Research article

A Comparison of the oxygenating differences of invasive non-native *Lagarosiphon major* and native *Ceratophyllum demersum*

Rhiann Mitchell-Holland*, Nicola Jane Morris and Peter Kenneth McGregor

Centre for Applied Zoology, Cornwall College Newquay, Newquay TR7 2LZ, UK

*Corresponding Author: Rhiann Mitchell-Holland. Email: rhiann01@hotmail.com

**Supervisor:** Peter McGregor

Native to Southern Africa, *Lagarosiphon major* is a submerged macrophyte that is recognized as a problematic, invasive non-native species in many countries including the UK. It is widely sold and promoted through the aquarium and water garden industry as an ‘efficient oxygenator’ for freshwater systems, irrespective of the absence of evidence to support this statement and evidence of its adverse ecological and economic impacts. A key concern, relating to its rapid growth rate and high fresh weight density, is that *L. major* can impose self-shading and limitation of photosynthetic and respiratory activity, causing it to consume more oxygen than it produces. Low dissolved oxygen (DO) conditions typify diminished water quality and seriously limit oxygen-dependent organisms. We measured over several months the DO, fresh weight and associated pond life abundances of *L. major* and a comparable UK-native macrophyte, *Ceratophyllum demersum*, established in small-pond conditions to determine which species best maintained a healthy freshwater environment. Both the time from establishment and species had significant effects on DO concentrations and pond life abundance; *L. major* produced the least amount of oxygen over time and had significantly less associated pond life compared to the native plant. *L. major* also increased significantly in overall fresh weight compared to *C. demersum*, indicating the higher invasive ability of the non-native species. In conclusion, our results suggest that *L. major* is not as good an oxygenator as *C. demersum* and that this native species should be promoted through the aquarium and water garden trades as an efficient oxygenator that improves water quality and habitat conditions over time.

**Key words:** invasive non-native species, macrophytes, dissolved oxygen, pond life, fresh weight, water quality

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**Introduction**

As a result of worldwide travel and trade, numerous invasive species have been introduced, both intentionally and inadvertently, into areas beyond their natural range (Westphal et al., 2008; Stiers, Njambuya, Triest, 2011). Aquatic plant species invasion has been recognized as one of the largest threats to freshwater ecosystems and biodiversity, with detrimental consequences for ecology and the economy (Pimentel et al., 2000; Strayer et al., 2003; Dudgeon et al., 2006; Riis et al., 2012). In cases where such plants have outcompeted and replaced native submerged vegetation (Rattray, Howard-Williams, Brown, 1994; Keenan, Baars, Caffrey, 2009), severe depletion of dissolved oxygen (DO) and diminished water quality has been the result (Caraco et al., 2006; Leppi, Arp, Whitman, 2016). Organisms, such as freshwater fish, invertebrates, plants and bacteria, rely on DO (the level of free, non-compound oxygen present in water) for survival, thus cannot...
withstand anoxic (a total depletion of oxygen) or even hypoxic (low oxygen) conditions for extended periods of time (Gray, Wu, Or, 2002; Caraco et al., 2006; Lennström, 2015). The presence and abundance of organisms and organic matter (and their associated biological processes) can greatly influence DO concentrations in a body of water (Caraco et al., 2006; Desmet et al., 2011; Kemler, 2013; Ribaudo, Bertran, Dutartre, 2014). For example, while photosynthesis contributes to an increase in DO (Desmet et al., 2011), the process of respiration by organisms, and decomposition of organic matter by microorganisms, can severely deplete the available DO for aerobic species (Caraco et al., 2006; Desmet et al., 2011; EPA, 2012; Annis, 2014). Despite high DO productivity during the day (Carrillo, Guarin, Guilhot, 2006; Ribaudo, Bertran, Dutartre, 2014), dense clusters of aquatic plants can cause water hypoxia at night, particularly in slow-moving water bodies, as the rate of oxygen consumption at the lower level of the bed cannot be replenished by diffusion from the atmosphere (Mazzeo et al., 2003; Loverde-Oliveira et al., 2009). Quantifying the impact of abundant macrophytes on basic water quality (oxygen dynamics, nitrogen retention and nutrient concentrations), Desmet et al. (2011) found that diurnal and seasonal fluctuations of DO were strongly correlated with plant growth/biomass density, temperature and solar irradiance, observing water hypoxia during the summer. Since light and temperature are triggers for biological processes, these diurnal and seasonal shifts can be affected by climatological conditions; such findings match literature knowledge about the impacts of dominating macrophytes on DO dynamics (National Heritage Trust, 2003; Tadesse, Green, Puhakka, 2004; Hussner, Hofstra, Jahn, 2011; Riis et al., 2012).

