

Seasonal growth and phenology of water hyacinth, curlyleaf pondweed, and Brazilian egeria in the Sacramento–San Joaquin River Delta

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ABSTRACT

The Sacramento–San Joaquin River Delta (hereafter the “Delta”) is a 28,000-ha (68,000 acre) tidal estuary formed by the Sacramento River and the San Joaquin River. The seasonal growth of water hyacinth (*Eichhornia crassipes* (Mart.) Solms), Brazilian egeria (*Egeria densa* Planch.), and curlyleaf pondweed (*Potamogeton crispus* L.) were studied to improve adaptive management of these species from May 2015 through December 2017 by sampling 3 separate sites by collecting 12 or 15 biomass samples taken with either a 0.1-m² quadrat (floating plants) or a 0.0225-m² Ekman dredge (submersed plants) at each site per month. Samples were sorted to relevant plant parts, dried at 70 C, and weighed. Water hyacinth biomass peaked in early fall, reaching as high as 2,500 g dry weight (gDW) m⁻². Leaves senesced in the winter, reaching a minimum of 300 gDW m⁻², composed mostly of stem bases. Egeria biomass did not vary significantly over the season, ranging between 200 and 400 gDW m⁻². Curlyleaf pondweed biomass reached a peak of 400 gDW m⁻² in midsummer, dying back to turions in the winter. Water hyacinth stem base total nonstructural carbohydrates (TNCs) ranged from almost 0 to 30% DW, with a distinct minima in June of each year. Curlyleaf pondweed turion TNCs ranged from 20 to 60% DW, with a peak in July and a low point in February. Egeria shoot TNC was consistently lowest in late spring (April or May). Phenological studies inform managers regarding the initiation of growth, and the timing of significant propagule formation.

Key words: *Egeria densa* Planch., *Eichhornia crassipes* (Mart.) Solms, TNCs, total nonstructural carbohydrates, water temperature.

INTRODUCTION

All too often, the management of weeds becomes strictly an exercise in chemistry or engineering—the selection of

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better herbicides or more powerful machines. The biology of weed species, however, is critical to developing successful weed management approaches in all sites, whether agricultural or natural areas, aquatic or terrestrial (Bhowmik 1997). The study of plant phenology, or the growth and life cycle of a plant through the year, is one such aspect of weed biology. Several components of phenology are pertinent to improving weed management: 1) production of critical life history stages or propagules, 2) germination or sprouting of perennating propagules, and 3) determination of low points in the carbohydrate storage of the plant. Madsen (1990) studied the seasonal growth and production of the seeds of waterchestnut (*Trapa natans* L.) in a New York reservoir, finding that this annual produced seeds throughout the summer and fall. When managers prevented seed production and maturation, the seed bank was reduced and the waterchestnut population declined (Madsen 1993c, Methe et al. 1993). In the midwestern and northeastern United States, curlyleaf pondweed (*Potamogeton crispus* L.) produces its turions in a synchronous manner in the early summer (Woolf and Madsen 2003). Through research on temperature sensitivity of herbicides (Netherland et al. 2000), an effective management program has been implemented in many lakes in this region preventing the development of new curlyleaf pondweed turions (Poovey et al. 2002, Johnson et al. 2012). A knowledge of the timing of seedling emergence or propagule sprouting can be used to improve weed management (Ghersa and Holt 1995, Otto et al. 2007). This principle is widely used in crop weed management and integrated pest management, but less commonly applied to weeds of natural areas (Ehler 2006, Swanton et al. 2008). Linde et al. (1976) identified a consistent low point in the carbohydrate storage in rhizomes of cattail (*Typha latifolia* L.), and found that this point was synchronous with anthesis. Pesacreta and Luu (1988) demonstrated the potential for examining carbohydrate partitioning in aquatic weed species. This approach has been applied with some success to Eurasian watermilfoil (*Myriophyllum spicatum* L.; Painter 1988, Madsen 1997), cattail (Linde et al. 1976), hydrilla (*Hydrilla verticillata* (L.f.) Royle; Madsen and Owens 1998) and water hyacinth (*Eichhornia crassipes* (Mart.) Solms; Madsen et al. 1993, 1995). Knowledge of when plants spread or propagule production occurs may also be used to contain invasive plants by managing the plants before the propa-

gules can disseminate (Madsen et al. 1988, Madsen and Smith 1997).

Water hyacinth (*Eichhornia crassipes* (Mart.) Solms) has been called the “worst aquatic weed in the world” (Holm et al. 1977). It is a rosette-forming free-floating aquatic weed, with leaves filled with aerenchyma, which serve for flotation. The plant forms large numbers of child plants on the end of stolons that coalesce into the formation of dense floating mats (Penfound and Earle 1948). Although it does flower prolifically and forms some viable seed, vegetative propagation predominates. Water hyacinth is native to the Amazon basin, and has been introduced around the world for water gardens (Holm et al. 1969). Water hyacinth has spread to all continents, except Antarctica (Kriticos and Brunel 2016). It was introduced to North America at the New Orleans Cotton Centennial Exposition in 1884, and subsequently spread to Florida and the southeastern states (Penfound and Earle 1948). The first record for water hyacinth in California is for Yolo County in 1904, and from there spread to the Delta and elsewhere (Bock 1968).

In tropical climates, it grows as an evergreen perennial (Penfound and Earle 1948). In subtropical climates where frost and cold weather cause leaf kill without affecting the stem base, it grows as an herbaceous perennial (Madsen et al. 1993). In the Delta of California, seasonal cold weather kills leaves in mid to late winter, and new leaves initiate regrowth in spring, typically in March (Spencer and Ksander 2005). Water hyacinth will not sprout from stem bases at water temperatures of 10 C or below, but will sprout at 15 C (Miskella and Madsen 2019).

Brazilian egeria (also Brazilian elodea, Brazilian waterweed; *Egeria densa* Planch., hereafter egeria) is a submersed evergreen perennial weed (Cook and Urmi-König 1984). Egeria is dioecious, but only plants bearing staminate flowers are found in North America and elsewhere in its introduced range (St. John 1961). The plant spreads predominantly by stem fragments and runners (Cook and Urmi-König 1984). A native of Brazil, Argentina, and Uruguay, it has been widely introduced to the rest of South America, North America, Europe, Asia, Japan, Australia, and New Zealand (Cook and Urmi-König 1984). In North America, it is found across the United States and into western Canada, but does not form nuisance growths throughout that range (U.S. Fish and Wildlife Service 2018). An evergreen perennial, it has green shoots throughout the year. In some locations, such as Japan, the biomass varies dramatically across the seasons (Haramoto and Ikusima 1988). In South Carolina’s Lake Marion, biomass varied from a low of 100 to a high of 400 g dry weight (gDW) m⁻² (Getsinger and Dillon 1984). Where dense growths occur, egeria can displace native vegetation, reduce turbidity, alter fish predator-prey interactions, and interfere with water flow (Tanner et al. 1990, Conrad et al. 2016, Hestir et al. 2016). These various impacts have caused some to describe egeria as an ecosystem engineer (Yarrow et al. 2009).

