An investigation of the reproductive ecology of crab's-claw in the Trent River, Ontario, Canada

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ABSTRACT

Crab's-claw (*Stratiotes aloides* L.) is an aquatic macrophyte native to northern Eurasia and often sold in North America in the aquarium and water garden plant trade. In 2008, the first wild crab's-claw population in North America was discovered in the Trent-Severn Waterway in Ontario, Canada. Lack of crucial information on the reproductive ecology of the plant in the invaded habitat is presenting a barrier to effective control and management strategies. Specifically, it is unknown the extent to which the plant is propagating via the production of turions and offsets. Further, the residency time of its turions is also unknown. A field study was completed to evaluate the density and biomass of plants as well as the number and fate of turions and offsets produced by different phenotypic forms of the plant. This was done to identify any potential variability in reproduction between forms in the area of infestation. The submerged phenotype was identified as creating, on average, significantly more turions and offsets than the emergent phenotype. Secondly, experiments were done to understand turion viability and residency times. It was found that turions of crab's-claw do not persist in sediment for longer than 8 to 9 mo; however, it is likely turions last no longer than the period between growing seasons. This may bode well for management as it could be that there is a period in the year where all of the crab's-claw biomass is vulnerable to control.

Key words: control and management, invasive aquatic macrophyte, offset, *Stratiotes aloides,* turion.

INTRODUCTION

In 2008, the first wild population of crab's-claw (*Stratiotes aloides* L.), herein referred to as CC, was found in North American inland waters. CC is thought to have been initially introduced from a water garden in the vicinity of the hamlet of Trent River in Kawarthas/Northumberland region of Ontario, Canada. As of 2015, the plant has spread west, downriver, to Percy's Reach, near Campbellford, ON, with another, separate, population in the Black River, a tributary of Lake Simcoe, to the east (Figure 1; R. McGowan, pers. comm.; OISAP 2016). It has established dense monodominant stands of vegetation within the river, with some stands over 20 ha in size, presenting a potential risk to the local

ecology and human values derived from the river ecosystem (OISAP 2016). This is the first documented establishment of a wild population of CC outside of its native range; as such there is limited information available as to how it may impact the ecology of the river and human values associated with the river. Data have shown that it often excludes phytoplankton from its stand through allelopathy and competition for nutrients (Crackles 1982, Mulderij et al. 2006). Forbes (2000) notes that waterfowl predation of CC has not been explicitly mentioned in previous studies, though, during this study of the Trent River CC population, Canada geese (*Branta canadensis*) were observed predating the leaf tips of emergent plants. The CC population in the Trent River was also observed in this study to have developed association with the invasive zebra mussel (*Dresseina polymorpha*), which is consistent with observed behavior in its native range (Lewandowski and Ozimek 1997). The lengthy, wide, and robust leaves of CC seem to provide an excellent surface for the zebra mussel, thus contributing to the perpetuation of another invasive (Lewandowski and Ozimek 1997, Toma 2006). CC is a member of the Hydrocharitaceae family, which includes other well-known invasives such as hydrilla [*Hydrilla verticillata* (L. f. Royle)]] and Brazilian egeria (*Egeria densa* Planch.) (Les et al. 2006). The family, despite being relatively small, has an incredibly morphologically diverse array of members (Les et al. 2006). A recent genetic review concerning CC classification argued that it should likely be placed within its own subfamily (Les et al. 2006). CC is dioecious; however, there have been rare cases of plants with a fertile stamen produced in a female flower (Cook and Urmi-König 1983). This inconsistent dioecious behavior indicates sexual phenotypic instability, and observational studies of the plant have noted that phenotypic expression of sex might be temperature dependent as no males are seen in the northerly reaches of its native range (Forbes 2000). However, even in ranges where both sexes are present, recruitment from seed is thought to be minimal relative to asexual recruitment (Cook and Urmi-König 1983, Smolders et al. 1995). In one field study by Erixon (1979) recruitment was observed as being greater than 100% per year, with plant densities doubling between June and September. Research on the Trent River population has documented a doubling in CC biomass between September and November, usually a time when the native plant community is senescing (Canning 2014). In an *in situ* study done in a laboratory by Renman (1989), recruitment (new plants being added to the population) was observed to be 70% with no mortality in the rest of the population.