An invasive non-native species of particular concern is Lagarosiphon major (Ridley) Moss. L (Hydrocharitaceae). Native to South Africa, this submerged macrophyte is a considerable potential threat to static water bodies in many countries, including the UK, where it is now well established (Bowmer, Jacobs, Sainty, 1995; NNSS, 2011; J. Newman, personal communication). In addition to the aforementioned problems associated with aquatic plant species invasion, L. major has been observed forming dense canopies that often occupy entire water volumes of slow-moving water bodies (Stiers, Njambuya, Triest, 2011). These thick mats block light penetration to other flora (eliminating their growth), restrict water movement and interfere with recreation activities, ultimately exacerbating flood risks (Schwarz and Howard-Williams, 1993; McGregor and Gourlay, 2002; Stiers, Njambuya, Triest, 2011).

As with other aquatic invasive species, L. major outcompetes native aquatic vegetation and affects associated populations of species as it has a rapid growth rate and is effectively perennial, surviving through the winter (Keenan, Baars, Caffrey, 2009; NNSS, 2011; J. Newman, personal communication). Furthermore, it is effective at removing CO₂ and HCO₃⁻ from water via photosynthesis, resulting in very high pH values that create further complications for many aquatic vertebrate and invertebrate species (Sand-Jensen, 1989; Hussner et al., 2014). Due to the decidedly invasive nature of L. major, which has already been banned in New Zealand and Australia (Natural Heritage Trust, 2003), it is an offence to plant or otherwise allow this species to grow in the wild in the UK, under Schedule 9 of the Wildlife and Countryside Act (NNSS, 2016). However, natural checks on the growth of L. major in the UK are insufficient, and control/eradication of the species is extremely costly and often ineffective (Caffrey, 1993; Caffrey and Monahan, 2006; Stiers, Njambuya, Triest, 2011; European Parliament, 2014).

Despite its environmental, ecological and economic impacts, L. major is a popular water garden/aquarium plant, often sold as Egeria or Elodea densa through the aquatics industry (NNSS, 2011; J. Newman, personal communication). The UK population of L. major has been intentionally planted as an ‘oxygenator’ and is often promoted through the trade as one of the best (Natural Heritage Trust, 2003; Nault and Mikulyuk, 2009; CBD, 2011; CABI, 2016; Royal Horticultural Society, 2016). Its English common name ‘oxygen weed’—referring to the species’ ability to add oxygen to the water as a result of its high photosynthetic rate (Rattray, Howard-Williams, Brown, 1994; CABI, 2016)—is the likely reason behind the industry’s promotion of the plant. However, the high biomass densities that are characteristic of this macrophyte are likely to lead to a higher consumption than production of oxygen, seriously limiting other aquatic species (Natural Heritage Trust, 2003; Nault and Mikulyuk, 2009). The trade of this plant as an ornamental through the Internet and mail order greatly increases its obtainability and ease of spread to new locations (Kay and Hoyle, 2001; Australia Natural Heritage Trust, 2003; CABI, 2016).

Much of the existing literature regarding L. major focuses on the core factors affecting aquatic plant growth and morphology, such as temperature/light conditions (Desmet et al., 2011; Riis et al., 2012), availability of carbon and nutrients (Hussner et al., 2014) or competitive abilities (Stiers, Njambuya, Triest, 2011; Martin and Coetzee, 2014). However, little attention has been paid primarily to the oxygenating abilities of L. major, with seemingly no existing literature that directly measures its effects on DO over time. Thus, in addition to filling this gap in the literature, our study aimed to compare L. major as an oxygenator with the UK-native macrophyte, Ceratophyllum demersum (rigid hornwort). C. demersum was chosen based on its similar morphological and growth characteristics to L. major, Ceratophyllum demersum is also widely sold as an oxygenating plant and is recognized as invasive outside of its natural range, although it does not share as many of the inherent risks as L. major (McGregor and Gourlay, 2002). Our experiment also measured and compared the differences in growth (fresh weight) and associated pond life abundance and diversity of the two species over 12 weeks to assess their invasiveness and habitat impact.
Materials and Methods