Curlyleaf pondweed (*Potamogeton crispus* L.) is a submersed aquatic weed that grows rooted in water up to 5 m (15 ft) deep, yet can form a surface canopy (Catling and Dobson 1985). The plant is rhizomatous, with long flexuous stems

that bear long, ovate denticulate leaves that have a distinctive venation (Catling and Dobson 1985). A native of Eurasia, Africa, and Australia, it is an invasive to North America (Bolduan et al. 1994). The oldest verified specimen in North America was found in Delaware in 1860 (Stuckey 1979). By 1900, it had spread throughout the northeastern part of the United States. By 1930, it had spread into the upper midwest states. Curlyleaf pondweed invaded southern California through a separate international introduction in 1900, and spread northward (Stuckey 1979). Nuisance growth of curlyleaf pondweed can suppress native vegetation and cause a flush of nutrients during the growing season through a combination of plant senescence and sediment nutrient flux (Bolduan et al. 1994, James et al. 2002). Curlyleaf pondweed is a perennial herbaceous plant. Although it forms viable seed, it also forms large numbers of dormant shoot buds known as turions (Wehrmeister and Stuckey 1992). In the northeastern and midwestern United States, the plant sprouts from turions in fall, remains largely quiescent over the winter, and then has eruptive growth of shoots in the spring (Bolduan et al. 1994). The plant forms turions and sets seed by the end of June, after which the shoots senesce (Wehrmeister and Stuckey 1992). This life-history cycle is similar to that observed in Japan (Sastroutomo 1981). Although turion formation is highly synchronous in midwestern lakes, the sprouting of turions is staggered (Woolf and Madsen 2003).

Superficially, one might expect that all there was to be known of phenology of these invasive plants was already known. However, phenology of a species responds to the environment of the site. For instance, the growth cycle of Eurasian watermilfoil (*Myriophyllum spicatum* L.) can vary from a single summer biomass peak to two separate biomass peaks (spring and fall), and a range of variations in between (Madsen 2005). Phenology studies for key invasive plants should be done in each region. Likewise, multiple phenology studies can refine our understanding of the drivers of plant life cycles. For instance, the typical phenology of sago pondweed (*Stuckenia pectinata* (L.) Boerner) is a herbaceous perennial across its temperate range, but studies of sago pondweed in the Baltic Sea found that the phenology can range from an herbaceous perennial to a stress-tolerant evergreen perennial in high-energy wave zones (Kautsky 1987).

As with other weed phenological studies, our goal in this study is to elucidate key points or aspects of the biology and life history of target species to improve their control (Wersal and Madsen 2018). In this paper, we present some preliminary observations on these three species and potential applications for their control in the Delta.

MATERIALS AND METHODS

Study site

Formed from the confluence of the Sacramento River from the northern half of the Central Valley of California, and the San Joaquin River flowing from the southern half of the Central Valley, the 28,000 ha (68,000 acre) Sacramento-San Joaquin River Delta (or “Delta”) is a critical estuary for

TABLE 1. SAMPLE SITE LOCATIONS FOR PHENOLOGICAL STUDIES OF WATER HYACINTH, CURLYLEAF PONDWEED, AND EGERIA IN THE SACRAMENTO–SAN JOAQUIN RIVER DELTA. SITE NUMBERS FOLLOWED BY AN ASTERISK INDICATE SITES NOT SHOWN ON THE MAP BECAUSE OF THE SHORT DURATION OF SAMPLING.

Site Name	Site Number (Reference Map)	Species Sampled	Dates Sampled (Once per Month)	Latitude N (Decimal Degrees)	Longitude W (Decimal Degrees)
Becky Bridge	W3	Water hyacinth	November 2015–October 2017	37.976026	–121.620335
Lambert Road	W2	Water hyacinth	May 2015–December 2017	37.933944	–121.432515
Trapper Slough	W3*	Water hyacinth	June 2015–October 2015	37.933890	–121.423505
Whiskey Slough	W1	Water hyacinth	May 2015–December 2017	37.944820	–121.416590
Quimby Island	P2*	Curlyleaf pondweed	August 2015	38.021772	–121.580169
Franks Tract	P1*	Curlyleaf pondweed	August 2015–January 2016	38.047169	–121.628302
Mildred Island	P2	Curlyleaf pondweed	September 2015–December 2017	37.999945	–121.510791
Holland	P1	Curlyleaf pondweed	February 2016–December 2017	37.993007	–121.576943
Mokelumne	P3	Curlyleaf pondweed	September 2015–December 2017	38.101779	–121.562820
Latham (Mildred)	E1	Egeria	May 2015–December 2017	37.984846	–121.531280
Columbia	E2	Egeria	November 2015–December 2017	38.044915	–121.521589
Connection	E3	Egeria	May 2015–December 2017	37.997611	–121.573532
Empire (Mildred)	E2*	Egeria	May 2015–October 2015	37.975952	–121.532340

its ecological and economic values (Delta Stewardship Council [DSC] 2013). Water from the Delta is used to irrigate California croplands and for domestic and industrial supply, and the Delta is used for commercial and recreational navigation. Specific sample sites for each species will be described below.

Water hyacinth

Water hyacinth was sampled at three locations per month in the Delta (Table 1, Figure 1). The sites varied slightly through the 2 yr of sampling. Whiskey Slough (site W1) was sampled throughout the program, from May 2015 to December 2017. Lambert Road (site W2) was also sampled throughout the study, from May 2015 to October 2017. Trapper Slough (W3) was initially sampled from June 2015 to October 2015, at which time a different location with more representative growth was selected. From November 2015 to October 2017, Becky's Bridge (W3) was sampled. At each of these sites, 12 biomass samples were collected each month using a 0.1-m² floating PVC quadrat (Madsen 1993a,b, Madsen and Wersal 2017). Plant samples were returned to the lab; sorted into leaves, stem bases, stolons, roots, and inflorescences; then dried at 70 C and weighed. No dead or senescent tissue was included in the samples. Plant samples were ground using a plant mill¹ to pass through a 0.4-mm screen. Samples from the same plant part, month, and site were grouped for total nonstructural carbohydrate (TNC) analysis to provide enough plant matter to measure the TNC content accurately, with the 12 samples per site composited into 3 samples per month per plant part per site. Ground plant samples were sent to an analytical lab² for analysis of TNCs, done by extracting and digesting nonsoluble carbohydrates (Smith 1969) and analyzing the free sugars using an high pressure liquid chromatography (HPLC) method. Total nonstructural carbohydrates are calculated from all resulting free sugars. At each site, air and water temperature were measured with a deployed temperature datasonde.³ Air-temperature datasondes were deployed within a radiation shield.⁴ Temperature datasondes collected a datum every 15 min, and data were downloaded

once per month using a data shuttle.⁵ Daily averages for air and water temperature were calculated and reported.

