

## Research Article

## A head start for an invasive species in a strongly seasonal environment? Growth of *Elodea canadensis* in boreal lakes

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### Abstract

Many invasive species are expanding northwards into boreal and subarctic habitats, but research on the factors favoring their establishment in these regions remains limited. In three Swedish lakes we investigated the growth of *Elodea canadensis* Michx, a highly invasive macrophyte that is spreading northwards in Europe and Alaska. We conducted an *in situ* growth experiment, maintained for ten months, in concert with two field macrophyte surveys, undertaken in summer and spring. We further compared the performance of propagules established during summer with those established under less favorable conditions in late autumn. We found that *E. canadensis* grew throughout the autumn, followed by winter dieback, with regrowth occurring early in the spring when water temperatures remained under 5 °C. *Elodea canadensis* plants were frequently found in our spring field survey, soon after ice melt, when almost all other species were still dormant. In the growth experiment, growth of individual shoots was positively associated with key abiotic variables (especially alkalinity) and also with increasing cover of *E. canadensis*. The tendency of propagule shoots to fragment from the main stems was also positively associated with increasing *E. canadensis* length and ambient population cover. Although propagules established in November initially did worse the following spring than those established in August, by the start of the following summer both groups were growing equally well, and had converged in morphology. The growth of *E. canadensis* throughout autumn and its early re-growth in spring, the capacity of propagules established even in late autumn to regrow well the following year, and the apparently self-reinforcing effect of increasing local population size on shoot growth all have the potential to benefit *E. canadensis* as it spreads north into boreal and subarctic regions.

**Key words:** Canadian waterweed, growth morphology, fragmentation, intraspecific facilitation, littoral zone, non-indigenous species

### Introduction

Overall, the Earth's vast boreal zone has been subjected to lower and patchier rates of biological invasion than other biomes (e.g. Rose and Hemanutz 2004; Langor et al. 2014). This reflects the remoteness of much of the region from centers of human settlement and activity, and its harsh winters and short growing seasons that hinder the establishment of invasive species from warmer regions (Rose and Hermanutz 2004; Sanderson et al. 2012). However, ongoing warming associated with global climate change,

along with increased human activity, is increasing the vulnerability of boreal habitats to biological invasions, and there are several notable examples of both terrestrial and aquatic organisms that have already penetrated deep within the region, impacting biodiversity and transforming ecosystem properties (Cameron and Bayne 2009; Ruokonen et al. 2012; Elmhagen et al. 2015; Bjelke et al. 2016; Carey et al. 2016). This highlights the pressing need for an improved understanding of the factors regulating the spread and establishment of invasive species in the region, including those species that are already well-established and extensively researched elsewhere.

*Elodea canadensis* Michx is a widespread invasive macrophyte that can form dense stands, with shoots reaching the water surface in optimal conditions (Cook and Urmi-König 1985; Mjelde et al. 2012). During the 19<sup>th</sup> century the species was introduced to Europe from its native range in temperate regions of North America (Simpson 1990). Only female plants have become established in Europe, so spread occurs through vegetative fragmentation only (Cook and Urmi-König 1985). However, changes in climate regimes appear to be favoring its establishment in northern Arctic and subarctic regions, both in Eurasia (Cook and Urmi-König 1985; Heikkinen et al. 2009; Hussner 2012) and beyond its native range in North America, as seen with the introduction of *E. canadensis* into subarctic regions of Alaska (Carey et al. 2016). This highlights the continuing need for research aimed at understanding the factors that contribute to its invasiveness and establishment. *Elodea canadensis* is tolerant of a wide range of temperatures (Cook and Urmi-König 1985; Nichols and Shaw 1986), though some laboratory evidence indicates that it performs poorly at low temperatures (Madsen and Brix 1997; Olesen and Madsen 2000). On the other hand, field evidence indicates that in colder climates, *E. canadensis* is capable of regrowing rapidly in the spring from dormant apices, and it has even been documented overwintering under the ice in central Ohio (US) (Stuckey et al. 1978). These attributes may give it an advantage even in boreal and subarctic regions of the world, where it has not yet completely invaded.