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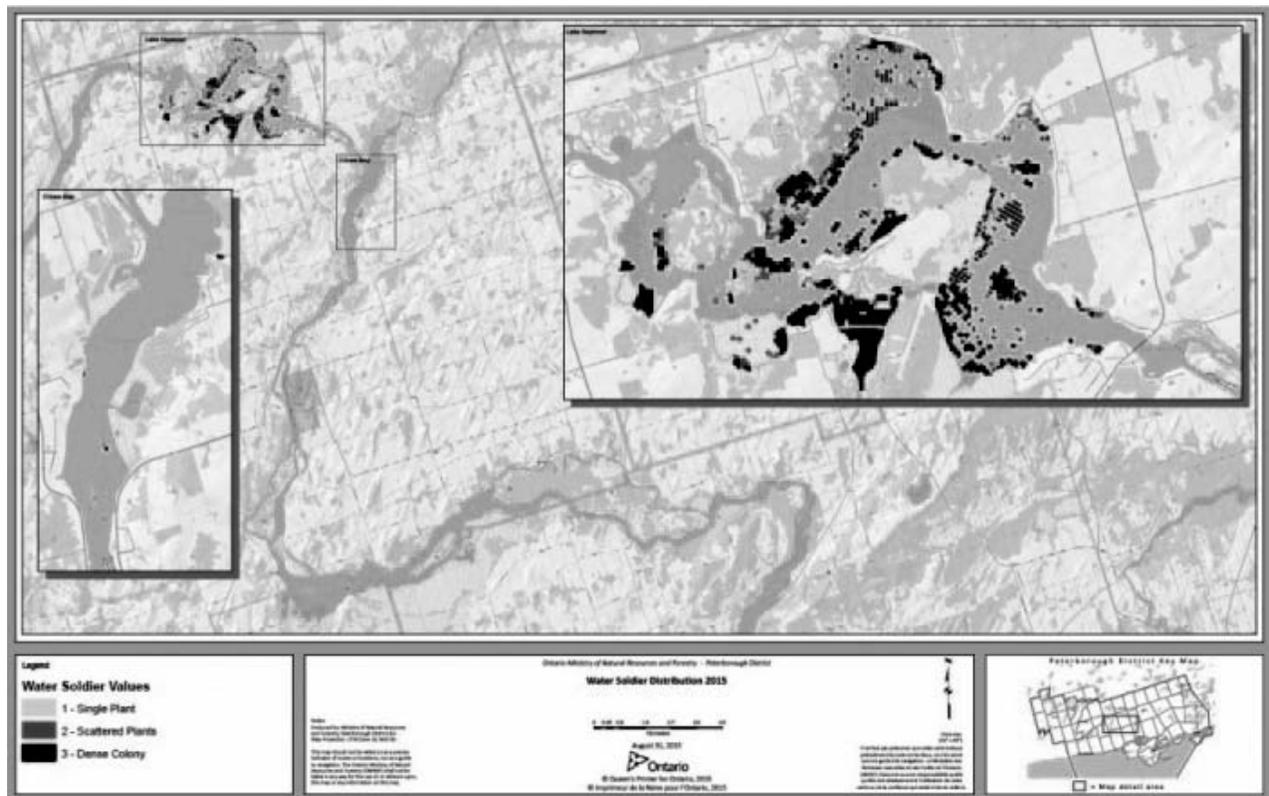
Figure 1. Crab's-claw distribution in east-central Ontario as of 31 August 2015 (OISAP 2016).

CC can behave as either a submerged or as an emergent aquatic plant. In the spring and summer some plants will generate photosynthetic gases in their leaves, allowing them to become buoyant and float to the water surface; when autumn returns CC will lose many of its leaves and sink back down to the sediment (Smolders et al. 2003). Beyond this, the plant has interesting phenotypic variety. CC is typically described as having two phenotypes, an emergent phenotype characterized by a plant with some or all leaves above the surface of the water and a submerged phenotype, with all leaves below the surface (Erixon 1979, Renman 1989, Efremov and Sviridenko 2008). However, it has been theorized that CC has as many as three (Strzalek 2004) or four morphologically distinct phenotypes (Toma 2006).