Egeria

Egeria was sampled at three locations per month in the Delta, although the sites varied slightly during the study (Figure 1, Table 1). Latham (E1) is a site located in the Mildred Island region of the Delta, along the channel outside the island levee. Latham was sampled monthly from May 2015 to December 2017. Empire (E2) is also in the Mildred Island region, and was sampled from May 2015 to November 2015. To be more representative of the Delta, this site was moved to a site named Columbia (E2), which is across the main stem of the San Joaquin near the Contra Costa Water District intake. Columbia was sampled from November 2015 to December 2017. Lastly, Connection Slough (E3) was sampled from May 2015 to December 2017. At these sites, 15 samples were taken each month using an Ekman dredge⁶ with an area of 0.0225 m². These plant samples were sorted into shoots, roots, and inflorescences. Plant samples were dried at 70 C and weighed. Only total biomass data will be discussed here. Plant samples were ground using a plant mill¹ to pass through a 0.4-mm screen. Samples from the same plant part, month, and site were grouped for TNC analysis to provide enough plant matter to have three composited samples per site per month and per plant part. Ground plant shoot samples were sent to an analytical lab² for analysis of TNCs, done by extracting and digesting nonsoluble carbohydrates (Smith 1969) and summing the analysis of free sugars using an HPLC method.

At sample locations, the water depth and plant canopy height was measured, either using a sounding rod or hydroacoustically.⁷ From these data, the percent of the water column inhabited by vegetation, or biovolume, was calculated (%PBV, Valley et al. 2015, Madsen and Wersal 2017). In addition, water temperature was measured with a deployed temperature datasonde.³ Water temperature sondes were deployed about 0.3 m above the sediment on PVC rods inserted at least 0.6 m into the sediment, at the average depth of the plant bed being studied. Because total tidal amplitude is up to 1.3 m, the water depth varied from 0.6 to 2.0 m. Temperature datasondes collected a datum

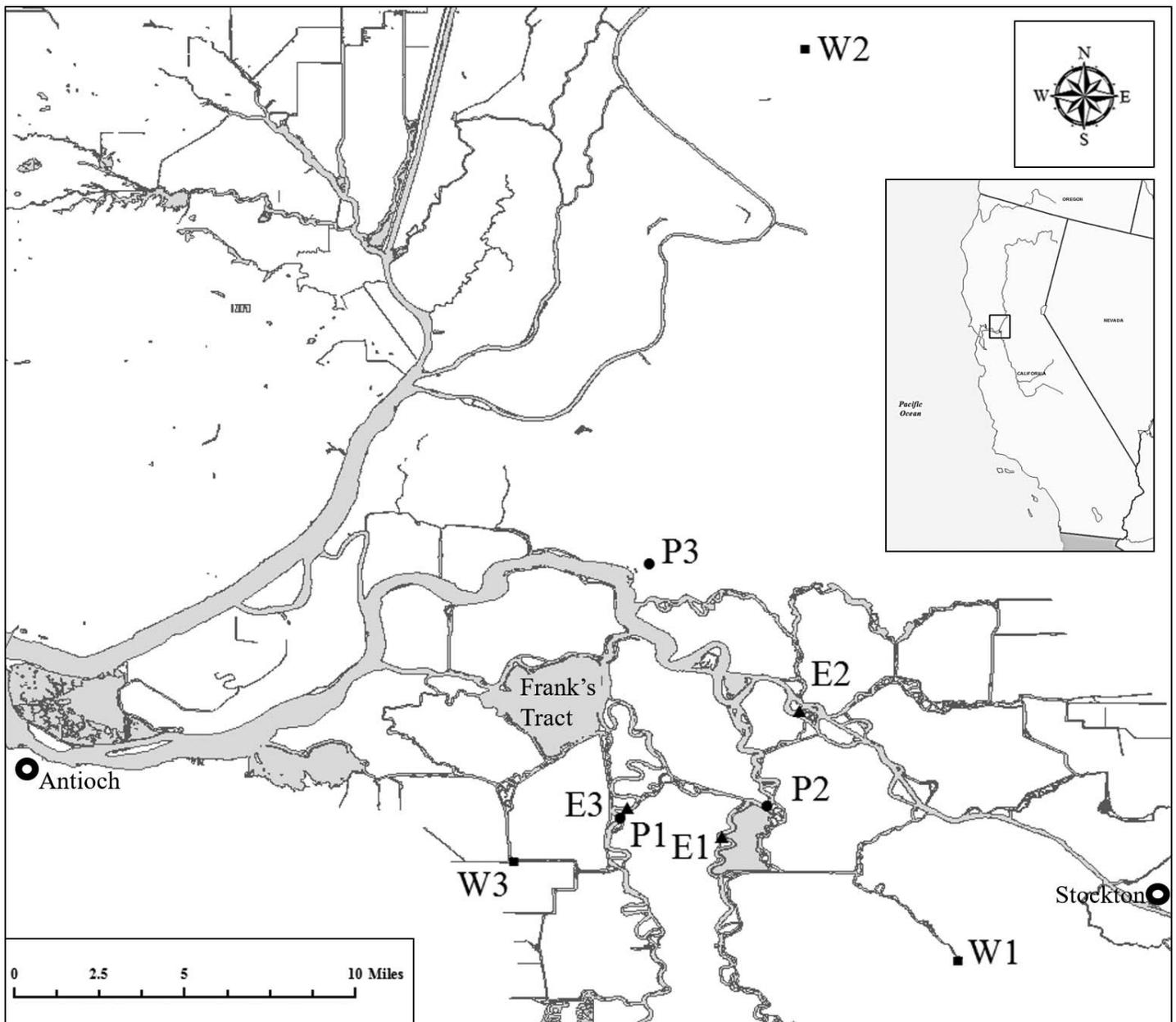


Figure 1. Map of the Sacramento–San Joaquin River Delta from Stockton, CA in the east to Kimball Island in the west. The map inset indicates the location of the map within the State of California. Sample site locations for each species are shown by a combination of letters and numbers. Letters: E, egeria; P, curlyleaf pondweed; W, water hyacinth. Site names are provided with site numbers in Table 1. Only sites used throughout the majority of the study are indicated.

every 15 min, and data were downloaded once per month using a data shuttle.⁵ Daily averages for air and water temperatures were calculated and reported for the three sites.

