynes 1977 & 2020). Recent phylogenetic analyses supported the transfer of the water-nymphs into the Hydrocharitaceae (APG II 2003, Ito et al. 2017, Bernardini and Lucchese 2018, Spaulding et al. 2019). Several other varieties of *Najas guadalupensis* have been described, none of which occur in New Jersey (Haynes and Wentz 1974, Haynes 1979). Haynes and Hellquist (1996) later reclassified them as subspecies. One of the subtaxa was recently determined to be synonymous with *Najas canadensis* (which is a hybrid derivative of *N. flexilis* and *N. guadalupensis* per Les et al. 2015) and the other two appear to be hybrids in which *N. guadalupensis* is the maternal parent (King 2017).



Left: Britton and Brown 1913, courtesy USDA NRCS 2025a. Right: Jordan Collins, 2022.

The stems of *Najas guadalupensis* var. *guadalupensis* are slender (0.1–0.8 mm wide), 1.1–7.5 dm in length, and much branched. The paired leaves are flat or slightly wavy and linear (0.3–2.8 cm x 0.2–1.8 mm), although their bases are wider and tapering. Numerous tiny teeth are present but they are not detectable without magnification. *N. guadalupensis* is monoecious, meaning that separate male and female flowers are present on the same plant. The flowers are tiny, stalkless, and axillary, with 1–3 per axil. The staminate flowers, which are 1.5–2.5 mm long and have four-celled anthers, are located on the upper part of the stem. The pistillate flowers are situated

lower on the stems: They are 1.5–2.0 mm in length and have four-lobed stigmas. The fruits are purplish-brown, longitudinally ribbed, and single-seeded. The seeds are spindle-shaped, 1.2–2.5 mm long, and 0.4–0.6 mm wide, and their surfaces are covered with a network of veins that form 10–20 rows of squarish pits. (See Britton and Brown 1913, Fernald 1950, Fassett 1957, Haynes 1979 & 2020, Gleason and Cronquist 1991, Bergstrom et al. 2006, Tiner 2009, Ricketson 2018).



Jordan Collins, 2022.



J. Rebman, 2019.

The examination of plant material with mature seeds is required for the identification of *Najas* species (Haynes 2020). Two other members of the genus (*N. flexilis*, *N. gracillima*) are native to New Jersey and one non-indigenous species (*N. minor*) has also been recorded in the state (Kartesz 2015). A comparative illustration of the four species' seeds was provided by Fassett (1957). The leaf bases of *N. minor* and *N. gracillima* are respectively fan-shaped or lobed. Both *N. flexilis* and *N. guadalupensis* have tapering leaf bases but *N. flexilis* has smooth, shiny seeds while those of *N. guadalupensis* are distinctly pitted and dull (Clausen 1936, Haynes 1979, Rhoads and Block 2007). A high level of variability has often been noted within *Najas guadalupensis* itself (Fernald 1923, Clausen 1936, Haynes 1977). Some of that might be attributable to hybridization but chromosomal differences between populations could also play a role. Diploid, triploid, hexaploid, heptaploid, and octoploid occurrences of *N. guadalupensis* have been documented throughout the species' range (Ito et al. 2017, King 2017).

Most *Najas* species, including *N. guadalupensis*, are generally depicted as having an annual life cycle (Les 1988, Philbrick 1991, Schuegraf 2004, de Boer et al. 2016). In North America, *N. guadalupensis* usually germinates in the spring, develops rapidly, and reaches peak biomass during the late summer (Sprenkle et al. 2004, Bergstrom et al. 2006). Flowering can begin as early as May in the southern states although July to August are typical further north, and fruit is likely to be present through September or October (Hough 1983, Tiner 2009, Howell 2015, Spaulding et al. 2019, Weakley et al. 2024). The plants usually die off completely during the winter and re-establish the following year (Montz 1978). In the southern hemisphere growth begins in October, seeds are produced in February, and the plants disappear by May (Schuegraf



2004). However, there is some evidence that *Najas guadalupensis* is facultatively perennial (Les et al. 2010, King 2017). Populations in the northernmost part of the species' range seldom produce fruit (Clausen 1936), and Fernald (1923) suspected that some Canadian occurrences had been initiated by vegetative dispersal events. Turions (densely leafy shoot tips that can overwinter) were first reported in *N. guadalupensis* var. *olivacea* by Rosendahl (1939), who noted that new plants were easily propagated from the structures. Stuckey et al. (1978) found intact *N. guadalupensis* (presumably var. *guadalupensis* based on location) plants wintering over in ice-covered Ohio ponds and observed new plants emerging from the stem tips the following spring. A turion was also recently discovered in a Connecticut population of *N. guadalupensis* var. *guadalupensis*. Although the water-nymph is more likely function as a perennial in the northern and eastern portions of its range, specimens have been collected during the wintertime in some southern locations (King 2017). Similar adaptability has been documented in *Najas marina*, which may be annual or perennial depending on where it is growing and produces turions in the places where it persists through the winter (Agami et al. 1986).

### **Pollinator Dynamics**

*Najas* species are hydrophilic, meaning that their pollen is transported by water (Philbrick 1991). In some hydrophilic species the pollen moves over the water's surface but in *Najas* the entire process takes place underwater (Haynes 1988, Ackerman 2000, Peredo et al. 2013). Typical pollen grains have a dual-layered outer wall but in hydrophilic plants the secondary layer (exine) is usually reduced and in *Najas* it is lacking altogether (Philbrick and Osborn 1994, Philbrick and Les 1996). Rosendahl (1939) observed that the pollen grains of *N. guadalupensis* were oblong-oval (averaging 51 x 27  $\mu$ ) and coarsely granular. *Najas* pollen is heavier than water so the grains usually sink after they are released, although some multi-directional distribution may occur via water currents (Cox 1988, Haynes 1988, Les 1988, Ackerman 2000). Pollen tubes can begin to form before the grains have reached a stigma, which improves the probability of contact by increasing the amount of surface area (Les 1988, Cox 1993). No means of preventing pollination between flowers on the same plant are known in *Najas* species (Les 1988).