Some populations of *E. canadensis* appear to go through a boom and bust dynamic, whereby the population grows extensively for several years and eventually dominates suitable habitats, before collapsing and then beginning to re-grow again (Rørslett et al. 1986; Simpson 1990; Strand and Weisner 2001; Simberloff and Gibbons 2004). It is unknown how many times such cycles are repeated before the population stabilizes at a lower population density. This boom and bust dynamic suggests a positive feedback between increasing *E. canadensis* density and population growth at local (within lake) scales, possibly reflecting accumulating impacts on resource control by the species (e.g. Rørslett et al. 1986) and/or the occurrence of allelopathic chemicals (Erhard and Gross 2006). In order to better understand both population growth and impacts of *E. canadensis*, a more complete picture of the factors regulating the growth and morphology of the species is required, not only during the active growing season but also during colder periods of the year.

To investigate the dynamics of *E. canadensis* growth and dieback in boreal lakes in Sweden, and

thereby gain insight into the factors likely to regulate its spread and establishment into new systems, we conducted a ten month long *in situ* growth experiment in conjunction with two macrophyte inventories (in late summer and early spring). Macrophyte growth is strongly seasonal in the region, with the growing season ranging from 160–175 days in the southern boreal to < 140 days in the north (Partanen and Hellsten 2005). With the exception of some bryophytes (e.g. *Fontinalis* spp.), submerged macrophyte assemblages are in general dominated by species – such as *Myriophyllum* spp., *Potamogeton* spp., *Chara* spp., and *Lemna* spp. – that die back during mid-late Autumn (October–November) as day lengths shorten and surface ice begins to form, and not regrowing significantly until late Spring (May–June) following ice- and snow-melt (Andersson and Willen 1999; Netten 2011). The specific aims of our *in situ* growth experiment were to (i) quantify the importance of *E. canadensis* population cover relative to key abiotic variables during both the establishment and growth of propagules in late summer and autumn and their subsequent regrowth after winter die-back the following spring; (ii) assess variation in the generation of apical stem buds, constituting potential propagules facilitating the further spread of the plant; and (iii) compare the spring-time regrowth of propagule fragments established in favourable conditions during late summer with those established during harsher conditions in early winter. The macrophyte inventories aimed (i) to quantify the ambient population size of *E. canadensis* at the commencement of our growth experiment, and (ii) assess the occurrence of *E. canadensis* relative to native macrophytes very early in the spring immediately after ice-melt. We hypothesized that growth would be regulated by key environmental variables such as nutrients, alkalinity, total organic carbon and temperature (Nichols and Shaw 1986; Bowmer et al. 1995; Mormul et al. 2012), and we expected an additional positive relationship with ambient population cover. We further hypothesized that propagules would successfully establish during both summer and late autumn, but that after winter dieback subsequent regrowth of the shoots the following spring would be greater for summer propagules, reflecting the more favorable environmental conditions during their initial establishment.

## Methods

Our fieldwork comprised an *in situ* growth experiment, conducted in pots over an extended seasonal profile, from August 2013 through to June 2014, and two macrophyte inventories conducted in August 2013 and at the end of March 2014. The inventories were

**Table 1.** Depth, sediment and macrophyte data for the 5 m wide transects in August 2013, including densities ( $\rho$ , quantified as percent coverage) of the invasive macrophyte, *Elodea canadensis*, all submerged macrophytes (including *E. canadensis*), helophytes and floating macrophytes, along with macrophyte species richness.

Lake	Transect	Max depth (cm)	Transect length (m)	Transect size (m <sup>2</sup> )	Dominant substrate	$\rho$ <i>Elodea canadensis</i> (%)	$\rho$ All submerged macrophytes (%)	$\rho$ Helophyte and floating macrophyte (%)	Macrophyte species richness
Lötsjön	Löt 1	128	18	90	Fine sed. < 0.2 mm	20	50	10	17
	Löt 2	113	8	40	Fine sed. < 0.2 mm	70	90	30	7
	Löt 3	113	12.5	43.75	Fine sed. < 0.2 mm	90	100	20	8
Sparren	Spa 1	121	13	65	Sand 0.2–2 mm	1	100	15	13
	Spa 2	125	20	100	Fine sed. < 0.2 mm	5	90	20	10
	Spa 3	113	10	50	Fine sed. < 0.2 mm	40	95	25	11
Ubby långsjön	Ubby 1	91	20	100	Gravel 2–20 mm	5	40	20	14
	Ubby 2	120	8	40	Sand 0.2–2 mm	5	20	20	10
	Ubby 3	93	20	100	Fine sed. < 0.2 mm	1	5	25	16

conducted to quantify initial density of *Elodea canadensis* during August, and macrophyte presence in early spring following ice-melt.