CC has three methods of propagation: by seed, offset, and turion (Forbes 2000). Seed production in the Trent-Severn Waterway population has been noted as being absent, which is consistent with information from its native range where, north of a particular line, in climates more similar to southern Ontario, male plants are found only rarely and no viable seed has been found (de Geus-Kruyt and Segal 1973, Forbes 2000). Further, even in areas where the plant reproduces sexually, it predominantly relies upon asexual reproduction by offset and by turion (Kornatowski 1979). Turions are frost-hardy propagules which can also act as long-range dispersal propagules as they susceptible to greater physical forces such as water current and wind-induced wave action (Erixon 1979). CC turion production begins in July and lasts until November (Erixon 1979, Kunze

et al. 2010, Canning 2014). It is known that axillary turions of aquatic macrophytes are able to both float and sink; this is thought to be caused by variable starch densities, which, at variable water temperatures (with constant pressure and therefore variable densities), are able to sink or float (Weber and Noodén 2005). A study by Erixon (1979) found that turions collected in January sank when replaced in the water. Offsets are stand-densifying propagules that have the ability to create their own rooting structures while attached to the mother plant. Offsets are vulnerable to fragmentation by current and wave action and can act as a long-range dispersal mechanism (Erixon 1979).

The mechanisms by which CC competes are of great interest in understanding potential interactions between CC and the newly invaded environments in Ontario. CC's ability to overwinter as a green plant gives it an additional resilience mechanism, contributing to its extremely low mortality rate from year to year (Renman 1989, Kunze et al. 2010). CC's phenotypic plasticity also lends to its ability to survive in lower light conditions. In a study by Harpenslager et al. (2015), it was observed that under lower light levels CC adapted by developing thinner leaves with a higher efficiency of photosystem II and higher chlorophyll content. In mesotrophic to eutrophic conditions with high photosynthetically active radiation (PAR) and high dissolved carbon dioxide (CO_2), CC is able to form dense emergent patches, with one study by Erixon (1979) reporting biomasses of 5,500 kg of dry weight per hectare in September (Harpenslager et al. 2015). These dense floating

patches are easily capable of heavily shading the bottom sediment, significantly reducing light resources available for other plants.

Due to the potential threat this plant poses to native ecosystems and its close proximity to the Great Lakes, the Ontario provincial government, in partnership with the Ontario Federation of Anglers and Hunters, has established a goal of complete eradication of CC from the Trent-Severn Waterway. In addition to ongoing studies as to appropriate management approaches, information on the reproductive ecology of the plant in this newly invaded region is lacking, presenting a barrier to effective management. Turion sediment residency time has been a large question for authorities managing CC because it is the only propagule in the current context that has the potential to act as a long-term resilience mechanism. Information on how long turions can persist in sediment will help determine the minimum repeat treatment period for any area invaded by CC. The viability of turions after overwintering is also unknown; additional information would provide a better estimation of the plants recruitment rates and ability to spread successfully on an annual basis.

Another gap in our knowledge is the difference in the quantity of propagules produced by each CC phenotype within the area of infestation. Although previous studies have examined the differences between propagule production in emergent and submerged phenotypes, it is prudent to check for consistency in a new range (Erixon 1979). This information may help identify targeting priorities; i.e., if a significant difference in propagule output between phenotypes exists, one may be identified as being more greatly contributing to spread than another.

MATERIALS AND METHODS

Study area

The study was conducted at two locations within the Kawarthas/Northumberland region of Ontario; the first location was a small (40 by 15 m), human-dug, hydrologically isolated pond in Blackstock, ON (44°05′57.52″N; 78°51′13.61″W) that is believed to have been colonized by CC sometime prior to 2011. The second location, near the hamlet of Trent River in the reach of the Trent-Severn Waterway known as Lake Seymour, was composed of two sets of sites (44°23′10.60″N; 77°50′22.05″W and 44°22′44.67″N; 77°49′33.75″W). The sampling sites at both locations consisted of a plant community largely dominated by CC (> 90% by sediment cover) with patches of both the emergent and submerged phenotypes.