Plant sample collection

Healthy plant samples of *C. demersum* (800 g) and *L. major* (800 g) were collected from two adjacent ponds (A6 and A8) at Penrose Water Gardens, Truro Cornwall (Fig. 1) on 7 October 2015. As pond A8 was larger than pond A6, samples were only collected within an area of similar size to pond A6 (boundary indicated by dotted line, Fig. 1), ensuring that both species derived from similar depth, light, temperature and growth conditions to limit the degree of variation in morphology. Samples were collected with a rake and by hand from randomly selected areas of the two ponds, avoiding sample selection bias and retaining sample independence. All samples were rinsed thoroughly on site (within ponds), and again later with settled tap water, to ensure no invertebrates or other plant species were present; any found were returned to their respective ponds, or a nearby garden pond at the study site.

Experimental setup

The experiment was conducted outdoors in Truro, Cornwall, between October 2015 and March 2016. Simulating small-pond conditions, 200 g of *L. major* and 200 g of *C. demersum* of similar size and root length were placed into plastic buckets containing 8 L of settled tap water. Tap water was left to stand for over 48 h prior to plant introduction (following Stiers, Njambuya, Triest, 2011) and had a mean (±S.E.) DO of 9.6 (±0.049) mg/L; thus simulated pond conditions were similar at the start of the experiment. In total, 12 buckets—four replicates of each species and four containing only water as controls—were left to establish for 6 weeks (from 29 October 2015 to 10 December 2016) before any measurements were taken. All buckets were situated on a raised decked area ~0.5 m above ground level. As highlighted by many researchers (Caraco et al., 2006; Desmet et al., 2011; Kemker, 2013; Ribaudo, Bertran, Dutartre, 2014), the presence and abundance of organisms and organic matter, and their associated biological processes (e.g. respiration and decomposition) can greatly alter water conditions. Gauze mesh coverings were considered to exclude organisms and organic matter. However, in order to retain natural light irradiance and temperature of the water, and in turn strengthen the integrity of the experiment (since contamination is a natural occurrence in ponds), the buckets were instead, monitored daily for major debris contamination (floating leaves, dead insects, etc.); anything found was removed with a sieve promptly.

Parameters measured

Six weeks after establishment, DO (mg/L) and temperature (°C) of the water in each bucket were measured twice a week for 12 weeks (10 December 2015–3 March 2016) using Hanna Instruments (Leighton Buzzard, UK) HI9142 portable waterproof DO meter and a TPI-315C (Crawley, UK) digital thermometer. Data collection always began at 1 h and 20 min after sunrise to control for diurnal effects on DO (informed by pilot study, personal observation) and collected in a balanced order to limit the degree of variation between buckets over time. The DO meter was left for 15 min before any measurements were taken to allow time for equilibration (following manufacturer’s recommendations), and a 1-min per bucket time limit was allocated for DO and temperature readings. Along with DO and temperature parameters, the date, hours since sunrise, general weather conditions (by visual inspection) and water volumes of each bucket were also recorded. Water levels were controlled every other day and kept at ~8000 cm³ per bucket. If a significant amount of water was lost or gained as a result of condensation or rainfall (i.e. ± >5 cm³ of original volume), it was replaced with settled tap water, or removed in order to keep conditions the same, and reduced the potential of algal growth or algae bloom through water replenishment (Paerl et al., 2001; Stiers, Njambuya, Triest, 2011). Buckets were rearranged every other day, again, in a balanced order, to reduce the effects of variation of light and temperature microclimate across buckets (Stiers, Njambuya, Triest, 2011). Plant fresh weight was measured in grams once every 2 weeks using an Analogue & Digital EK-300i compact balance scales. Upon removal from water buckets (by hand), plant samples were left to drain on the top of a gauze mesh (placed over the bucket) for 1 min per plant to replenish water and prevent inaccurate fresh weight readings due to added weight. It was during this stage that the associated pond life, i.e. invertebrate species, were individually counted and recorded manually. The weighing process presented an opportunity to inspect the plants and water bucket contents, whilst causing the least disturbance to organisms present. Plastic, transparent tubs were used to transfer plant samples from the gauze mesh to the scales and back into their corresponding buckets and also to transfer any organisms found safely to a nearby pond (~10 m away from study site).