The pollination process in *Najas guadalupensis* is likely to be similar to that of *N. marina*, which was described in detail by Huang et al. (2001). The male *Najas* flowers elongated and changed position shortly before they released copious amounts of pollen into the water. Pollen dispersal was completed in under an hour. The grains sunk slowly but were sometimes carried upward by water currents, and they were frequently deposited on leaf sheaths then redispersed by moving water. Grains that landed in close proximity to female flowers developed branched pollen tubes which enabled them to access stigmas without landing on them directly.

### **Seed Dispersal and Establishment**

*Najas* species, including *N. guadalupensis*, have been noted to produce a copious amount of seeds (Philbrick 1991, Spaulding et al. 2019). That seems counterintuitive for plants that have single-seeded fruits but it is likely explained by the rapid vegetative proliferation that occurs during a single growing season. The plants spread laterally by producing adventitious roots at

the nodes, and new plants can also become established from stem fragments (Philbrick and Les 1996, King 2017). *N. guadalupensis* is often one of the most abundant species present in the places where it occurs (Montz 1978, Dierberg et al. 2002, Brush and Hilgartner 2000, Goldberg and Trent 2020). It is sometimes identified as weedy (Bruton 1950, Bonilla-Barbosa 2013) or even as potentially invasive (Hellquist 1977, de Boer et al. 2016).

Waterfowl are probably the primary dispersal agents of *Najas* seeds. *N. guadalupensis* and other water-nymphs are an important food source for ducks, and seeds that pass through the birds' digestive tracts remain viable and are often deposited in favorable habitat (Bruton 1950, Fassett 1957, Bergstrom et al. 2006, Brochet et al. 2009, King 2017, Spaulding et al. 2019, Volk 2019). Bruton (1950) noted that adherence to feet and feathers of waterfowl might also result in some seed dispersal. Seeds that are not consumed by birds are likely to sink (Davis 1985). In places where *N. guadalupensis* produces turions those organs may be dispersed vegetatively by water movement.

Humans have probably played an unintentional part in the dispersal of *Najas guadalupensis*. The species is widely used in the fish culture trade and as an ornamental plant in aquaria (de Boer et al. 2016, King 2017), so careless disposal could introduce it into new bodies of water. As with many other aquatic plants, seeds or viable fragments of *Najas* species can be transported to different locations by clinging to boats, trailers, or fishing gear (Volk 2019).

## **Habitat**

*Najas guadalupensis* var. *guadalupensis* is found in a multitude of aquatic settings around the world. It occurs at elevations of 0–1500 meters above sea level (Haynes 2020). Natural habitats include lakes, ponds, streams, and rivers—including freshwater tidal areas (Coddington and Field 1978, Hough 1983, Carter and Rybicki 1986, Angelo and Boufford 2000, Mora-Olivo and Retana 2005, Rhoads and Block 2007, Tiner 2009, England 2014, Spaulding et al. 2019, Weakley et al. 2024). Southern Water-nymph is also right at home in man-made ponds or lakes, reservoirs, canals, and rice fields (Blackburn et al. 1968, Wentz and Stuckey 1971, Rhoads and Block 2007, King 2017). In New Jersey, the species has been found in ponds near the coast, inland lakes, and the tidal portion of a river (Clausen 1936, Schuyler 1981, Ferren 1982, NJNHP 2024).

The habitats utilized by *Najas guadalupensis* are generally unshaded (Weakley et al. 2024). In lakes, *N. guadalupensis* grows in the infralittoral zone where the majority of submergent aquatic plants are typically found (Howell 2015). At one New Jersey site the plants were rooted in less than a meter of water (NJNIHP 2024). Hellquist (1977) noted that the species was extremely abundant in about a meter of water and Montz (1978) recorded it growing at depths of about two meters. Southern Water-nymph has also been documented in a lagoon where the water level drops to just a few centimeters during the late fall and winter months (Mora-Olivo and Retana 2005). *N. guadalupensis* can occur in mixed populations with other *Najas* species, and it has been reported as co-dominant with *Ruppia maritima*, *Vallisneria americana*, or *Zannichellia palustris* at various locations (Brush and Hilgartner 2000, Schuegraf 2004, Morse et al. 2007, Goldberg and Trent 2020).

*Najas guadalupensis* sometimes occurs in brackish habitats. The species is most likely to thrive at low salinity levels, although it has some tolerance for moderate salinity. Excessive exposure can result in reduced growth or mortality (Alcocer and Hammer 1998, Brush and Hilgartner 2000, Schuegraf 2004, Bergstrom et al. 2006, Poirrier et al. 2010, Morris and Dobberfuhl 2012, Goldberg and Trent 2020). Hellquist (1977) indicated that New England plants were found in moderately alkaline waters. *N. guadalupensis* also appears to be tolerant of high nutrient loads in waterways; in fact, Wentz and Stuckey (1971) suggested that the spread of the plants in Ohio had been enhanced by the eutrophication of lakes and rivers. Peltier and Welch (1970) found that the species' annual growth was not affected by nitrogen or phosphorous levels, and Dierberg et al. (2002) determined that *N. guadalupensis* has the capacity to sequester large amounts of phosphorous.

### **Wetland Indicator Status**

*Najas guadalupensis* is an obligate wetland species, meaning that it almost always occurs in wetlands (U. S. Army Corps of Engineers 2022).

### **USDA Plants Code (USDA, NRCS 2025b)**

The USDA code for *Najas guadalupensis* ssp. *guadalupensis* is NAGUG. No separate code is listed for *N. guadalupensis* var. *guadalupensis*.

### **Coefficient of Conservancy (Walz et al. 2020)**

CoC = 3. Criteria for a value of 3 to 5: Native with an intermediate range of ecological tolerances and may typify a stable native community, but may also persist under some anthropogenic disturbance (Faber-Langendoen 2018).