Offset and turion production by river populations

The first portion of this research was to determine the differences in the reproductive ecology between emergent and submerged phenotypes. Data were collected in two sampling periods (August 2013 and September 2015) at the Trent-Severn Waterway location. The August 2013 sampling period was used to collect information on stand density, stand biomass, and individual biomass by phenotype; this occurred

at the site with coordinates 44°23′10.60″N; 77°50′22.05″W. Patches were selected by having a diver move along a 50-m transect, with each patch encountered sampled. A patch was defined as a distinct area of sediment covered by a single phenotype of CC. One sample was taken from each patch by spearing a pole of polyvinyl chloride (PVC) piping into the sediment and placing a 0.5 by 0.5–m quadrat overtop of the spear, with all vegetation present within the quadrat harvested by hand. Upon harvest, each individual plant was placed within its own plastic garbage bag. In total, 5 emergent patches and 14 submerged patches were sampled. Any roots were removed from the sampled plants and all remaining biomass was spun in a salad spinner to remove excess moisture. All of the spun biomass was then placed on a scale until the mass reading stabilized (± 1 g).

The September 2015 sampling period was used to collect information on turion and offset production by phenotype of CC. Sampling was done in a small bay within the Lake Seymour reach of the Trent River; this area was chosen as it received relatively little disturbance from boat traffic and other recreational users of the water body. Two submerged CC sites and six CC sites were chosen for sampling in late September 2015. Sites were defined as a 2 by 2–m area within a single patch of CC of a particular phenotype. Samples were taken at each site by spearing a pole of PVC piping into the sediment and placing a 0.5 by 0.5–m quadrat over the top of the spear, holding a corner of the quadrat to the spear to maintain relative position for sampling. Samples were taken within the quadrat until 15 plants had been harvested or there were no plants left within the site. Each plant then had its associated turions and offsets counted and recorded. For statistical analysis, Student's t tests and Mann-Whitney Rank Sum tests were used (based on the normality or nonnormality of the particular data, respectively). All statistical comparisons were considered significant at a P value of less than 0.05 (alpha). All statistical analysis was done in the software program SigmaPlot 12.0.[1]

Turion persistence

The turion persistence study was conducted at both the pond and the river sites in early August 2013, prior to the fall and winter release of turions, by collecting bulk sediment samples using a standard Ponar® Grab sediment sampler[2] with a 523-cm^2 sample area (Kunze et al. 2010). At the pond site, transect lines were set up covering half the length of the pond with five lines, each 5 m apart and with six sampling points per line, each 2 m apart, with a total of 30 sampling points. The Ponar Grab sediment sampler was dropped once at each point and the contents of the sample were emptied into a 5-mm wire mesh screen. Water was then poured through the screen to dissolve the sediment and reveal any turions. The number of turions per 523 cm^2 and the depth of the sample were recorded. River site sampling was conducted by recording 10 global positioning system (GPS) positions within the site. At each GPS position, five samples were taken from different positions off the boat. Samples were collected and processed as previously mentioned in the pond site. The number of turions per 523 cm^2 and the depth of the sample were recorded.
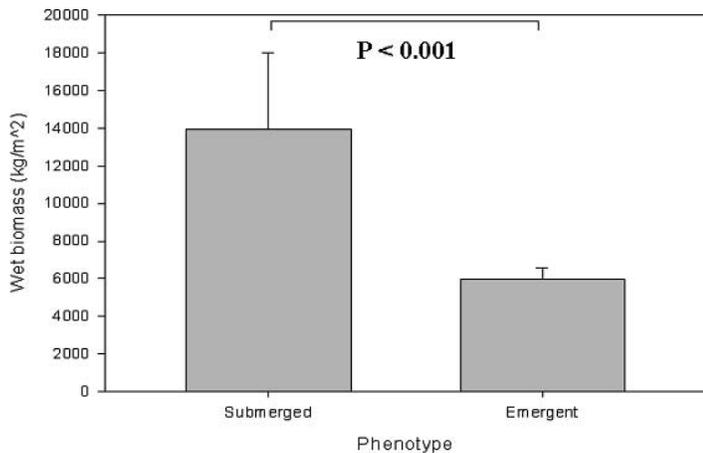
Figure 2. Mean ± SD wet biomass density (kg m^{-2}) by phenotype from population sampling in early August. Line with P value below indicates significances level between bars (Student's t test).

Figure 3. Mean ± SD wet biomass per plant (g) by phenotype from population analysis in early August. Line with P value below indicates significances level between bars (Student's t test).