#### Study sites

The macrophyte inventories and plant growth experiment were conducted in three lakes in the Uppland region of Central Sweden, all of which were invaded by *E. canadensis* (supplementary material Table S1). Within each lake, we selected three separate bays, characterized by soft, fine-grain sediments (sand and silt), and comprising reed-free areas along a shoreline otherwise dominated by *Phragmites australis* (Cav.) Steud. We selected the bays to encompass a broad range of *E. canadensis* cover (Table 1), as a necessary precondition to test our research questions about the role of ambient population size in regulating growth. Within each bay, a single transect was established based on the macrophyte inventory conducted in August 2013 (see section on macrophyte inventory and Tables 1 and 2).

#### Water chemistry

Water samples were taken for chemical analysis at each transect within the three lakes once during August and once in October 2013, and again in May 2014. Secchi depth was measured on site using a secchi disc (diameter, 30 cm). Temperature, turbidity and oxygen were measured on site using a Manta<sup>TM</sup> multiprobe (Eureka Water Probes, Austin TX). Water samples were analyzed at the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences following international (ISO) or European (EN) standards (Fölster et al. 2014 and references therein). Analyzed variables included pH, alkalinity and conductivity, along with total nitrogen,

**Table 2.** Occurrence of species sampled at the end of March 2014 quantified as percentage of species presences per sampling plot, pooled across all lakes and transects.

Species	% occurrence $\pm$ SE
<i>Elodea canadensis</i>	48 $\pm$ 10
<i>Fontinalis antipyretica</i>	38 $\pm$ 13
<i>Elodea nuttallii</i>	11 $\pm$ 11
<i>Chara</i> sp.	10 $\pm$ 6
Small-leafed bryophytes	9 $\pm$ 5
<i>Eleocharis acicularis</i>	6 $\pm$ 4
<i>Lemna trisulca</i>	6 $\pm$ 3
<i>Phragmites australis</i>	4 $\pm$ 4
<i>Sparganium</i> sp.	2 $\pm$ 2
<i>Carex</i> sp.	1 $\pm$ 1
Small marchantiophyte	1 $\pm$ 1
Empty squares	19 $\pm$ 6

ammonium, nitrate, total phosphorous and phosphate (PO<sub>4</sub>). Absorbance (at 420 and 436 nm) and total organic carbon (TOC) were additionally quantified for estimating water colour and carbon content. Specific analytical methods are given in Appendix 1. Temperature and light sensor loggers were placed within each transect at 50 cm depth and set to record temperature and light intensity every two hours throughout the study period.

#### Macrophyte inventories

We conducted two macrophyte surveys, one in August 2013 and another at the end of March 2014. In the summer survey, macrophyte coverage was dense so we employed an intensive sampling approach that quantified species abundances as coverage per square meter. This detailed approach was not necessary for the spring survey, when macrophyte coverage was extremely sparse and the aim was primarily to quantify which species were regrowing early in the

season following winter dieback. Accordingly, for the spring survey we adopted a less intensive sampling methodology where macrophyte abundances were quantified as the percent occurrence of species across all sampled plots. These differences in sampling methodologies preclude quantitative statistical analysis of species abundances between the two surveys.