Curlyleaf pondweed

Curlyleaf pondweed was sampled at three locations per month in the Delta, though the sites shifted early in the project cycle (Figure 1, Table 1). Initially, we sampled curlyleaf pondweed in Frank's Tract (P1) from August 2015 to January 2016. Waterfowl depredation on turions, however,

was sufficient to eliminate curlyleaf pondweed from this site. We sampled Holland Slough (P1) from February 2016 to December 2017. Quimby Island (P2) was sampled only once, in August 2015. Mildred Island (P2), which is a site at the north end of the Mildred Island complex, was sampled September 2015 to December 2017. Mokulemne River (P3) was sampled from September 2015 to December 2017. At these sites, 15 samples were taken each month using an Ekman dredge⁶ with an area of 0.0225 m². These plant samples were sorted into shoots, turions, inflorescences, roots, and rhizomes, and the number of turions and sprouting turions in the sample counted. Plant samples were

dried at 70 C and weighed. Only total biomass data will be discussed here. Plant samples were ground using a plant mill¹ to pass through a 0.4-mm screen. Samples from the same plant part, month, and site were grouped for TNC analysis to provide enough plant matter to have three composited samples per site per month and per plant part. Ground plant samples were sent to an analytical lab² for analysis of turion TNCs, done by extracting and digesting nonsoluble carbohydrates (Smith 1969) and summing the analysis of free sugars using an HPLC method.

At sample locations, the water depth and plant canopy height was measured by using a sounding rod, or hydro-acoustically.⁷ In addition, water temperature was measured with a deployed temperature datasonde. Temperature datasondes collected a datum every 15 min, and data were downloaded once per month using a data shuttle.⁵ Daily averages for air and water temperatures were calculated and reported for the three sites. Monthly mean and standard error of plant biomass data were computed using Statistix.⁸

RESULTS AND DISCUSSION

Water hyacinth

Water hyacinth biomass was lowest in spring (March or April) and highest in the autumn (October; Figure 2). Water hyacinth growth in the Delta follows a seasonal pattern that is more representative of an herbaceous perennial, like water hyacinth growth in northern Texas (Madsen et al. 1993), Mississippi (Luu and Getsinger 1990), or northern Florida (Center and Spencer 1981) than that of an evergreen perennial such as in northern Argentina (Neiff et al. 2001), tropical Brazil (Greco and Freitas 2002), or southern Louisiana (Penfound and Earle 1948). Water hyacinth leaves in the Delta will die back entirely from January to March in response to cold temperatures (Spencer and Ksander 2005). Water hyacinth will alternate between these life-history strategies depending on the presence or absence of sufficiently low temperature to kill exposed leaves. However, so long as stem bases are in the water, they will be protected from freezing and the plant will survive (Owens and Madsen 1995). The vast majority of overwintering is done by vegetative growth from overwintering stem bases. Although most think of water hyacinth as a tropical plant, there is no reason it should not establish and thrive in temperate locations such as Illinois or southern Ontario (Adebayo et al. 2011, VonBank et al. 2018).

Air and water temperatures track each other closely ($R^2 = 0.99$, $P < 0.001$). Average air temperatures reached a minimum of 3–5 C in January of each year, and a maximum of 30 C or more in July and August (Figure 2A). The biomass minima for all three sites in both years occurs much later than the temperature minima, in March or April (Figure 2B). The biomass maxima occurred in the fall, in September or October. The sites differ in the times of the maxima and slope of increase, but follow the same slope of decrease and minima. In late October and November, the mats break up, with a large number of small mats floating in the rivers and navigable channels. It is unknown whether this is a dispersal strategy, like autofragmentation in Eurasian watermilfoil

(*Myriophyllum spicatum* L., Madsen et al. 1988), or is the product of another natural or human action.

The maximum biomass at the Lambert site reached as high as 2,900 gDW m⁻² in September 2016, whereas the maximum biomass at the Becky's Bridge site was 2,100 gDW m⁻². The high biomass values are comparable to those observed in Florida before the introduction of any of the biological control agents (Center et al. 1999). Although one introduced biological control agent (*Neochetina bruchi* Hustache) is widely distributed in the Delta, it is not having a significant impact on growth, though it does cause leaf damage (Hopper et al. 2017). Research is ongoing to find ecotypes of *Neochetina eichhorniae* (Warner) that are more cold tolerant, and thus will thrive in typical Delta temperatures (Reddy et al. 2019).

TNCs are the energy storage compound plants use to store and transfer photosynthetic products in the plant. These include a variety of sugars (glucose, fructose, and sucrose) and starch. Plants may store large amounts of TNCs in the fall, then utilize them during regrowth in the spring (Madsen 1991). For water hyacinth, the site specialized for carbohydrate storage is the stem base (Madsen et al. 1993). Although one population did not exceed a maximum of 12% DW TNC, the plants at the Becky's Bridge site reached maxima of from 20 to 30% of DW, which occurred in December or January. A maximum of 20% DW starch in the stem base was observed for a water hyacinth population in Texas (Madsen et al. 1993). Luu and Getsinger (1990) reported TNCs of up to 30% DW in the stem bases of water hyacinth grown in Mississippi. The seasonal dynamic is such that TNC begins to increase in July and August, when water hyacinth is actively growing.

The phenology of water hyacinth suggests three tactics for managing water hyacinth in the Delta. Management, particularly herbicide applications, should begin as early in the spring as possible to capitalize on the low point in TNC storage (Pesacreta and Luu 1988). Treatment early in the season will have greater success than waiting later in the season (Madsen et al. 1995). Secondly, retreatment should happen while the plants are small and lower density, rather than waiting until the rosettes are larger or at higher density. Treatment is more effective on small plants than large plants (Lopez 1993), due to a combination of better herbicide coverage and lower biomass to control. The key to stopping water hyacinth is to kill or remove stem bases. Although plants are not actively growing in the winter, removal of stem bases will prevent their regrowth in the following spring. Harvesting operations targeting large accumulations of water hyacinth stem bases will maximize removal of regrowth potential and minimize the amount of other plant material to be removed.