### **Distribution and Range**

*Najas guadalupensis* var. *guadalupensis* is native throughout much of the western hemisphere, including North, Central, and South America and some parts of the Caribbean. It is introduced in Trinidad and Tobago as well as in several European and Middle Eastern countries (POWO 2025). The map in Figure 1 depicts the extent of *N. guadalupensis* var. *guadalupensis* in the United States and Canada.

The USDA PLANTS Database (2025b) shows records of *Najas guadalupensis* var. *guadalupensis* in seven New Jersey counties: Atlantic, Burlington, Camden, Monmouth, Ocean, Passaic, and Sussex (Figure 2). It has also been reported in Morris County (Clausen 1936, Mid-Atlantic Herbaria 2025). The data include historic observations and do not reflect the current distribution of the species.

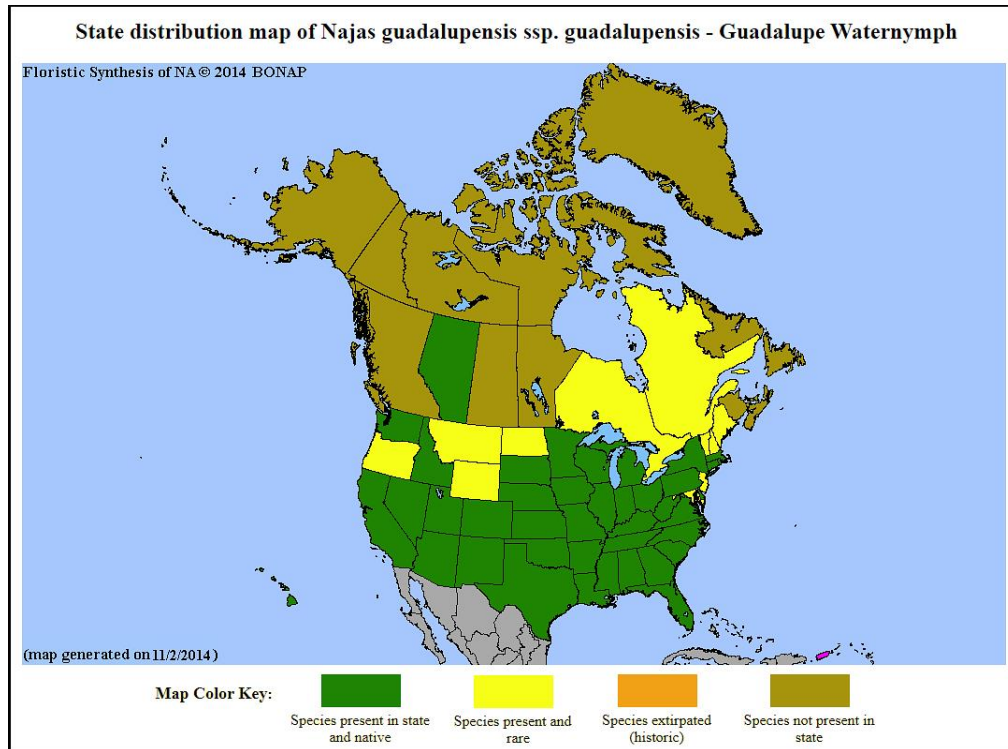


Figure 1. Distribution of *N. guadalupensis* var. *guadalupensis* in the United States and Canada, adapted from BONAP (Kartesz 2015).

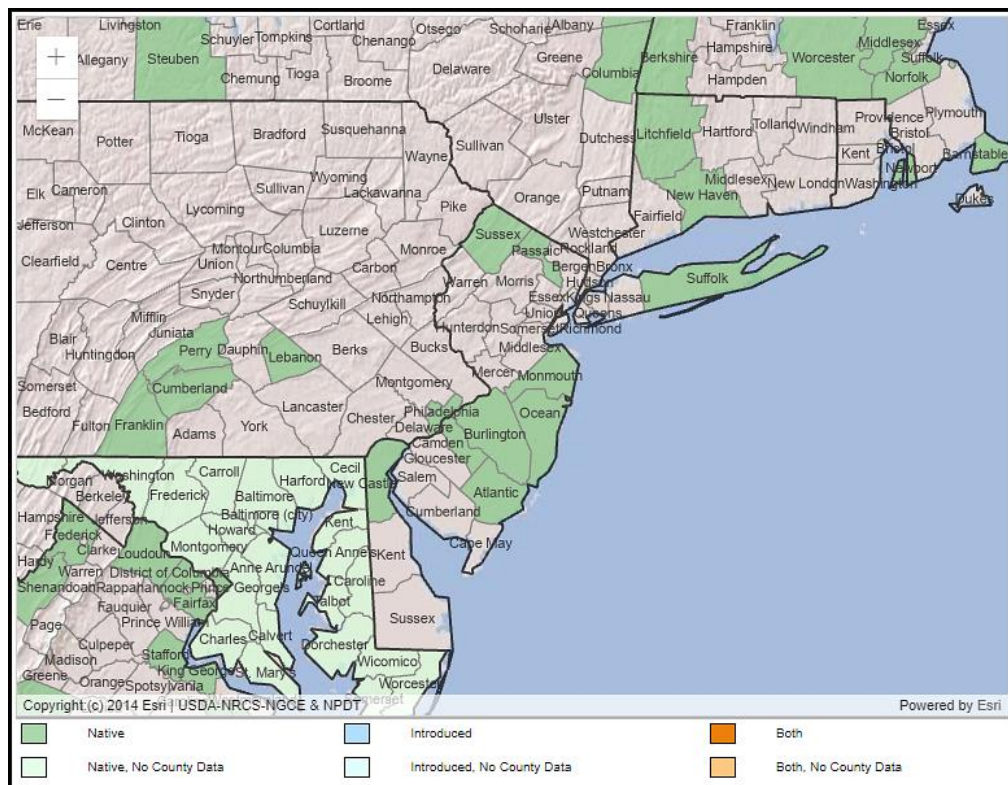


Figure 2. County records of *N. guadalupensis* var. *guadalupensis* in New Jersey and vicinity (USDA NRCS 2025b).