For the first macrophyte inventory, conducted in August 2013, we used a combination of the methodology applied in the national Swedish macrophyte inventory (Naturvårdsverket 2010) and the Finnish belt method (Leka and Kaninen 2003). Macrophytes were sampled along a 5m-wide transect extending perpendicular from the shoreline, with each transect subdivided into quadrats of  $2.5 \times 2.5 \text{ m}^2$  within which species coverage was quantified. Sampling along each transect was conducted from the shoreline to a standardized maximum depth of 115 cm, in line with the depth interval over which the *Elodea canadensis* growth experiment was conducted (see below). Consequently, transect length varied depending on the slope of the lakebed and how rapidly the maximum depth was reached, and ranged between 7.5–20 m, with the number of quadrats similarly varying from 8 to 16. All quadrats were inventoried in all transects. An aqua-scope and snorkeling were used to aid in visually quantifying species presence and estimating species coverage within each quadrat, with a rake used to aid an additional search for rare and small species. The subdivision of transects into quadrats was used to facilitate the inventory and was not part of the design of the growth experiment (see below).

The second macrophyte inventory was conducted at the end of March 2014, after ice-melt (see supplementary information for air temperature from November to March, Table S2). Within the same transects sampled during 2013, a narrow (0.25 m) transect was delineated to the same maximum depth as previously (115 cm), and inventoried by placing a  $0.25 \times 0.25 \text{ m}^2$  quadrat at 0.2 m depth intervals, or more frequently when the slope was relatively flat, with the presence of different species at each sample point recorded (Naturvårdsverket 2010). Species occurrence across the whole transect was then calculated as the number of quadrats a species was recorded from as a percentage of all surveyed quadrats.

#### *Growth experiment: Summer propagules*

Standard garden flower pots (height: 14 cm, diameter: 16 cm, volume: 2.2 L) were filled with a 1:4 soil and sand mixture (particle size: 0–4 mm; soil properties are detailed in Table S3, supplementary information). *Elodea canadensis* shoots were collected from a pond at the Swedish University of Agricultural

Sciences, Ultuna, Sweden (59,814251°N; 17666423°E) for transplantation into our three lakes, where *E. canadensis* was already well established. Transplantation of propagules from one population of a highly invasive species into another carries the risk of increasing the genetic diversity of the recipient population, and possibly enhancing its adaptive potential (Lambertini et al. 2010; Riis et al. 2010; Huotari et al. 2011). However, genetic analysis of specimens from the source population and our three study lakes, based on six markers, indicate that all belong to a single group (M. Mjelde, unpublished data).

The collected shoots were washed and kept in tap water in holding tanks for three days prior to the experiment. Then, 1350 shoots with intact apex buds were cut to a length of 20 cm, and divided into 270 sets of five. The wet weight of each set of five shoots was obtained following removal of excess water by spinning in a salad spinner for 20 seconds. These sets of five shoots were then stored moist in plastic bags during transport to the study sites. On site, each set of five shoots was planted in each pot, 5 cm deep (see supplementary material Figure S1). These initial shoots had no lateral shoots or roots when planted.

The pots were deployed during August 2013 in the same replicate transects across the three lakes sampled for the summer and spring macrophyte inventories. The pots were evenly spaced in a single cluster over a  $4.5 \text{ m}^2$  area, at a standard water depth of  $65 \pm 18 \text{ cm}$  (mean  $\pm$  1SD). In total, 30 pots were placed in each transect, allowing for retrieval of five pots at each of six retrieval dates. After a two week acclimation period, the first set of five pots was retrieved (for examples of retrieved pots, see Figure S2). Regular sampling was performed at the start of each month until November, and then following ice-melt at the beginning of April, with a final retrieval date in early summer (June 2014).

On retrieval of pots, all shoot and root material was removed from each pot and placed in a plastic bag for transport to the laboratory. The shoots were washed to remove sediment and organisms, and then placed in a sonication bath for 2 min to remove periphyton and particulate detritus. Total plant length, combining across all initial shoot main stems and new lateral shoots in each pot but excluding roots, were measured to the nearest 0.5 cm. Plant parts that were degraded were regarded as indicative of senescence, and were also measured to the nearest 0.5 cm (see supplementary material Figure S3). New lateral shoots, roots and leaf whorls were counted. Internode length was based on the total plant length divided by the number of leaf whorls. We also recorded the number of potential propagule fragments produced.

Propagule fragmentation was assessed by carefully inspecting the main stem and lateral shoots of each plant, and quantifying instances where the apical buds (i.e. the active growth point, which easily breaks off) were missing on retrieval. This was recorded both on initial main-stem and new lateral shoots (see supplementary material Figure S3). Finally, the roots were separated from the above ground material (shoot) and both were dried at 60 °C for 48 h, and then weighed separately, allowing us to quantify root:shoot ratios.