Data analysis

All statistical analyses were carried out in Minitab® (17 Statistical Software (2010)).
Results

The DO concentration of the experimental ponds was significantly affected by treatment (L. major, C. demersum, control) over the duration of the experiment (Fig. 2A; general linear methods; treatment: $F_{11, 264} = 53.4, p < 0.0001$; days: $F_{24, 264} = 11.1, p < 0.001$). Whilst the pond temperature changed over the course of observations (Fig. 2B; $F_{24, 264} = 5003.4, p < 0.001$), there was no significant effect of treatment (Fig. 2B; $F_{11, 264} = 1.4, p = 0.160$); therefore temperature effects were not responsible for the DO changes between the treatments.

The pond life abundances associated with native C. demersum ponds were significantly higher than non-native L. major (Fig. 3; $F_{7, 42} = 4.6, p = 0.001$). Establishment time of the plants also had a significant effect on the number of invertebrate species present (Fig. 3; $F_{6, 42} = 3.1, p = 0.013$). The pond life associated with L. major and C. demersum (pond life was absent in the control buckets) ranged from 0 to 13 freshwater invertebrate ‘species’ from a single sample observation.

The fresh weight of the two species differed significantly during the experimental period; L. major samples increased by $-16\%$ (Fig. 4; $F_{7, 42} = 70.3, p = 0.000$). However, establishment time had no significant effect on fresh weight (Fig. 4; $F_{6, 42} = 1.5, p = 0.209$).

Qualitatively, there was a notable difference, particularly with L. major, in the appearance of the samples at the start of the experiment compared to the end (Figs 5 and 6). Similarly, after measurements had ceased and the simulated pond conditions were left for a further 2 weeks (17/03/16), there were striking visual differences between native and non-native plants. All L. major replicates were in a state of decomposition, unlike C. demersum replicates, which appeared to remain in a healthy condition (Fig. 7).
This research demonstrates for the first time the oxygenating efficacies, growth rates and associated pond life abundances of two macrophyte species, native, *C. demersum* and non-native, *L. major*, established under small-pond conditions. The results showed significant differences between the species’ DO concentrations over time, with *C. demersum* maintaining higher levels of DO than *L. major* (Fig. 2A). Fluctuations in overall DO concentrations were associated with temperature changes (Figs 2A and B) and were explicable in terms of the known effects of temperature on DO; as temperature increases, the solubility of oxygen decreases as gases are typically more soluble at colder temperatures (Tadesse, Green, Puhakka, 2004; Desmet et al., 2011; Hussner, Hofstra, Jahns, 2011; Riis et al., 2012; Kemker, 2013). For example at around 49, 59, 87 and 115 days from establishment, where mean temperatures reached maxima (13.2°C, 13.3°C, 12.5°C and 10.7°C, respectively), mean DO concentrations of all samples decreased considerably (Fig. 2A). However, as there were no significant differences between the temperatures of the treatments (Fig. 2B), it was clear that temperature was not the cause of the significant DO variations that occurred between the treatments.

*Ceratophyllum demersum* consistently had higher associated pond life abundance, with a more diverse collection than *L. major*—often there was no associated biodiversity (Fig. 3). Although little has been published on the preferences and tolerance levels of native fish and invertebrate species for DO, previous research has documented that the requirement for most freshwater fish is >6 mg/L, and around 5 mg/L for freshwater insects (Davis, 1975). Wurts (1993) proposed that DO levels <3 mg/L are insufficient to support aquatic life (e.g. fish), with more recent literature (Leppi, Arp, Whitman, 2016), suggesting that many freshwater organisms will be adversely affected when DO falls below a level of 2 mg/L for prolonged periods. Whilst DO reached a maximum of 11.9 mg/L in *C. demersum* and control buckets over the course of the experiment, one *L. major* replicate caused DO to fall to a minimum of 1.1 mg/L (Supplementary data, Table 1); this is well below the level which is classed as sustainable for most aquatic life. Other *L. major* replicates often fell below the recommended healthy requirements for native freshwater invertebrates (5 mg/L), with even the mean values (4.5 and 3.9 mg/L) falling to near-lethal levels on several occasions (Fig. 2A). Oxygen availability is known to be a major

Figure 5. *Lagarosiphon major* (left) and *C. demersum* (right) samples in 24-cm-diameter buckets at the start of the experiment (photographs: R. Mitchell-Holland, 2016).

Figure 6. *Lagarosiphon major* (left) and *C. demersum* (right) samples in 24-cm-diameter buckets at the end of the experiment (photographs: R. Mitchell-Holland, 2016).