Egeria

Water temperature in the areas supporting egeria growth had a daily average ranging from 5 C in January to 25 C in December (Figure 3A). Plant response to these temperatures is much less obvious for egeria than for either water hyacinth or curlyleaf pondweed (below). There is a general tendency for lower biomass in the winter and higher

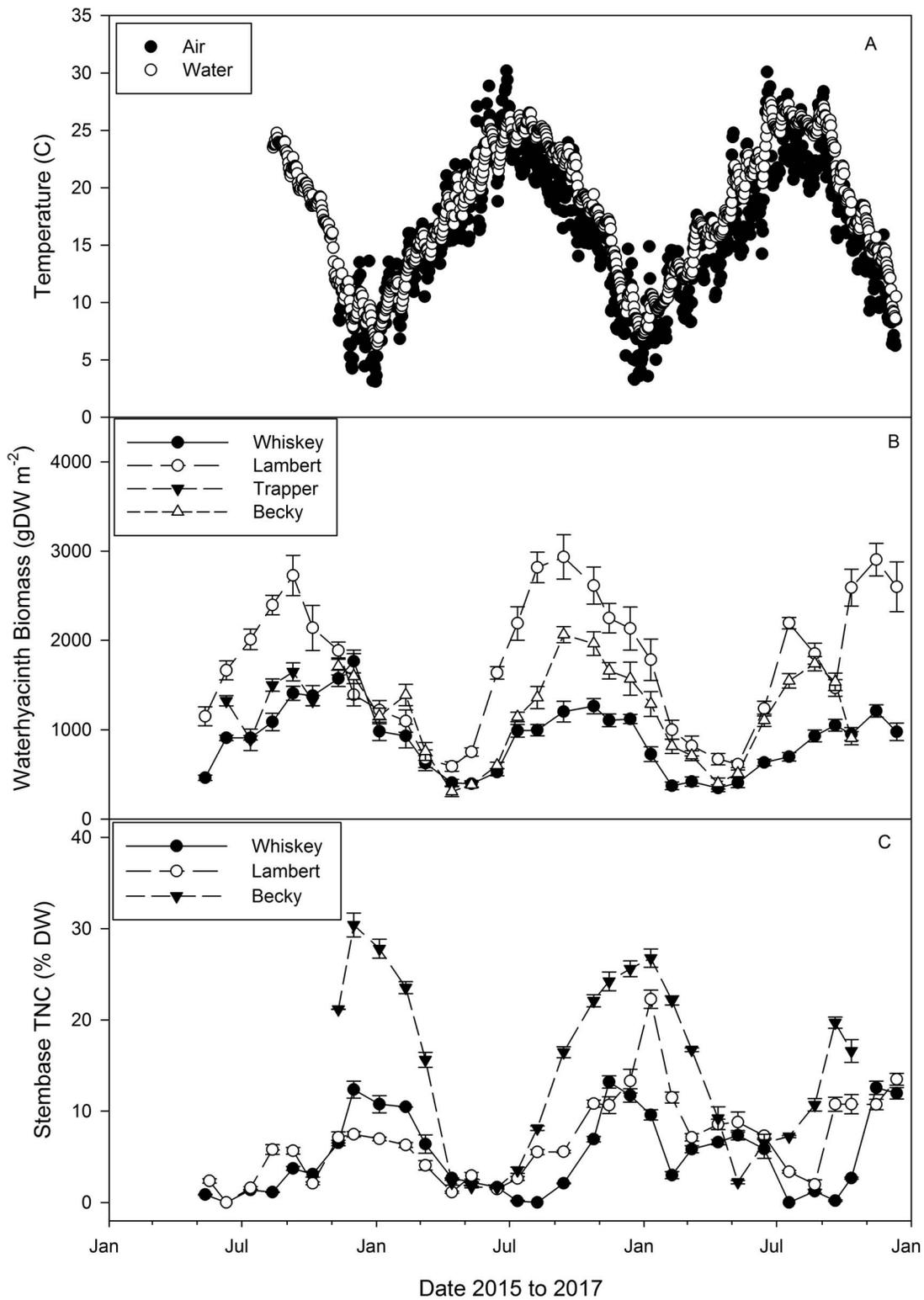


Figure 2. Water hyacinth (*Eichhornia crassipes*) phenology data collected at three sites in the Sacramento–San Joaquin River Delta from May 2015 to December 2017. See Table 1 for site names and numbers. (A) Daily average of air (solid circles) and water (open circles) temperature (in C) for May 2015 to December 2017. (B) Water hyacinth total biomass (g dry weight [gDW] m⁻²) at four sites. (C) Stem-base total nonstructural carbohydrate (TNC) as percentage of dry weight for three sites. Bars indicate a ± 1 standard error of the mean at a given site.