## Conservation Status

*Najas guadalupensis* var. *guadalupensis* is considered globally secure. The G5T5 rank means the variety has a very low risk of extinction or collapse due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats (NatureServe 2025). The map below (Figure 3) illustrates the conservation status of *N. guadalupensis* var. *guadalupensis* in the United States and Canada. Southern Water-nymph has not been ranked in many of the states where it occurs, although a few have identified it as secure or apparently so. The species is vulnerable (moderate risk of extinction) in one state, imperiled (high risk of extinction) in one state and one province, and critically imperiled (very high risk of extinction) in four states and one province.

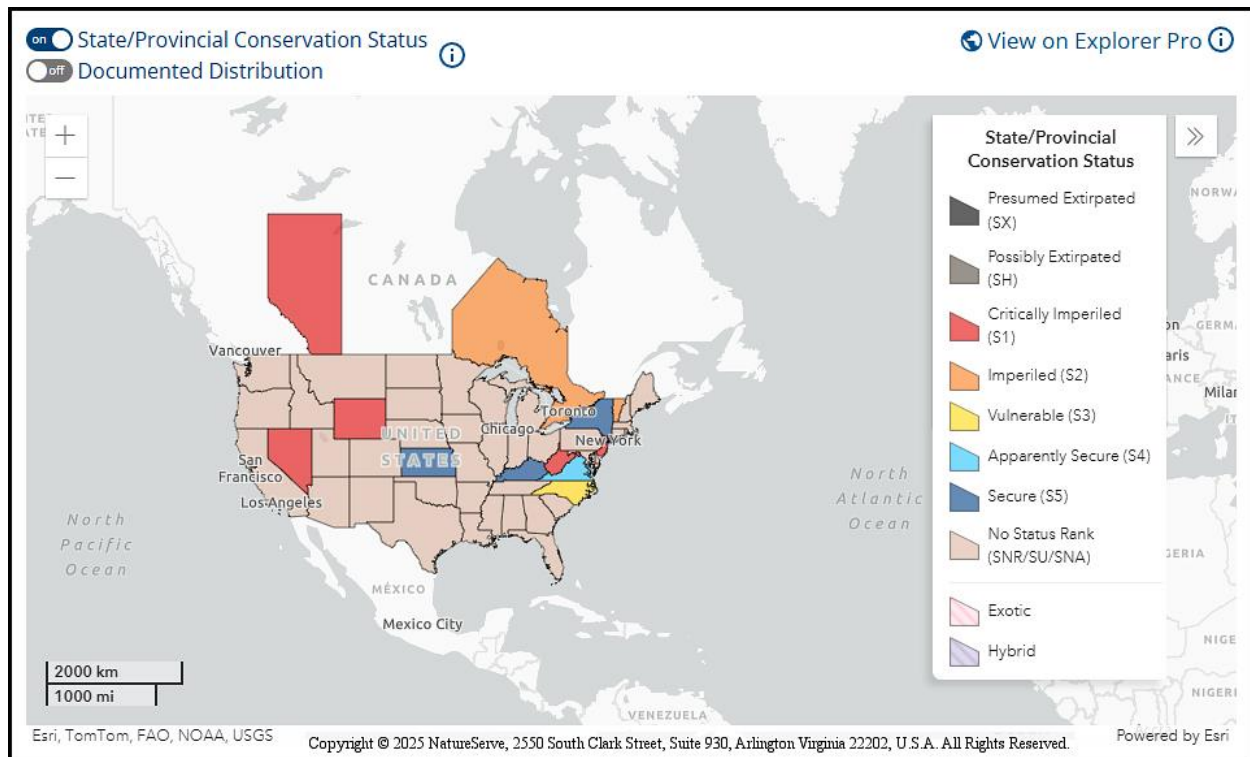


Figure 3. Conservation status of *N. guadalupensis* var. *guadalupensis* in the United States and Canada (NatureServe 2025).

*Najas guadalupensis* var. *guadalupensis* is critically imperiled (S1) in New Jersey (NJNHP 2024). The rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *N. guadalupensis* var. *guadalupensis* has also been assigned a regional status code of HL, signifying that the species is eligible for protection under the jurisdiction of the Highlands Preservation Area (NJNHP 2010).

*Najas guadalupensis* was not documented in New Jersey until the 1930s, when specimens were collected in Morris and Ocean counties (Clausen 1936). During the early 1980s records were reported from Camden, Monmouth, Ocean, Passaic, and Sussex counties (Schuyler 1981, Ferren 1982, Hough 1983), although Hough noted that some of the identifications were tentative. Only

two occurrences are presently tracked by the Natural Heritage Program and both are thought to be extant (NJNHP 2024).

### **Threats**

No threats to New Jersey's known populations of *Najas guadalupensis* var. *guadalupensis* have been reported to date (NJNHP 2024). Ferren (1982) noted that the habitat of a former occurrence was potentially vulnerable to dumping, siltation, or tidal fluctuations. The reasons for the rarity of *N. guadalupensis* in the state are unclear since the species disperses well, utilizes a broad range of aquatic habitats, and is often characterized as weedy. No range-wide concerns have been identified for Southern Water-nymph, although some local populations might be affected by development, pollutants, herbicides, or invasive species (Johnson 2024).

One invasive aquatic plant that is particularly likely to threaten *Najas guadalupensis* populations is Water-thyme, *Hydrilla verticillata* (Carter and Rybicki 1986). *H. verticillata* was first detected in Florida during the 1960s and it has rapidly spread throughout much of the continental United States, including New Jersey. Multiple biotypes are known and both monoecious and dioecious strains are present in the country. The species grows rapidly and forms dense mats that can shade out native submersed aquatics. Possible allelopathic effects have also been reported (Jacono et al. 2020). Water-thyme is considered highly threatening to native plant communities in New Jersey (FoHVOS 2025). Shortly after *H. verticillata* was introduced in Florida it replaced *Najas guadalupensis* in some locations. The displacements occurred rapidly, within two years of *Hydrilla*'s appearance in the canals observed by Blackburn et al. (1968).