Figure 7. Water buckets containing *L. major* samples (left) and *C. demersum* (right) 2 weeks post experiment.
factor determining the occurrence and abundance of many aquatic communities (Ruse, 1996; Gabriels et al., 2007; Desmet et al., 2011) as low DO concentrations characterize diminished water quality and have adverse effects on associated species (Hussner et al., 2014). This can explain why L. major consistently had significantly less associated biodiversity than C. demersum—particularly evident in L. major replicate 1 (Supplementary data, Table 2), which had the lowest mean DO overall (5.4 mg/L) and no associated pond life over the study period. The significant effect of time on pond life abundance can also be explained by the significant effect of time on DO, which increased with C. demersum, and decreased with L. major samples. Across all C. demersum samples, levels never fell below 6.4 mg/L throughout the study period, thus, were consistently sustainable for aquatic life. Furthermore, the literature states that certain species may be indicators of water quality. For example, shrimps (Crangonyx pseudogracilis), which were only associated with C. demersum samples, are often only present in good-quality ponds (Freshwater Habitats Trust, 2016). Caddis flies, which were abundant in C. demersum samples but absent in L. major, and water snails may mean that the water quality is relatively good (Freshwater Habitats Trust, 2016). Water slaters (Asselus aquaticus) and sludge worms (Tubifex tubifex) were the most abundant species associated with L. major. Such pollution-tolerant species may be indicators of relatively poor water quality (Freshwater Habitats Trust, 2016). Overall, these findings demonstrate that the native plant was associated with freshwater invertebrates while the non-native plant was not (Supplementary material, Table 2).

Outside of its normal growing season, L. major grew more than the native species in terms of overall growth, with an end mean weight of 233.1 g compared to the 198.3 g mean of C. demersum samples. L. major not only increased in fresh weight but also exhibited a wider variability in growth patterns across replicates, deviating quite far from its initial 200 g start-weight at times (Supplementary data, Table 3). In comparison, C. demersum showed no growth. This indicates that L. major has an ability to be more invasive, with high unpredictability in its growth rates, which poses many issues when implementing guidelines in relation to the trade and promotion of this species for aquarium and pond use. The fresh weight findings from this study are in line with previous research results (Stiers, Njambuya, Triest, 2011; Martin and Coetzee, 2014). Rattray, Howard-Williams, Brown (1994) revealed that, in comparison to the macrophyte Myriophyllum triphyllum, L. major has a greater ability to increase both height and fresh weight during the colonization stage. A similar study by Stiers, Njambuya, Triest (2011), using a direct comparison of the two species used in this experiment (in similar pond conditions), found that L. major outperformed C. demersum in relative growth rate (RGR) (based on total length and weight) under two different sediment conditions. More recently, in a comparison of the competitive abilities of L. major and Myriophyllum spicatum, Martin and Coetzee (2014) found that L. major had a faster RGR and was overall a superior competitor to M. spicatum.

However, as observed in Ranunculus circinatus by Larson (2007) and Myriophyllum spicatum by Angelstein et al. (2009), any treatment used for manipulating the plants (i.e. by hand when weighing) can be a potential stress factor and impose loss of vitality. Thus, this may have influenced the weight differences observed between the two species in this experiment, as well as decomposition and fragmentation. After only a few weeks of establishment, although fragmentation of both species was observed, it was more apparent in C. demersum samples. By January, one L. major replicate (Lm 1) was beginning to decompose and was severely decomposed by February. As stated by Rattray, Howard-Williams, Brown (1994) and Nault and Mikulyuk (2009) decomposing mats of L. major create extremely low oxygen levels in the water, which clarifies the consistently low DO concentrations of that particular sample (lowest DO readings overall—1.1 mg/L). However, these observations do not concur with the literature that states that L. major is effectively perennial (Keenan, Baars, Caflrey, 2009) as none of the samples survived through the winter and were all heavily decomposed by the end of the experiment (Fig. 7). This may be because the small, simulated pond conditions are more susceptible to temperature change, which limits the ability to extrapolate the results to a natural ecosystem. Furthermore, although many submerged macrophytes are able to tolerate changes in temperature well (Roonley, Kalf, Habel, 2003), L. major is thought to be unable to withstand temperatures below 10°C, dying or becoming dormant when exposed (Australia Natural Heritage Trust, 2003; CABl, 2016). Therefore, the mean temperature of 7.29°C over the data collection period may have been a contributing factor for the decomposing/dying plants.