Turion incubation and sprouting

A laboratory experiment was set up to assess overwintering dynamics and turion viability by incubating three sets of five sealed plastic containers containing six turions each at 4 C for 2, 3, and 4 mo (Berhardt and Duniway 1986; Adamec 1999). Turions used with the experiment were harvested in November using a throw rake to collect plants, from which a total of 90 mature turions were harvested. In order to best simulate winter conditions in the river, sediment from the river was used to line the bottom of the containers and river water was used to fill the containers to control for any impact nutrient and substrate conditions may have on sprouting. Light and temperature were controlled for by placing the turions in a dark refrigerator set at 4 C to mimic the overwintering conditions in Lake Seymour. Each turion was weighed and its position in the tray recorded. Once the appropriate incubation time was achieved, each set of containers was brought into a growth chamber with growing conditions established at 20 C and a 12-h light–dark cycle. The percentages of sprouting were assessed by container and by mass.

RESULTS AND DISCUSSION

Plant density results

Emergent communities were found to have a significantly higher mean wet biomass density (Student's t test; $P < 0.001$) than submerged communities, on average 13.9 kg m^{-2} and 6.00 kg m^{-2}, respectively (Figure 2). Additionally, individual emergent plants were found to have significantly more wet biomass on average (Student's t test; $P < 0.001$) than submerged plants, 279 g and 94 g respectively (Figure 3), which is a finding consistent with the literature (Toma 2006).

The disparity in biomass density, despite lack of a significant difference in absolute plant numbers and individual plant biomass between emergent and submerged phenotypes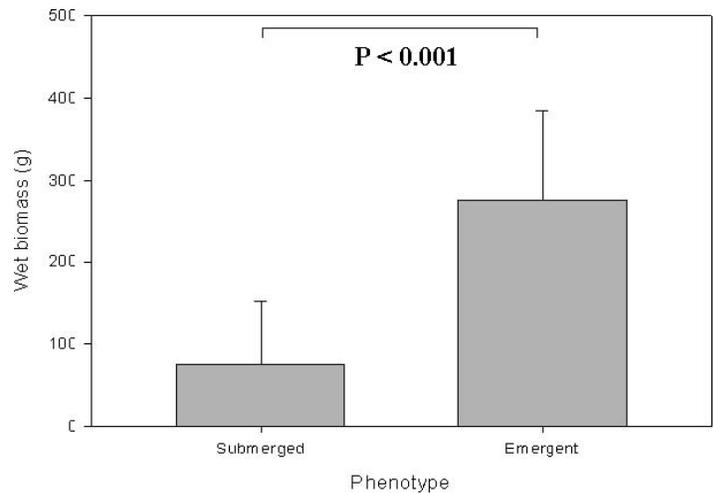 could possibly be explained by the emergent plants' increased access to CO_2 and light (Bowes and Salvucci 1989). In highly productive, shallow, freshwater riverine ecosystems both water and nutrients are rarely lacking; however, due to the high turbidity and heavy competition as a product of the high nutrient availability, light, as well as the limited diffusion of CO_2 into water, becoming the chief limiting factors (Bowes and Salvucci 1989). It has been well established that CC in its submerged form produces a significant quantity of marl, meaning that the submerged form uses a large amount of dissolved bicarbonate (HCO_{3-}) for its photosynthetic processes, a more energetically expensive process than dissolved CO_2 assimilation (Brammer 1979, Madsen and Sand-Jensen 1991). In a study by Harpenslager et al. (2015) it was found that under low dissolved CO_2 levels, submerged CC would use HCO_{3-} to supplement carbon needs; however, this resulted in lower rates of photosynthesis, decreased emergent leaf formation, and increased precipitation of marl (calcium carbonate) on leaves. Further, this study found that, even with high levels of CO_2, at low levels of PAR submerged plants formed less biomass and produced no emergent leaves compared to those exposed to high PAR (Harpenslager et al. 2015). Hence, the more free availability of both CO_2 and light for emergent plants could explain the large disparity in individual plant biomass as well as biomass density between these two phenotypes of the plants.