### **Climate Change Vulnerability**

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Najas guadalupensis* var. *guadalupensis* populations to climate change. The plant was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climatic conditions in accordance with the guidelines described by Young et al. (2016) and the state climatic computations by Ring et al. (2013). Based on available data *N. guadalupensis* was assessed as Less Vulnerable, meaning that climate change is not expected to have a notable detrimental impact on its extent in New Jersey by 2050.

Some of the effects of changing climatic conditions in New Jersey include higher temperatures, shifting precipitation patterns that increase the frequency and intensity of both droughts and floods, and rising seas along the coast (Hill et al. 2020). Both of the state's extant populations of *Najas guadalupensis* are situated in permanent bodies of water that are not likely to dry out completely during periods of drought, and neither one is in a location that will be directly affected by sea level rise. As the climate continues to warm the greatest threats to submerged aquatic plants are expected to result from rising temperatures and decreased water clarity (Short et al. 2016). The water-nymph has typically been more abundant in the southern part of its range (Coddington and Field 1978), so it may benefit from higher temperatures. Wentz and Stuckey

(1971) suggested that a gradual warming of water bodies might have facilitated the spread of *N. guadalupensis* in Ohio, and projected climate change scenarios in Norway increase the probability that the species will become invasive in that nation (de Boer et al. 2016). *N. guadalupensis* has already adjusted to cooler northern sites by adopting a perennial habit so the warming climate might further a northward range expansion. The impacts of reduced water clarity are harder to project, although Bergstrom et al. (2006) noted that *Najas* species are generally tolerant of low light.

The existing level of threat to *Najas guadalupensis* populations from *Hydrilla verticillata* is unlikely to be altered by climate change. Low temperatures can inhibit the northward spread of Water-thyme, but the monoecious form of *H. verticillata* is more cold-tolerant (Maki and Galatowitsch 2008, Zhu et al. 2017) so the invasive species will probably keep pace with *N. guadalupensis* in terms of range expansion. Other significant competitors may also emerge; for example, Koncki and Aronson (2015) identified several aquatic species that are likely to spread into the northeast as a result of climate change and one of those (*Salvinia molesta*) has already been designated as a developing threat in New Jersey (FoHVOS 2025).

### **Management Summary and Recommendations**

Neither of New Jersey's two known *Najas guadalupensis* var. *guadalupensis* populations has been formally assessed. Site visits are needed to determine the size and viability of the occurrences and to identify potential threats. Monitoring efforts should focus on the presence and extent of invasive aquatic plants, including *Hydrilla verticillata* and a number of others that have already become widely established in the state (FoHVOS 2025). Site-specific management plans may be needed depending on the outcome of the initial surveys. The control of invasive aquatic species can be particularly challenging—some specific guidelines and additional references are available from Kaufman and Kaufman (2007), Hussner et al. (2017), and FoHVOS (2025).

Scattered reports from the past century raise the possibility that there may be additional undiscovered populations of *Najas guadalupensis* var. *guadalupensis* in New Jersey. The water-nymph could be overlooked in places where it occurs in mixed species populations or underreported due to the difficulty of making a positive identification. Careful searches of potential habitats, particularly in counties where *N. guadalupensis* was previously reported, might prove to be fruitful.

### **Synonyms**

The accepted botanical name of the species is *Najas guadalupensis* (Spreng.) Magnus var. *guadalupensis*. Orthographic variants, synonyms, and common names are listed below. Many current sources follow Haynes and Hellquist (1996) in identifying it as a subspecies rather than a variety (Kartesz 2015, ITIS 2025, POWO 2025, USDA NRCS 2025b) although Weakley et al. (2024) retains it as a variety. Recent work by King (2017) has challenged the validity of all previously described subtaxa in *N. guadalupensis*.

## Botanical Synonyms

*Najas guadalupensis* (Spreng.) Magnus ssp. *guadalupensis*  
*Najas guadalupensis* var. *curassavica* (A. Braun) Urb.  
*Najas arcana* Subils & Hunz.  
*Najas flexilis* var. *curassavica* A. Braun  
*Najas flexilis* var. *fusiformis* Chapm.  
*Najas flexilis* var. *gollmeriana* A. Braun  
*Najas flexilis* var. *punctata* A. Braun  
*Najas microdon* var. *curassavica* (A. Braun) A. Braun  
*Najas punctata* (A. Braun) Rendle  
*Najas urbaniana* O. Schmidt  
*Naias guadalupensis* (Spreng.) Morong  
*Caulinia guadalupensis* Spreng.

## Common Names

Southern Water-nymph  
Common Naiad  
Southern Naiad  
Guadalupe Waternymph  
Guppy Grass  
Bushy Pondweed

## References

- Ackerman, J. D. 2000. Abiotic pollen and pollination: Ecological, functional, and evolutionary perspectives. *Plant Systematics and Evolution* 222: 167–185.
- Agami, Moshe, Sven Beer, and Yoav Waisel. 1986. The morphology and physiology of turions in *Najas marina* L. in Israel. *Aquatic Botany* 26: 371–376.
- Alcocer, J. and U. T. Hammer. 1998. Saline lake ecosystems of Mexico. *Aquatic Ecosystem Health and Management* 1(3–4): 291–315.
- Angelo, Ray and David E. Boufford. 2000. Atlas of the flora of New England, monocots except Poaceae and Cyperaceae. *Rhodora* 102(909): 1–119.
- APG (Angiosperm Phylogeny Group) II. 2003. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141: 399–436.
- Bergstrom, Peter W., Robert F. Murphy, Michael D. Naylor, Ryan C. Davis, and Justin T. Reel. 2006. Underwater Grasses in Chesapeake Bay and Mid-Atlantic Coastal Waters: Guide to Identifying Submerged Aquatic Vegetation. Maryland Sea Grant College Publication No. UM-SG-P1-2006-01. 76 pp.
- Bernardini, B. and F. Lucchese. 2018. New phylogenetic insights into Hydrocharitaceae. *Annali Di Botanica* 8: 45–58.
- Blackburn, R. D., P. F. White, and L. W. Weldon. 1968. Ecology of submersed aquatic weeds in south Florida canals. *Weed Science* 16(2): 261–266.