However, even outside of the species’ usual growth season, and with findings limited by low temperature (considered minimal given that its optimum is 20–23°C), L. major grew more (Fig. 4) and caused oxygen depletion. This strongly suggests that the impacts associated with L. major (rapid growth, diminished DO) will be exacerbated during its growth season (Wilcock et al., 1998). Furthermore, although data from the on the provisional mean temperature for the UK were below the 1981–2010 long-term average, global surface temperate data from NASA (2016) have reached an all-time high, which is predicted to rise. Elevated temperatures and increased light irradiation are likely to significantly increase L. major growth rates and heighten invasion risks, further impacting DO and threatening oxygen-dependent organisms (Hussner, Hofstra, Jahn, 2011).

While longitudinal studies conducted on natural ponds over the summer months (typical growth period) are recommended to strengthen the validity of this study’s findings, the results clearly suggest that invasive non-native L. major has detrimental impacts on its freshwater environment. As this
species was not an efficient oxygenator (quite the opposite of its sale title), results could inform current practice and legislation negotiations in relation to the legal trade of L. major in the UK, offering a safer, more effective alternative (C. demersum) to the aquatic oxygenating plant industry.

In conclusion, L. major is detrimental to freshwater ecosystems, causing DO depletions and creating unfavourable living conditions for pond life, which deteriorates over time. These detriments are likely to be exacerbated during the usual growth season of L. major, and in the future as a result of global warming increases.

Supplementary data

Supplementary data are available at BIOHOR online.

Authors’ biography

Rhiann Mitchell-Holland attended Cornwall College Newquay from 2013 to 2016 and obtained anFdSc in Wildlife Education and Media, and a BSc in Applied Zoology. Currently a presenter and educator at Newquay Zoo, Cornwall, Rhiann’s particular fields of interest include the risks, prevention and management of invasive non-native species in the UK, wildlife management, biodiversity conservation and education, and sustainability. Rhiann aims to apply her skills in research and the development of wildlife/environmental management and conservation plans to combat current threats and protect our biological resources. Rhiann designed the details of the study, conducted research, analysed data, wrote the paper and had primary responsibility for final content. Nicola Morris co-supervised the project (conception and study oversight) and provided essential materials. Peter McGregor co-supervised the project (conception, development, data collection and statistical advice and study oversight) and contributed to paper write-up.

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References

Angelstein, S., Wolfram, C., Rahn, K. et al. (2009) The influence of different sediment nutrient content on growth and competition of Elodea nuttalli and Myriophyllum spicatum in nutrient-poor waters, *Fundamental and Applied Limnology*, 175, 49–57.

Annis, R. B. *Water Resources Institute: Dissolved Oxygen*, accessed at: https://www.gvsu.edu/wri/education/instructors-manual-dissolved-oxygen-30.htm (2014) (15 March 2015).

Australia Natural Heritage Trust. (2003) *Lagarosiphon - Lagarosiphon major. Weed Management Guide*, Natural Heritage Trust, Australia.

Bowmer, K. H., Jacobs, S. W. L. and Sainty, G. R. (1995) Identification, biology and management of Elodea canadensis, *Hydrocharitaceae*, *Journal of Aquatic Plant Management*, 33, 13–19.

CABI. (2016) *Lagarosiphon major (African elodea)*, accessed at: http://www.cabi.org/isc/datasheet/30548 (2 April 2016).

Caffrey, J. M. (1993) Plant management as an integrated part of Ireland’s aquatic resource, *Hydrobiology*, 5, 77–96.

Caffrey, J. M. and Monahan, C. (2006) Control of Myriophyllum verticillatum L. in Irish canals by turion removal, *Hydrobiologia*, 570, 211–215.

Caraco, N., Cole, J., Findlay, S. et al. (2006) Vascular plants as engineers of oxygen in aquatic systems, *Bioscience*, 56, 219–225.

Carrillo, Y., Guarin, A. and Guillot, G. (2006) Biomass distribution, growth and decay of Egeria densa in a tropical high-mountain reservoir (NEUSA, Colombia), *Aquatic Botany*, 85, 7–15.

CBD (The Convention on Biological Diversity)., *Information about GB Non-native Species Risk Assessments*, accessed at: file://Users/anettelumb/Downloads/RA_Lagarosiphon_major_(Curly_Waterweed).pdf (11 November 2015).

Davis, J. C. (1975) Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review, *Journal of the Fisheries Research Board of Canada*, 32, 2295–2332.