No significant difference was found in mean plant density between emergent and submerged phenotypic forms (Mann-Whitney Rank Sum test; $P = 0.008$) (Figure 6). However the submerged phenotype had much greater variation, ranging from 32 to 96 plants m^{-2}, compared to 40 to 60 plants m^{-2} for emergents (Figure 6). This could be explained by an unequal and lower sample size in the emergent data, resulting in a Type 1 error ($n = 5$ vs. $n = 14$); however, submerged plants must live within a much greater range of PAR levels, especially in a eutrophic system like the Trent-Severn Waterway, as PAR levels attenuate rapidly due to high water turbidity. This great range of PAR levels may
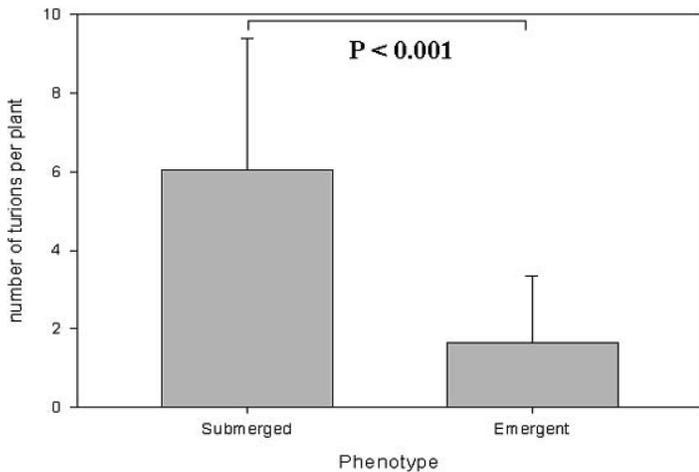
Figure 4. Mean ± SD number of turions per plant phenotype from population analysis in October. Line with *P* value below indicates significances level between bars (Mann-Whitney Rank Sum test).

partly explain this high variability in submerged plants; a study by Harpenslager et al. (2015) found less new biomass was produced by submerged CC at lower PAR levels.

There were significantly more turions produced, on average, by the submerged plants (6 turions plant^{-1}) than by emergent plants (1.7 turions plant^{-1}) (Figure 4) (Mann-Whitney Rank Sum test, $P < 0.001$). There were also significantly more offsets produced, on average, by submerged (6.2 offsets plant^{-1}) than emergent plants (4.1 offsets plant^{-1}) when measured in early August (Figure 5) (Mann-Whitney Rank Sum test, $P < 0.001$). When combined with information on stand density, this might indicate that submerged patches are priority targets to reduce propagule output. However, this study represents a comparative snapshot of propagule production by phenotype; annual data documenting patch size increases by phenotype, in nature, would provide valuable information on expected rate of spread.
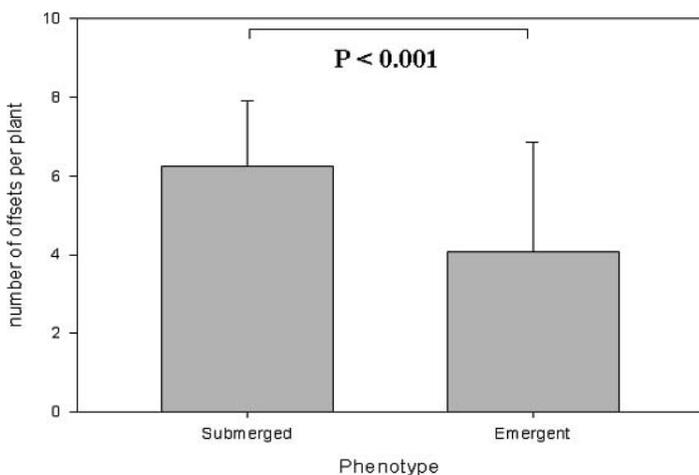

Figure 5. Mean ± SD number of offsets per plant by phenotype from population analysis in early August. Line with *P* value below indicate significances level between bars (Mann-Whitney Rank Sum test).

TABLE 1. TURION SPROUTING RATE BY INCUBATION PERIOD.

Incubation Period	2 mo	3 mo	4 mo
Sprouting rate	100%	100%	100%
Mean turion mass	0.36 g	0.34 g	0.33 g
Maximum turion mass	0.18 g	0.16 g	0.12 g
Minimum turion mass	0.46 g	0.52 g	0.48 g

Turion persistence

No turions were found at the pond site or the river site, suggesting that no turions of CC stay dormant longer than 8 to 9 mo, given sampling occurred in early August and mature turions begin detaching in late fall (November to December) (Kunze et al. 2010). Rather than being reflective of sampling errors, this conclusion is likely reasonable considering that studies using similar equipment and methods have been used to assess the presence of turions of other plants (Sutton and Portier 1985); that the limited distribution area for any turions at the pond site, given it was human constructed, hydrologically isolated, and small (40 by 15 m) are all factors favorable for detection; and that curlyleaf pondweed (*Potamogeton crispus* L.) turions were found in the sediment samples taken from the river site, showing that the method was capable of finding turions when they are present. This conclusion is also largely consistent with literature on turion persistence of similar species. It has been documented that hydrilla axillary turions last for a year at most (Van and Steward 1990). Similar maximum persistence periods (10 to 12 mo) have also been found for the axillary turions of the genus *Utricularia* as well as other carnivorous aquatic macrophytes (Adamec 1999).