#### *Growth experiment: Autumn propagules*

In November 2013, an additional three sets of five pots each were added to each lake transect, and intermixed with the previously deployed pots, but with unique labels. This was done to evaluate the establishment success of vegetative shoot propagules late in the season. The procedures for collection, preparation and deployment of these additional pots were identical to those detailed above for the pots deployed in August. These additional pots were first sampled after a two week acclimation period, and then again at the beginning of April and June 2014.

#### *Analysis of water chemistry data*

Principal component analysis (PCA) was performed on a set of environmental variables (Table S1) known to regulate the growth and distribution patterns of *Elodea canadensis* (Nichols and Shaw 1986; Bowmer et al. 1995; Mormul et al. 2012), using the R-package *vegan* (Oksanen et al. 2013; R Core Team 2013). These variables included water chemistry parameters measured in August (alkalinity, PO<sub>4</sub>, and TOC), together with variables extending from August to October (light intensity at 50 cm depth, and degree-days). We chose to focus on water chemistry measured in August through October as representative of the environmental conditions predominating during the peak growing period in our study; however analysis of our data using water chemistry sampled on other dates, or against the mean of all dates, yielded similar results to those presented here. We used the PCA axis describing most of the variation in environmental conditions for subsequent analyses to construct a general linear mixed model for analyzing variation in the growth and morphology of *E. canadensis*.

#### *Analysis of the growth experiment: Summer propagules*

Variation in total biomass (root and shoot dry weight; g DW pot<sup>-1</sup>) and internode length (the length in cm

between leaf whorls; cm) of *E. canadensis* during autumn (August to November) was analyzed using a general linear mixed model (GLMM) using the R (R Core Team 2013) package *lme4* (Bates et al. 2014). P-values for the GLMM were obtained using the R package *car* (Fox and Weisberg 2011). A mixed model was used in order to partition variability arising from those factors we had specific hypotheses about (fixed factors) from that arising from other sources of variation (random factors) between the lakes, transects and sample dates (Quinn and Keough 2002). Thus, time (months) and transect nested within lake were defined as random slopes to account for variation between months and the spatial proximity of transects within lakes, respectively. Two continuous predictors were analyzed as fixed factors: axis 1 from the PCA of environmental variables (hereafter Env-PC1), and initial *E. canadensis* cover at each transect, as a proxy for ambient population density. This model allowed us to separate the effects of these variables in regulating growth, and address our aims regarding the relative roles of the abiotic environment and ambient population size. Our measure of initial cover was the percent coverage inventoried during August (i.e. at the commencement of the experiment). We observed no marked increase or decrease in the cover of *E. canadensis* over our repeated autumn visits, suggesting that maximal cover for the year had already been reached prior to commencement of the study. The correlation between Env-PC1 and *E. canadensis* cover was not significant ( $r = 0.60$ ,  $p = 0.09$ ), and did not cause any bias in the analysis according to diagnostic statistics and plots (Quinn and Keough 2002).

#### *Analysis of the growth experiment: Comparing the summer and autumn propagules*

The growth and morphology of propagule shoots established in August *versus* November, all collected the following spring (April and June), was compared using a GLMM, with “establishment month” set as a fixed factor with two levels (August vs November) and lake transects as a random variable (Fox and Weisberg 2011; R Core Team 2013; Bates et al. 2014; Halekoh and Højsgaard 2014). In this analysis we had sufficient replication to test for interactions between establishment period and sample month (April and June) as a fixed factor. Morphological variables including total biomass (g DW pot<sup>-1</sup>), plant length (cm pot<sup>-1</sup>), internode length (cm), green length per shoot (cm; (total plant length – total senescence length) / total number of stem and lateral shoots), number of shoots, root-to-shoot weight ratio and number of fragmented shoots (counts of all shoots

lacking an apical bud) (per pot) were evaluated as response variables.