Desmet, N. J. S., Van Belleghem, S., Seuntjens, P. et al. (2011) Quantification of the impact of macrophytes on oxygen dynamics and nitrogen retention in a vegetated lowland river, *Physics and Chemistry of the Earth, Parts A/B/C*, 36, 479–489.

Dudgeon, D., Arthington, A. H., Gessner, M. O. et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges, *Biological Reviews*, 81, 163–182.

EPA., *What are Suspended and Bedded Sediments (SABS)?* accessed at: http://water.epa.gov/scitech/datraitools/warsss/sabs.cfm (28 February 2016).

EU. (2016) Commission Implementing Regulation (EU) 2016/1141, accessed at: http://eur-lex.europa.eu/legal-content/EN/TXT/?qid=1468477158043&uri=CELEX:32016R1141 (6 June 2017).

European Parliament., *Invasive Alien Species* (2014), accessed at: http://www.europarl.europa.eu/RegData/etudes/workingdocument/join/2014/518746/IPOL-ENVI AT(2014)518746 EN.pdf (11 October 2015).

Freshwater Habitats Trust., *Shrimp*, accessed at: http://freshwaterhabitats.org.uk/habitats/pond/identifying-creatures-pond/shrimp/ (10 May 2016).

Gabriels, W., Goethals, P. L. M., Dedecker, A. P. et al. (2007) Analysis of macrobenthic communities in Flanders, Belgium, using a stepwise input variable selection procedure with artificial neural networks, *Aquatic Ecology*, 41, 427–441.
Google Maps., Penrose Water Gardens, accessed at: https://www.google.co.uk/maps/place/penrose+water+gardens/ (2016) (20 March 2016).

Gray, J. S., Wu, R. S. and Or, Y. Y. (2002) Effects of hypoxia and organic enrichment on the coastal marine environments, Marine Ecological Progress Series, 238, 249–279.

Hussner, A., Hofstra, D. and Jahns, P. (2011) Diurnal courses of net photosynthesis and photosystem II quantum efficiency of submerged Lagarosiphon major under natural light conditions, Flora, 206, 904–909.

Hussner, A., Hofstra, D., Jahns, P. et al. (2014) Response capacity to CO2 depletion rather than temperature and light effects explain the growth success of three alien Hydrocharitaceae compared with native Myriophyllum triphysum in New Zealand, Aquatic Botany, 120, 205–211.

Kay, K. H. and Hoyle, S. T. (2001) Mail order, the internet, and invasive aquatic weeds, Journal of aquatic Plant Management, 39, 88–91.

Keenan, E., Baars, J.-R. and Caffrey, J. M. (2009) Changes in littoral invertebrate communities in lough corrib in response to an invasion by Lagarosiphon major, in Pieterse A., Rytkonen A.-M. and Hellsten S. (eds), Aquatic Weeds, Finnish Environment Institute, Finland, pp. 24–28.

Kemker, C., Dissolved Oxygen: Fundamentals of Environmental Measurements. Fondriest Environmental, accessed at: http://www.fondriest.com/environmental-measurements/parameters/water-quality/dissolved-oxygen/#2 (22 February 2016).

Larson, D. (2007) Growth of three submerged plants below different densities of nymphoides peltata (SG, Gmel) Kuntze, Aquatic Botany, 86, 280–284.

Lenntech., Why oxygen dissolved in water is important, accessed at: http://www.lenntech.com/why_the_oxygen_dissolved_is_important.htm (27 January 2015).

Leppi, J. C., Arp, C. D. and Whitman, M. S. (2016) Predicting late winter dissolved oxygen levels in Arctic lakes using morphology and landscape metrics, Environmental Management, 57, 463–473.

Loverde-Oliveira, S. M., Moraes Huszar, V. L., Mazzeo, N. et al. (2009) Hydrology-driven regime shifts in a shallow tropical lake, Ecosystems, 12, 807–819.

Martin, G. D. and Coetzee, J. A. (2014) Competition between two aquatic macrophytes, Lagarosiphon major (Ridley) Moss (Hydrocharitaceae) and Myriophyllum spicatum Linnaeus (Haloragaceae) as influenced by substrate sediment and nutrients, Aquatic Botany, 114, 1–11.

Mazzeo, N, Rodriguez-Gallego, L, Kruk, C. et al. (2003) Effects of Egeria densa Planch. beds on a shallow lake without piscivorous fish, Hydrobiologia, 506 (1), 591–602.