- Bonilla-Barbosa, Jaime Raúl. 2013. Mexican aquatic weeds: Distribution and importance. Preliminary results of weed distribution models in Mexico. Proceedings of the 6<sup>TH</sup> Biennial Weeds Across Borders Conference (2012): 199–210.
- Britton, N. L. and A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada in three volumes: Volume I (Ferns to Buckwheat). Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 680 pp.
- Brochet, Anne-Laure, Matthieu Guillemain, Hervé Fritz, Michel Gauthier-Clerc, and Andy J. Green. 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. *Ecography* 32(6): 919–928.
- Brush, Grace S. and William B. Hilgartner. 2000. Paleoecology of submerged macrophytes in the upper Chesapeake Bay. *Ecological Monographs* 70(4): 645–667.
- Bruton, Charles. 1950. *Najas guadalupensis* (Spreng.) Magnus, Its Ecology and Control. Master's Thesis, Oklahoma State University, Stillwater, OK. 35 pp.
- Carter, Virginia and Nancy Rybicki. 1986. Resurgence of submersed aquatic macrophytes in the tidal Potomac River, Maryland, Virginia, and the District of Columbia. *Estuaries* 9(4): 368–375.
- Clausen, Robert T. 1936. Studies in the genus *Najas* in the northern United States. *Rhodora* 38: 333–345.
- Coddington, Jonathan and Katharine G. Field. 1978. Rare and Endangered Vascular Plant Species in Massachusetts. Report prepared by the New England Botanical Club, Cambridge, MA. 67 pp.
- Collins, Jordan. 2022. Three photos of *Najas guadalupensis* ssp. *guadalupensis* from California. Shared via iNaturalist at <https://www.inaturalist.org/observations/132351315>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>
- Cox, Paul Alan. 1988. Hydrophilous pollination. *Annual Review of Ecology and Systematics* 19: 261–279.
- Cox, Paul Alan. 1993. Water-pollinated plants. *Scientific American* 269: 68–74.
- Davis, Frank W. 1985. Historical changes in submerged macrophyte communities of Upper Chesapeake Bay. *Ecology* 66(3): 981–993.
- de Boer, Hugo, Maria G. Asmyhr, Hanne H. Grundt, Inga Kjersti Sjøtun, Hans K. Stenøien, and Iris Stiers. 2016. Assessment of the risks to Norwegian biodiversity from the import and keeping of aquarium and garden pond plants. Scientific Opinion on the on Alien Organisms and Trade in Endangered species of the Norwegian Scientific Committee for Food Safety ISBN: 978-82-8259-240-6, Oslo, Norway.



Dierberg, F. E., T. A. DeBusk, S. D. Jackson, M. J. Chimeney, and K. Pietro. 2002. Submerged aquatic vegetation-based treatment wetlands for removing phosphorous from agricultural runoff: Response to hydraulic and nutrient loading. *Water Research* 36(6): 1409–1422.

England, J. Kevin. 2014. The Vascular Flora of Marengo County, Alabama. Master's Thesis, University of West Alabama, Livingston, AL. 269 pp.

Faber-Langendoen, D. 2018. Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments. NatureServe, Arlington, VA. 52 pp.

Fassett, Norman C. 1957. A Manual of Aquatic Plants. Second Edition. University of Wisconsin Press, Madison, WI. 405 pp.

Fernald, M. L. 1923. Notes on the distribution of *Najas* in northeastern America. *Rhodora* 25(295): 105–109.

Fernald, M. L. 1950. Gray's Manual of Botany. Dioscorides Press, Portland, OR. 1632 pp.

Ferren, Wayne W. Jr. 1982. Critical tidal river-palustrine and estuarine wetlands of southern New Jersey. In William J. Cromartie (ed.). New Jersey's Endangered Plants and Animals. Stockton State College Center for Environmental Research, Pomona, NJ.

FoHvos (Friends of Hopewell Valley Open Space). 2025. New Jersey Invasive Species Strike Team. Invasive species list with control recommendations. Available online at <https://www.fohvos.info/invasive-species-strike-team/info-center/>

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition. The New York Botanical Garden, Bronx, NY. 910 pp.

Goldberg, Nisse and Tiffany Trent. 2020. Patterns in submerged aquatic vegetation in the lower St. Johns River, Florida, from 2001 to 2019. *Journal of Aquatic Plant Management* 58: 135–145.

Haynes, Robert R. 1977. The Najadaceae in the southeastern United States. *Journal of the Arnold Arboretum* 58(2): 161–170.

Haynes, Robert R. 1979. Revision of North and Central American *Najas* (Najadaceae). *SIDA, Contributions to Botany* 8(1): 34–56.

Haynes, R. R. 1988. Reproductive biology of selected aquatic plants. *Annals of the Missouri Botanical Garden* 75: 805–810.