Additional analyses were used to assess variation in other aspects of plant morphology potentially varying with growth. Linear regression was used to analyse the relationship between total plant length (cm) and number of lateral shoots and extent of propagule fragmentation, and additionally between the number of lateral shoots and amount of propagule fragmentation (per pot) for the Autumn (August to November) and for the Spring datasets (April and June, including both the August and November established propagules) (R Core Team 2013). Data was standardized or log-transformed in all analyses when inspection of residual plots indicated non-normality and heterogeneous variances, to satisfy parametric assumptions.

## Results

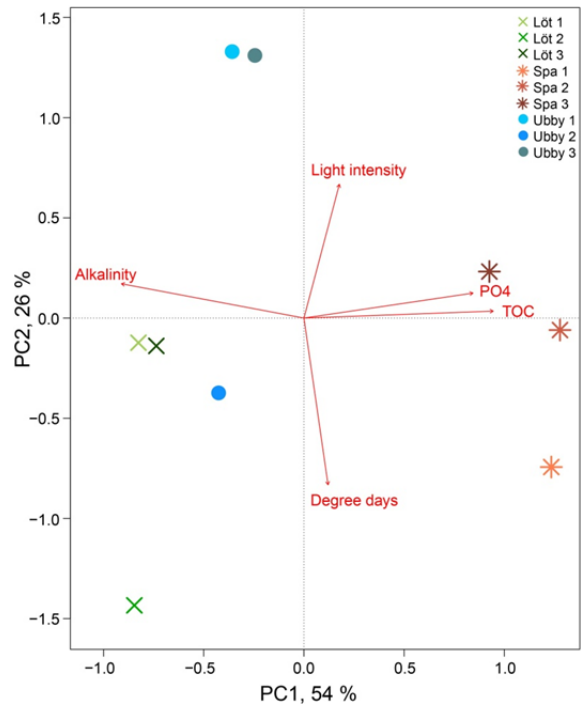
### Environmental variables

In our PCA of environmental data, PC axis 1 explained 54% of the total variance, representing a gradient from more alkaline to less alkaline transects, which were also characterized by higher concentrations of TOC and PO<sub>4</sub>. PC2 explained 26% of the variance, primarily reflecting variability in light and temperature (Figure 1, see also supplementary material Table S4). PC axis 1 (Env-PC1) was used as the predictor variable in our general linear models below.

### Macrophyte inventories: Ambient *Elodea canadensis* cover during summer, and occurrence in early spring

Our summer macrophyte inventory confirmed that *Elodea canadensis* was present in all transects, with percent coverage varying from c. 1–90% among sample quadrats (Table 1). Other species present in several transects included *Fontinalis antipyretica* Hedw., *Nuphar lutea* (L.) Sm., and *Potamogeton* spp., with richness of native macrophytes ranging from 6–10 species. For an overview of the different macrophyte groups, submerged macrophytes, helophytes and floating macrophytes, and *E. canadensis* density see Table 1.

Most of the species found in the summer survey had not or only barely begun regrowing when we conducted the second macrophyte inventory at the end of March 2014, so were absent from most or all of our transects. The only species found at similar frequency to *E. canadensis* in spring was the bryophyte *F. antipyretica* (Table 2, see also supplementary material Table S5).



**Figure 1.** Principal component analysis (PCA) of key environmental variables for *E. canadensis* growth (supplementary material Table S1) quantified at the transect scale. Percentage variance explained by the respective PCs are given for each axis. The legend specifies the different lake transects (Lake Löttsjön (Löt 1 to 3), Lake Sparren (Spa 1 to 3) and Lake Ubbby Långsjön (Ubbly 1 to 3). TOC = Total organic Carbon.

### Growth experiment: The roles of environment and ambient *Elodea canadensis* cover

Overall, a biomass pattern of autumn growth, winter dieback and spring regrowth was observed ( $g\ DW\ pot^{-1}$ , Figure 2) for *E. canadensis* in our growth experiment. This pattern was observed across all lakes, although the maximum biomass achieved varied among lakes (supplementary material Figure S4). *Elodea canadensis* biomass was affected by an interaction between initial cover of *E. canadensis* and Env-PC1 (Table 3). The negative slope of this interaction (Table 3) indicates that biomass was highest when both initial *E. canadensis* cover and alkalinity were highest (associated with the negative end of the Env-PC1 gradient). Month, fitted as a random effect, contributed to 12.94% of variance to the response variable. This variation is reflected in the progressively increasing regression slopes in models relating initial *E. canadensis* coverage and biomass from the first retrieval date in August through the subsequent three retrieval dates (supplementary material Figure S5).