McGregor, P. G. and Gourlay, H. (2002) Assessing the Prospects for the Biological Control of Lagarosiphon (Lagarosiphon major (Hydrocharitaceae)), Department of Conservation, New Zealand.

NASA, Global temperature. Accessed at: http://climate.nasa.gov/ (2016) (10 May 2016).

Natural Heritage Trust., Lagarosiphon – Lagarosiphon major. Weed Management Guide. Canberra, Australia: Department of Sustainability, Environment, Water, Population and Communities, accessed at: http://www.weeds.gov.au/publications/guidelines/alert/pubs/l-major.pdf (2015) (6 October 2015).

Nault, M. E. and Mikuluky, A. (2009) African Elodea (Lagarosiphon major): A Technical Review of Distribution, Ecology, Impacts, and Management, Wisconsin Department of Natural Resources Bureau of Science Services, Madison, Wisconsin, USA.

NNSS., Information about GB Non-native Species Risk Assessments, accessed at: file:///Users/anneltumb/Downloads/RA_Lagarosiphon_major_(Curly_Waterweed).pdf (2015) (10 March 2015).

NNSS., England and Wales: The Countryside Act 1981. Accessed at: http://www.nonnativespecies.org/index.cfm?pageid=67 (2016) (2 January 2016).

Pael, H. W., Fulton, R. S., Moisander, P. M. et al. (2001) Harmful freshwater algal blooms, with an emphasis on Cyanobacteria, The Scientific World Journal, 1, 76–113.

Pimentel, D., Lach, L., Zuniga, R. et al. (2000) Environmental and economic costs of nonindigenous species in the United States, Bioscience, 50, 53–65.

Rattray, M. R., Howard-Williams, C. and Brown, J. M. (1994) Rates of early growth of propagules of Lagarosiphon major and Myriophyllum triphysum in lakes of differing trophic status, New Zealand Journal of Marine and Freshwater Research, 28, 235–241.

Ribaud, C., Berthin, V. and Dutartre, A. (2014) Dissolved gas and nutrient dynamics within an Egeria densa Planch. bed, Acta Botanica Gallica, 161, 233–241.

Riis, T., Olsen, B., Clayton, S. J. et al. (2012) Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species, Aquatic Botany, 102, 56–64.

Rooney, N., Kalff, J. and Habel, C. (2003) The role of submerged macrophyte beds in phosphorus and sediment accumulation in Lake Memphremagog, Quebec, Canada, Limnology Oceanography, 48, 1927–1937.

Royal Horticultural Society., Lagarosiphon major (curly waterweed), accessed at: https://www.rhs.org.uk/plants/9805/Lagarosiphon-major/Details?returnurl=%2Fplants%2Fsearch-results (2016) (29 March 2016).

Ruse, L. P. (1996) Multivariate techniques relating macroinvertebrate and environmental data from a river catchment, Water Research, 30, 3017–3024.

Sand-Jensen, K. (1989) Environmental variables and their effect on photosynthesis of aquatic plant communities, Aquatic Botany, 34, 5–25.

Schwarz, A. and Howard-Williams, C. (1993) Aquatic weed bed structure and photosynthesis in two New Zealand lakes, Aquatic Botany, 46, 263–281.

Stiers, I., Njambuya, J. and Triest, L. (2011) Competitive abilities of invasive Lagarosiphon major and native Ceratophyllum demersum in
monocultures and mixed cultures in relation to experimental sediment dredging, *Aquatic Botany*, 95, 61–166.

Strayer, D. L., Lutz, C., Malcom, H. M. et al. (2003) Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river, *Freshwater Biology*, 48, 1938–1949.

Tadesse, I., Green, F. B. and Puhakka, J. A. (2004) Seasonal and diurnal variations of temperature, pH and dissolved oxygen in advanced integrated wastewater pond system* treating tannery effluent, *Water Research*, 38, 645–654.

Westphal, M. I., Browne, M., MacKinnon, K. et al. (2008) The link between inter-national trade and the global distribution of invasive alien species, *Biological Invasions*, 10, 391–398.

Wilcock, R. J., Nagels, J. W., McBride, G. G. et al. (1998) Characterisation of lowland streams using a single-station diurnal curve analysis model with continuous monitoring data for dissolved oxygen and temperature, *New Zealand Journal of Marine and Freshwater Research*, 32, 67–79.

Wurts, W. A. (1993) Dealing with oxygen depletion in ponds, *World Aquaculture*, 24, 108–109.