Haynes, Robert R. Page updated November 5, 2020. *Najas guadalupensis* subsp. *guadalupensis*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed November 20, 2024 at [http://floranorthamerica.org/Najas\\_guadalupensis\\_subsp.\\_guadalupensis](http://floranorthamerica.org/Najas_guadalupensis_subsp._guadalupensis)

- Haynes, Robert R. and C. Barre Hellquist. 1996. New combinations in North American Alismatidae. *Novon* 6: 370–371.
- Haynes, Robert R. and W. Alan Wentz. 1974. Notes on the genus *Najas* (Najadaceae). *SIDA, Contributions to Botany* 5(4): 259–264.
- Hellquist, C. Barre. 1977. Observations on some uncommon vascular aquatic plants in New England. *Rhodora* 79: 445–452.
- Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.
- Hough, Mary Y. 1983. New Jersey Wild Plants. Harmony Press, Harmony, NJ. 414 pp.
- Howell, Nathan Devine. 2015. Guide to the Littoral Zone Vascular Flora of Carolina Bay Lakes. Master's Thesis, North Carolina State University, Raleigh, NC. 363 pp.
- Huang, Shuang-Quan, You-Hao Guo, Gituru W. Robert, Yao-Hua Shi, and Kun Sun. 2001. Mechanism of underwater pollination in *Najas marina* (Najadaceae). *Aquatic Botany* 70: 67–78.
- Hussner, A., I. Stiers, M. J. J. M. Verhofstad, E. S. Bakker, B. M. C. Grutters, J. Haury, J. L. C. H. van Valkenburg, G. Brundu, J. Newman, J. S. Clayton, L. W. J. Anderson, and D. Hofstra. 2017. Management and control methods of invasive alien freshwater aquatic plants: A review. *Aquatic Botany* 136: 112–137.
- ITIS (Integrated Taxonomic Information System). Accessed January 31, 2025 at <http://www.itis.gov>
- Ito, Yu, Norio Tanaka, Stephan W. Gale, Okihito Yano, and Jie Li. 2017. Phylogeny of *Najas* (Hydrocharitaceae) revisited: Implications for systematics and evolution. *Taxon* 66(2): 309–323.
- Jacono, C. C., M. M. Richerson, V. H. Morgan, E. Baker, and J. Li. 2020. *Hydrilla verticillata* (L. f.) Royle. U.S. Geological Survey, Nonindigenous Aquatic Species Database, Gainesville, FL, and NOAA Great Lakes Aquatic Nonindigenous Species Information System, Ann Arbor, MI. Accessed April 18, 2025 at [https://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?Species\\_ID=6&Potential=Y&Type=2&HUCNumber](https://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?Species_ID=6&Potential=Y&Type=2&HUCNumber)
- Johnson, J. 2024. *Najas guadalupensis* ssp. *guadalupensis* conservation status factors. NatureServe, Arlington, VA. Accessed April 12, 2025 at [https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.153529/Najas\\_guadalupensis\\_ssp\\_guadalupensis](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.153529/Najas_guadalupensis_ssp_guadalupensis)
- Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (<http://www.bonap.net/tdc>). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Kaufman, Sylvan Ramsey and Wallace Kaufman. 2007. *Invasive Plants: Guide to the Impacts and Control of Common North American Species*. Stackpole Books, Mechanicsburg, PA. 458 pp.

King, Ursula. 2017. *Genome Evolution in *Najas* and *Hydrilla* (Hydrocharitaceae)*. Doctoral Dissertation, University of Connecticut, Storrs, CT. 282 pp.

Koncki, Natalie G. and Myla F. J. Aronson. 2015. Invasion risk in a warmer world: Modeling range expansion and habitat preferences of three nonnative aquatic invasive plants. *Invasive Plant Science and Management* 8(4): 436–449.

Les, Donald H. 1988. Breeding systems, population structure, and evolution in hydrophilous angiosperms. *Annals of the Missouri Botanical Garden* 75: 819–835.

Les, Donald H., Sallie P. Sheldon, and Nicholas P. Tippery. 2010. Hybridization in hydrophiles: Natural interspecific hybrids in *Najas* (Hydrocharitaceae). *Systemic Botany* 35(4): 736–744.

Les, Donald H., Elena L. Peredo, Ursula M. King, Lori K. Benoit, Nicholas P. Tippery, Cassandra J. Ball, and Robynn K. Shannon. 2015. Through thick and thin: Cryptic sympatric speciation in the submersed genus *Najas* (Hydrocharitaceae). *Molecular Phylogenetics and Evolution* 82: 15–30.

Maki, Kristine C. and S. M. Galatowitsch. 2008. Cold tolerance of the axillary turions of two biotypes of *Hydrilla* and Northern Watermilfoil. *Journal of Aquatic Plant Management* 46: 42–50.

Mid-Atlantic Herbaria. 2025. Accessed at <https://midatlanticherbaria.org/portal/index.php> on April 12, 2025.

Montz, Glen N. 1978. The submerged vegetation of Lake Pontchartrain, Louisiana. *Castanea* 43(2): 115–128.

Mora-Olivo, Arturo and Alejandro Novelo Retana. 2005. La vegetación acuática y semiacuática. In G. Sánchez-Ramos, P. Reyes-Castillo, and R. Dirzo (eds.), *Historia Natural de la Reserva de la Biosfera El Cielo, Tamaulipas, México*. Instituto de Ecología A. C., Xalapa, Veracruz, Mexico.

Morong, Thomas. 1893. The Naiadaceae of North America. *Memoirs of the Torrey Botanical Club* 3(2): 1–65 + 55 plates.

Morris, Lori and Dean Dobberfuhl. 2012. Submerged aquatic vegetation patterns in the lower St. Johns River Basin. Appendix 9.A. in the St. Johns River Water Supply Impact Study, Division of Water Resources, St. Johns River Water Management District, Palatka, FL. 14 pp.

Morse, Caleb A., Craig C. Freeman, and Ronald L. McGregor. 2007. New, corrected, and interesting records for the Kansas vascular flora. *Journal of the Botanical Research Institute of Texas* 1(1): 753–761.

NatureServe. 2025. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed April 12, 2025 at <https://explorer.natureserve.org/>

NJNHP (New Jersey Natural Heritage Program). 2010. Explanation of Codes Used in Natural Heritage Reports. Updated March 2010. Available at [https://nj.gov/dep/parksandforests/natural/docs/nhpcodes\\_2010.pdf](https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf)

NJNHP (New Jersey Natural Heritage Program). 2024. Biotics 5 Database. NatureServe, Arlington, VA. Accessed March 15, 2024.