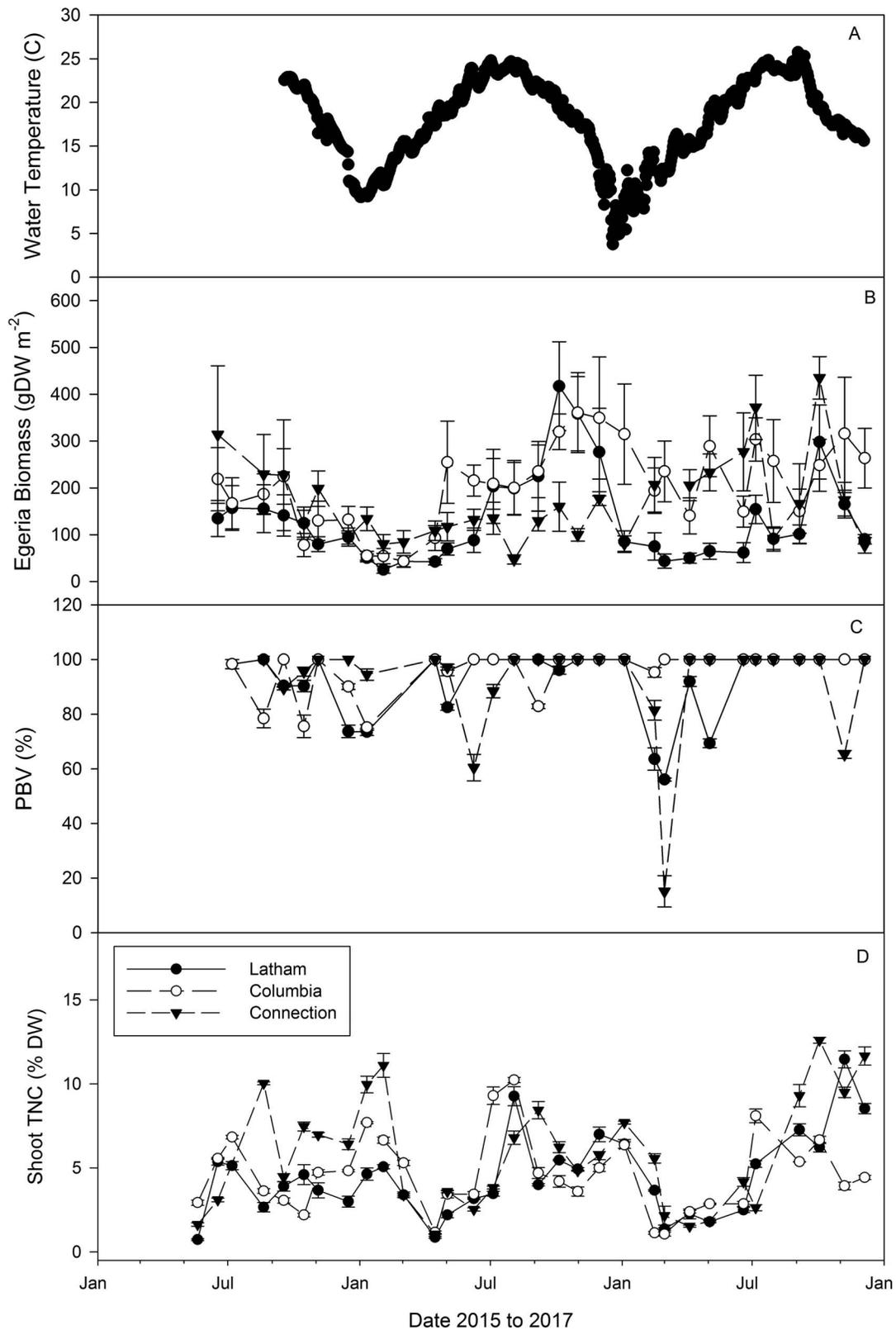


Figure 3. *Egeria* (*Egeria densa*) phenology data collected at three sites in the Sacramento–San Joaquin River Delta from May 2015 to December 2017. (A) Daily average water temperature (C) for three sites. (B) *Egeria* total biomass (g dry weight [gDW] m⁻²) at three sites. (C) Percent of the water column composed of egeria biovolume (%PBV) as determined by hydroacoustics or direct measurement. (D) Shoot total nonstructural carbohydrate (TNC) content as % dry weight (DW) for stems collected at three sites in the Delta. Bars indicate +1 standard error of the mean.

biomass in mid to late summer, but no clear and synchronous pattern between sites existed (Figure 3B). Concerned that this might be an artifact of sampling, we examined the biovolume of egeria, which is the percent of water column filled by plant shoots. Considering that these sites are influenced by tidal variations of 1–1.3 m (3–4 ft), the plant canopy is consistently at or near the surface on most dates except for February 2017 (Figure 3C). The biomass values are not erroneous; the mats of vegetation tend to persist across the seasons. This is contrary to observations by Getsinger and Dillon (1984) of egeria growth in Lake Marion, SC. They observed distinct seasonal growth with a pronounced low in the winter, and two peaks in biomass. Likewise, Haramoto and Ikusima (1988) observed a much more pronounced seasonal cycle in growth for an egeria population in Lake Kasumiga-ura in Japan. The maximum biomass for this study (430 gDW m^{-2}) is comparable to the 370 gDW m^{-2} in Lake Marion (Getsinger and Dillon 1984). The maximum biomass for egeria in a tropical high mountain reservoir in Colombia was observed to be 522 gDW m^{-2} (Carrillo et al. 2006). In the Hawkesbury-Nepean River of Australia, egeria invaded and displaced the native *Vallisneria americana* Michx., reaching a peak biomass of 800 gDW m^{-2} in one site (Roberts et al. 1999). Peak biomass for most sites in the Delta is occurring in October, with the lowest biomass in March (Figure 3B).

Although egeria biomass patterns were not expressive of seasonal variation, the allocation of TNCs showed a pronounced minimum in the spring (March or April) to coincide with regrowth of the plant. Spring low TNC was 2.5–3% DW, whereas peak TNC was as high as 11% DW (Figure 3D). Egeria does not have a specialized storage structure, so 10% DW for TNC is consistent with what is seen in other plants storing starch in an unmodified stem (Madsen 1991). The pattern of spring low in TNC and a summer or fall maximum is consistent with observations made by Pennington and Sytsma (2009) in Disappointment Slough in the Delta, as well as a reservoir in Oregon. Haramoto and Ikusima (1988) observed much higher starch storage in egeria in Japan, of up to 25% DW.

Egeria is a noted ecosystem engineer that alters sedimentation, suspended solids, and water flow (Yarrow et al. 2009). Roberts et al. (1999) documented egeria outcompeting native vegetation. Caudill et al. (2019) has documented that, with intensive management, a native plant community can be restored by controlling egeria. Hestir et al. (2016) has demonstrated that egeria has altered turbidity in the Delta, lowering its habitat suitability for the endangered Delta smelt (*Hypomesus transpacificus* McAllister). In addition, the dense beds of submersed plants serve as habitat for introduced predatory fish like largemouth bass (*Micropterus salmoides* Lacepede) that prey on the endangered Delta smelt (Conrad et al. 2016). Therefore, managing egeria is of critical importance to maintaining the habitat for both endangered fish species (Delta smelt) and other migratory fish.

These phenological observations support an early treatment window for egeria, using herbicides in March or April as regrowth begins. In addition, retreatment should occur within 2–4 wk rather than waiting for plants to grow and rebuild carbohydrate reserves. However, this approach is as

yet untested, and needs to have verification at the mesocosm or field scale through a trial. Despite these suggestions, managers should recognize that egeria does not have a specialized storage organ or propagule, so management targeting the green shoots will be removing the only plant portion viable for regrowth.

Curlyleaf pondweed

Curlyleaf pondweed has a life history that is driven by both water temperature and photoperiod; these environmental triggers interact to stimulate the formation of new turions in the spring and summer and turion sprouting in the fall or winter (Wehrmeister and Stuckey 1992, Bolduan et al. 1994). In the Delta study sites, water temperature varied from a minimum of 5 C in January to a maximum of 25 C in September (Figure 4A). Curlyleaf pondweed biomass, composed mostly of shoot material, increased from a minimum of 10 gDW m^{-2} or less (mostly turions) in January to a maximum of 230 gDW m^{-2} in July (Figure 4B). The timing of these peaks and valleys in the growth cycle differ only slightly from elsewhere in the country in the later peak biomass and later minimum. In Minnesota, Woolf and Madsen (2003) reported maximum biomass in June. Similar in seasonal amplitude, Rogers and Breen (1980) reported maximum shoot biomass in late spring in South Africa. Like the Minnesota study, they found no standing biomass in summer. In a study in Mississippi, Turnage et al. (2018) found standing biomass throughout the year, with biomass declining during the summer and active growth in the fall and winter. We observed standing biomass into the fall at our sites. Curlyleaf pondweed phenology may well be a continuum of responses between the patterns observed in Minnesota and Mississippi, with California somewhere in the middle.