Turion viability and overwintering dynamics

Sprouting rates for all containers in all sets were 100% following incubation at 4 C, thus viability was unaffected by incubation period (Table 1). Further, variations in turion mass also seemed to have no effect on sprouting as, despite some turions being up to three times more massive than others, there was no failure to sprout (Table 1). Similar to the conclusions drawn by Van and Steward (1990) concerning hydrilla axillary turions, this extremely high viability likely helps explain the extremely low persistence. In addition, as Van and Steward (1990) note, because the turion is designed for dispersal, has a relatively low mass, no hard outer coating, and stays on the surface of the sediment, it will tend to be highly influenced by fluctuations in the external environment, contributing further to the extremely low persistence of the turion (Strzalek 2004).

Given that turions are the only propagule of the wild CC population currently in North America with the capability of dormancy, knowing that there may be a period within which there are no dormant propagules, and that, based on the results of the turion lifespan experiment, there are no multiyear propagule banks, the chance of an eradication strategy succeeding is significantly higher than if these conditions weren't present. However, the extremely high viability of turions will make managing the plant even more challenging as the small plants into which turions develop
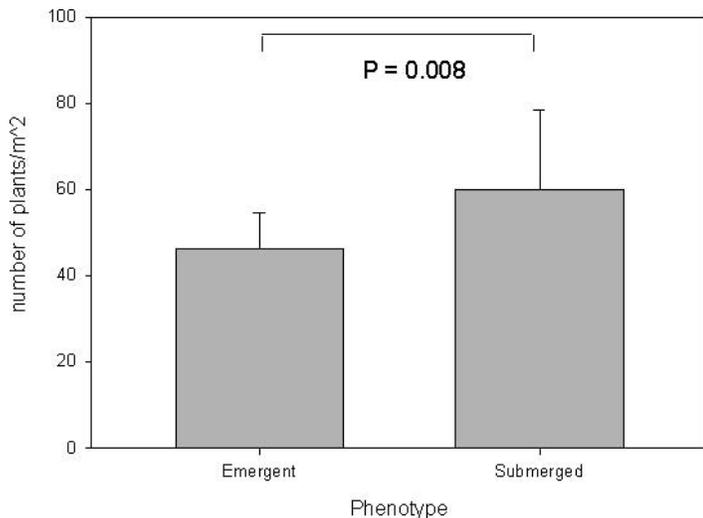
Figure 6. Mean ± SD plants m^{-2} by phenotype from population analysis in early August. Line with *P* value below indicates significances level between bars (Mann-Whitney Rank Sum test).

may be extremely difficult to find. This makes the study and modeling of their range and movement through the environment a potential next step.

It can be concluded that the turions of CC persist for at most 8 to 9 mo and that there may be a significant period within which no turions are present in sediment at all during the summer months. The turions of CC have an extremely high viability rate (around 100%) regardless of mass and length of incubation. This may mean that CC recruitment from turions is extremely high, given its ability to live in a suppressed state (Harpenslager et al. 2015). Analysis of patch density, and number of turions and offsets produced per plant showed that the submerged phenotype produced both more turions and offsets and that patch densities of both phenotypes were not significantly different. This suggests that submerged patches are priority targets for reducing propagule output. However, this study represents a comparative snapshot of propagule production by phenotype; annual data documenting patch size increases by phenotype, in nature, would provide valuable information on expected rate of spread. It was also found that emergent phenotypes have denser biomass and larger plants than submerged phenotypes, likely due to increased access to CO$_2$ and light.

SOURCES OF MATERIALS

[1]Sigmaplot 12.0, Systat Software Inc., 1735 Technology Dr #430, San Jose, California

[2]Ponar Grab sediment sampler, Hoskins Scientific, 4210 Morris Drive, Burlington, Ontario

ACKNOWLEDGEMENTS

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