Peltier, W. H. and E. B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. *Weed Science* 18: 7–9.

Peredo, Elena L., Ursula M. King, and Donald H. Les. 2013. The plastid genome of *Najas flexilis*: Adaptation to submersed environments is accompanied by the complete loss of the NDH complex in an aquatic angiosperm. *PLoS ONE* 8(7): e68591.

Philbrick, C. Thomas. 1991. Hydrophily: Phylogenetic and evolutionary considerations. *Rhodora* 93(873): 36–50.

Philbrick, C. Thomas and Donald H. Les. 1996. Evolution of aquatic angiosperm reproductive systems. *BioScience* 46(11): 813–826.

Philbrick, C. T. and J. M. Osborn. 1994. Exine reduction in underwater flowering *Callitriche* (Callitrichaceae): Implications for the evolution of hypohydrophily. *Rhodora* 96: 370–381.

Poirrier, Michael A., Kathy Burt-Utley, John F. Utley, and Elizabeth A. Spalding. 2010. Submersed aquatic vegetation of the Jean Lafitte National Historical Park and Preserve. *Southeastern Naturalist* 9(3): 477–486.

POWO. 2025. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed April 12, 2025 at <http://www.plantsoftheworldonline.org/>

Rebman, J. 2019. Photo of *Najas guadalupensis* ssp. *guadalupensis* from California. Shared via iNaturalist at <https://www.inaturalist.org/observations/31634985>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

Rhoads, Ann Fowler and Timothy A. Block. 2007. *The Plants of Pennsylvania*. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.

Ricketson, Jon M. 2018. Vascular plants of Arizona: Najadaceae, water-nymph family. *Canotia* 14: 31–35.

Ring, Richard M., Elizabeth A. Spencer, and Kathleen Strakosch Walz. 2013. Vulnerability of 70 Plant Species of Greatest Conservation Need to Climate Change in New Jersey. New York Natural Heritage Program, Albany, NY and New Jersey Natural Heritage Program, Department of Environmental Protection, Office of Natural Lands Management, Trenton, NJ, for NatureServe #DDCF-0F-001a, Arlington, VA. 38 pp.

Rosendahl, C. O. 1939. Additional notes on *Najas* in Minnesota. *Rhodora* 41: 187–189.

Schuegraf, Monica A. 2004. Establishment of Seagrass Decline and Causative Mechanisms in Pearl Lagoon, Nicaragua through use of Traditional Ecological Knowledge, Sediment Coring and Direct Visual Census. FES Outstanding Graduate Student Paper Series, Volume 9, Number 1, York University, Toronto, Ontario. 40 pp.

Schuyler, Alfred E. 1981. 1980 field trips. *Bartonia* 48: 49–51.

Short, Frederick T., Sarian Kosten, Pamela A. Morgan, Sparkle Malone, and Gregg E. Moore. 2016. Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany* 135: 3–17.

Spaulding, D. D., T. W. Barger, H. E. Horne, and B. J. Finzel. 2019. Flora of Northern Alabama, part 4. Basal Monocots. *Phytoneuron* 47: 1–132.

Sprenkle, Elizabeth Silverman, Leonard A. Smock, and John E. Anderson. 2004. Distribution and growth of submerged aquatic vegetation in the Piedmont section of the James River, Virginia. *Southeastern Naturalist* 3(3): 517–530.

Stuckey, Ronald L., John R. Wehrmeister, and Robert J. Bartolotta. 1978. Submersed aquatic vascular plants in ice-covered ponds of central Ohio. *Rhodora* 80(824): 575–580.

Tiner, Ralph W. 2009. Field Guide to Tidal Wetland Plants of the Northeastern United States and Neighboring Canada. University of Massachusetts Press, Amherst, MA. 459 pp.

U. S. Army Corps of Engineers. 2022. National Wetland Plant List, version 3.6. <https://nwpl.sec.usace.army.mil/> U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2025a. *Najas guadalupensis* illustration from Britton, N. L. and A. Brown, 1913, An illustrated flora of the northern United States, Canada and the British Possessions, 3 vols., Kentucky Native Plant Society, New York, Scanned By Omnitek Inc. Image courtesy of The PLANTS Database (<http://plants.usda.gov>). National Plant Data Team, Greensboro, NC.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2025b. PLANTS profile for *Najas guadalupensis* ssp. *guadalupensis* (Southern Water nymph). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed April 12, 2025 at <http://plants.usda.gov>



Volk, Kaitlin M. 2019. Assessing the Invasive Potential of *Najas minor* in Maine. Honors Thesis, Colby College, Waterville, ME. 35 pp.

Walz, Kathleen S., Jason L. Hafstad, Linda Kelly, and Karl Anderson. 2020. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservancy (CoC) Values for Species and Genera (update to 2017 list). New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ.

Weakley, A. S. and Southeastern Flora Team. 2024. Flora of the Southeastern United States. Edition of March 4, 2024. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2203 pp.

Wentz, W. A., and R. L. Stuckey. 1971. The changing distribution of the genus *Najas* (Najadaceae) in Ohio. Ohio Journal of Science 71(5): 292–302.

Young, Bruce E., Elizabeth Byers, Geoff Hammerson, Anne Frances, Leah Oliver, and Amanda Treher. 2016. Guidelines for Using the NatureServe Climate Change Vulnerability Index, Release 3.02, 1 June 2016. NatureServe, Arlington, VA. 65 pp.

Zhu, Jinning, Xuan Xu, Qing Tao, Panpan Yi, Dan Yu, and Xinwei Xu. 2017. High invasion potential of *Hydrilla verticillata* in the Americas predicted using ecological niche modeling combined with genetic data. Ecology and Evolution 7: 4982–4990.