Turion density reached as high as $1,500 \text{ turions m}^{-2}$ (Figure 4C). The turion densities observed in the Delta are consistent with those reported for Minnesota ($1,500$ – $2,500 \text{ turions m}^{-2}$; Woolf and Madsen 2003). In most sites, we observed a minimum in turion density in January, and a maximum in late summer (Figure 4C). This would suggest that turions are formed in late summer (July–August) and turions sprouting in winter. Sastroutomo (1980) reports that turions in Japan are formed in summer, before plant senescence, under conditions of long photoperiod and water temperatures up to 24 C. Woolf and Madsen (2003) documented that in Minnesota lakes, new turions were formed in June and July, before stem senescence. Warmer water temperatures would precipitate earlier turion formation and senescence.

The Woolf and Madsen findings led to a strategy of managing curlyleaf pondweed before the formation of new turions (Netherland et al. 2000, Skogerboe et al. 2008). This strategy has been widely applied in the midwestern and northeastern United States (Johnson et al. 2012). We did not see evidence of synchronous turion production in the Delta.

Turion TNC was relatively constant throughout the year, with the exception of a minimum in winter (Figure 4D). Turion TNC was as high as 56% DW in Frank's Tract, and otherwise reached 45% DW in the other sites (Figure 4D). Turions are a specialized structure for dormancy, and tend

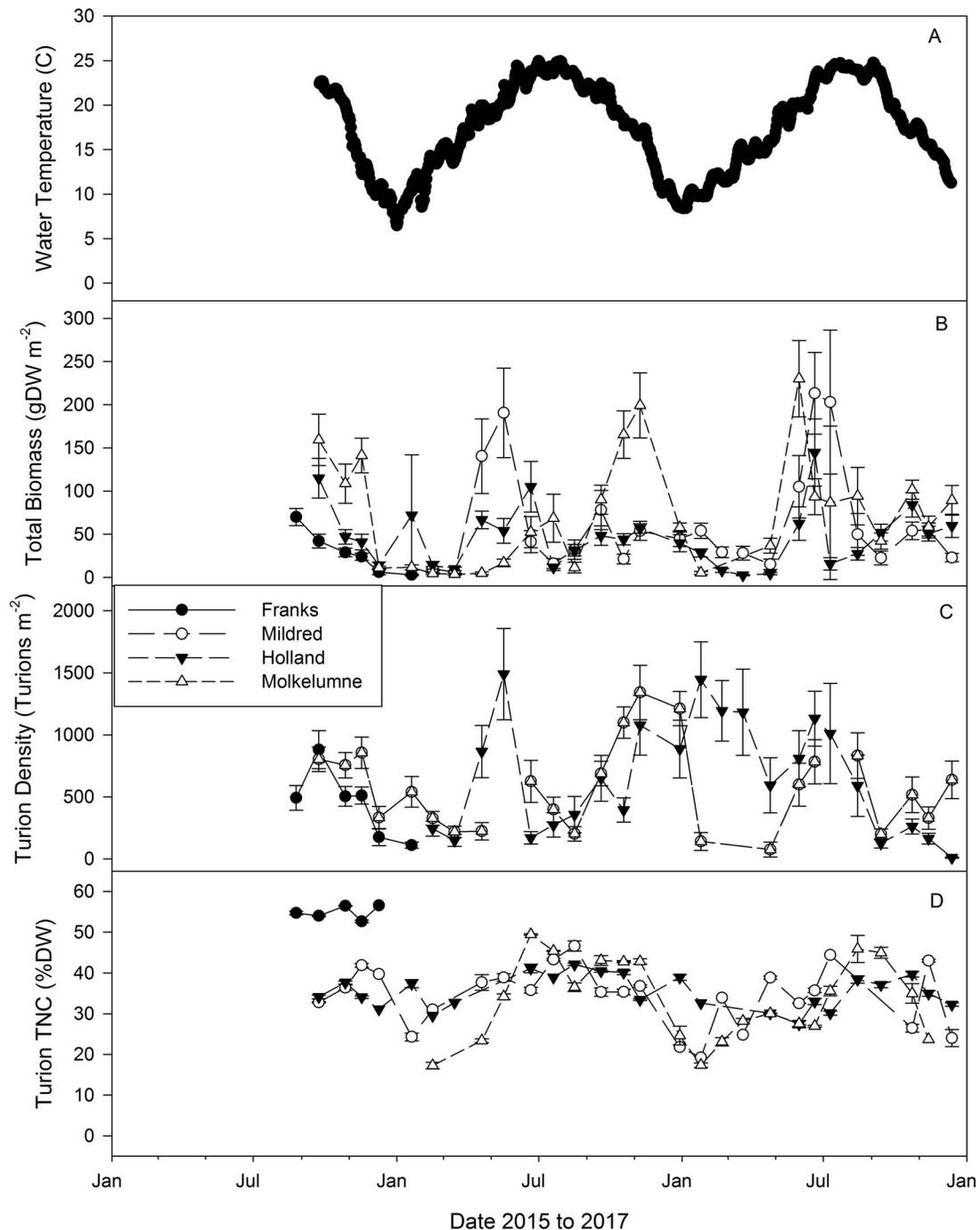


Figure 4. Curlyleaf pondweed (*Potamogeton crispus*) phenology data collected at three sites in the Sacramento–San Joaquin River Delta from August 2015 to December 2017. (A) Daily average water temperature (C) for three sites. (B) Curlyleaf pondweed total biomass (g dry weight [gDW] m⁻²) at four sites. (C) Turion density (turions m⁻²) for four sites. (D) Turion total nonstructural carbohydrate (TNC) content as % dry weight for turions collected at three sites in the Delta. Bars indicate +1 standard error of the mean.

to have higher starch concentrations than unspecialized stem tissue (Madsen 1991). TNC storage observed at other locations ranged from 44 to 66% DW in Minnesota (Wolf and Madsen 2003).

Rather than seeing a synchronous timing of turion formation, we observed synchronous sprouting of turions (Figure 5B). Turions sprouted in December and January,

when water temperatures were approaching their minimum (Figure 5A). We observed 30–50% of all turions sprouting during this time frame, and little sprouting at other times (Figure 5C). This is in contrast to lakes in Minnesota, where Wolf and Madsen (2003) observed sporadic sprouting throughout the fall, winter and spring. One difference may be that in the Delta, the cold water temperatures occur

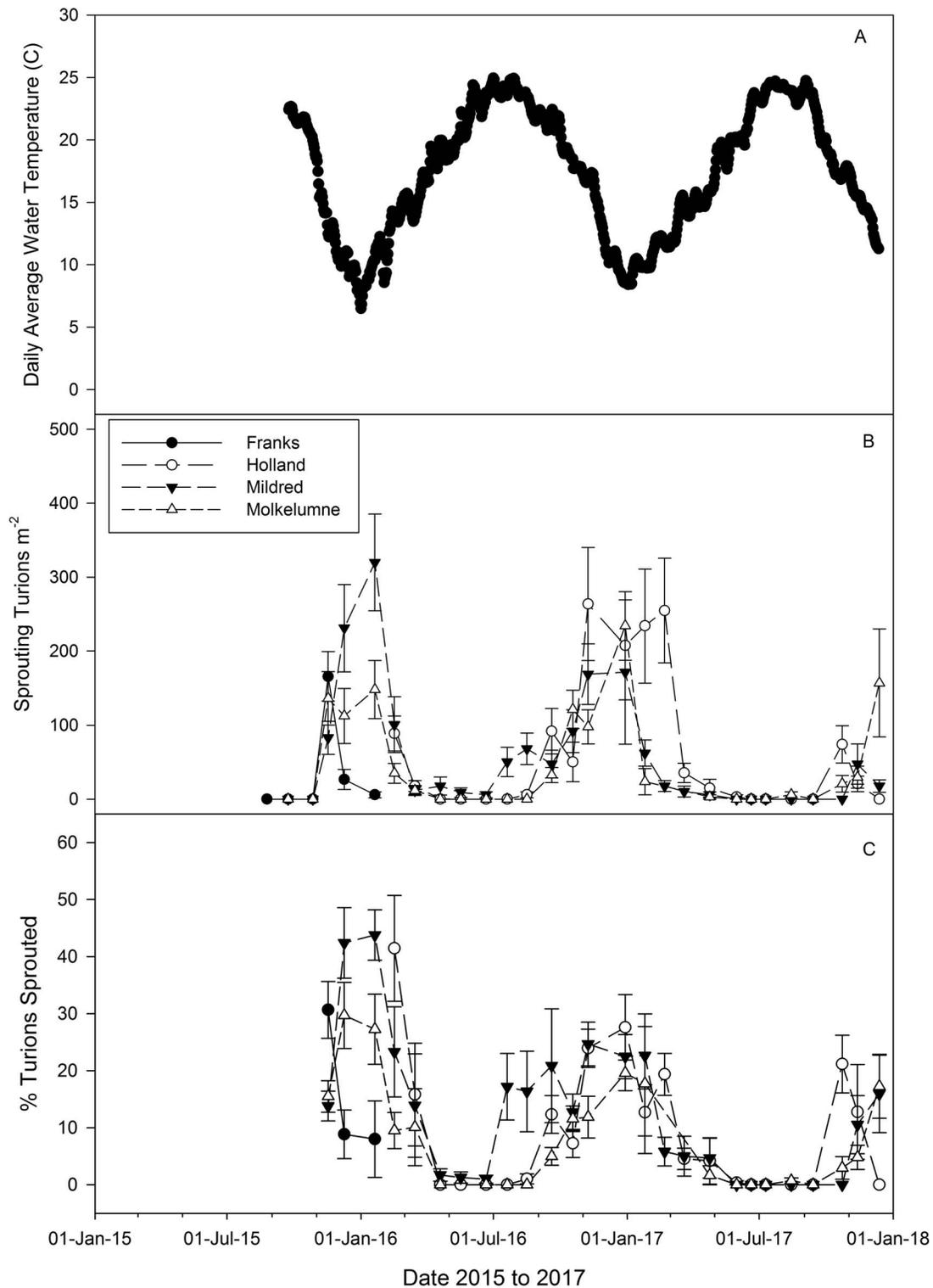


Figure 5. Curlyleaf pondweed (*Potamogeton crispus*) phenology data collected at three sites in the Sacramento–San Joaquin River Delta from August 2015 to December 2017. (A) Daily average water temperature (C) for three sites. (B) Number of turions sprouting per square meter for four sites. (C) Percent of all turions that sprouted for August 2015 to December 2017. Bars indicate +1 standard error of the mean.

in a narrow window, whereas in Minnesota they extend from fall through early spring. Sastroutomo (1981) reports that nondormant turions will sprout after a cold treatment of 5 C for as little as 1 wk.

The phenology of curlyleaf pondweed in the Delta suggests a different management approach than the Midwest. In the Midwest and Northeast, lakes with curlyleaf pondweed are treated in early spring (April) before turions

are formed, thus preventing a new generation of curlyleaf pondweed (Skogerboe et al. 2008). This timing is propitious in these regions, as it occurs before fish spawning and before native plants are active, helping to preserve plant diversity. However, we did not observe an opportunity for spring treatment of curlyleaf for the Delta. In addition, runoff may be heavy in the spring, preventing herbicide use, and this is a time when some endangered fish species are transiting the Delta. Rather, treatments may target sprouting turions in January or February, before heavy runoff and migration of fish into the Delta.

In combating invasive aquatic weeds, using the biology of the plant as part of the management strategy can enhance the ability to weaken the plant (Nichols and Shaw 1986). By studying the phenology and carbohydrate allocation of the target plant, a strategy can be developed to reduce the long-term population of the target aquatic weed (Madsen 2007, Wersal and Madsen 2018). These studies will be used to develop new approaches for managing these species in the Delta; for instance, timing the initiation of management to water temperature or water flow rather than exclusively the calendar, using degree-day relationships to determine how rapidly plants will regrow, or targeting a reduction of propagules (stem bases or turions) as a metric of success. For each species, a more in-depth examination of the data collected will provide some of these answers.

SOURCES OF MATERIALS

¹Wiley Mini-Mill, Thomas Scientific, 1654 High Hill Road, Swedesboro, NJ 08085.

²University of California–Davis Analytical Lab, Hoagland Annex, One Shield Avenue, Davis, CA 95616.

³HOBO Pendant Temperature Data Logger, Onset Computer Corporation, 470 MacArthur Boulevard, Bourne, MA 02532.

⁴Solar Radiation Shield SR1, Onset Computer Corporation, 470 MacArthur Boulevard, Bourne, MA 02532.

⁵HOBO Waterproof Shuttle, Onset Computer Corporation, 470 MacArthur Boulevard, Bourne, MA 02532.

⁶Ekman Dredge, AMS, Inc., 105 Harrison Street, American Falls, ID 83211.

⁷Lowrance HDS 7 and transducer, Lowrance (owned by Navico), 4500 S 129th East Avenue No. 200, Tulsa, OK 74134.

⁸Statistix 10, Analytical Software, 2105 Miller Landing Road, Tallahassee, FL 32312.

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