**Table 3.** Significance tests and regression slopes from GLM analysis testing total dry weight and internode length against Env-PC1, initial cover of *E. canadensis* (*E. can*) and the interaction between the two. Random effects were time (in months) and transects nested within lakes.

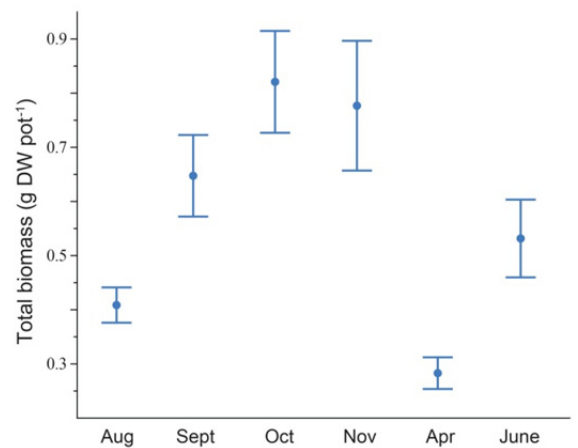
	Df	Residuals Df	F-value	Total dry weight	
				P-value	Slope, estimate $\pm$ SE
Intercept					-1.49 $\pm$ 0.22
Env-PC1	1	28	0.02	0.883	0.17 $\pm$ 0.13
<i>E. can</i> density	1	28	8.38	0.007	-1.84 $\pm$ 0.94
Env-PC1 $\times$ <i>E. can</i> density	1	30	9.66	0.004	-3.76 $\pm$ 1.21
Internode length					
Intercept					-1.05 $\pm$ 0.22
Env-PC1	1	28	27.36	<0.001	-0.57 $\pm$ 0.17
<i>E. can</i> density	1	28	13.07	0.001	-0.54 $\pm$ 0.35
Env-PC1 $\times$ <i>E. can</i> density	1	30	12.79	0.001	1.45 $\pm$ 0.75

Internode length (cm) of the plants was also positively affected by the interaction between high initial cover of *E. canadensis* and Env-PC1 (interaction;  $F_{(1,30)} = 12.79$ ,  $p = 0.001$ ; Table 3 for slopes). Internode length increased more strongly with initial density when TOC and  $PO_4$  were higher, given both these variables increased along PC1 (Figure 1). Unfortunately the high correlation between TOC and  $PO_4$  ( $R^2 = 0.85$ ) prevents further separation of the relative importance of these variables in explaining variation in internode length.

#### Growth experiment: Effect of establishment period on propagule growth

In spring, shoots established in August had a higher total dry weight ( $F_{(1,137)} = 8.75$ ,  $p < 0.005$ ; mean  $\pm$  SE:  $0.38 \pm 0.04$  and  $0.27 \pm 0.03$  g DW pot<sup>-1</sup>, respectively) and higher total plant length (cm pot<sup>-1</sup>) ( $F_{(1,137)} = 11.71$ ,  $p < 0.001$ ) than for those established in November. This length difference is reflected in the greater number of lateral shoots observed on propagules established in August ( $F_{(1,137)} = 51.95$ ,  $p < 0.001$ ). There were no interactions between establishment period and time (all  $F_{(1,137)} < 2.16$ ,  $p > 0.14$ ) for biomass, length and number of shoots.

In addition to old above-ground biomass that survived the winter, re-growth of shoots of *E. canadensis* in the pots was observed in early April, when in-lake temperatures had not yet exceeded 5 °C ( $2.73 \pm 0.13$  cm (mean  $\pm$  1SE) green length per shoot for all plants samples in April). Further, there was no difference in mean green length per shoot between propagules established in August versus November during the spring ( $F_{(1,137)} = 0.19$ ,  $p = 0.661$ ). Similarly, there was no interaction between establishment period and time ( $F_{(1,137)} = 0.38$ ,  $p = 0.539$ ). Few roots were observed on November propagules at the beginning of April.

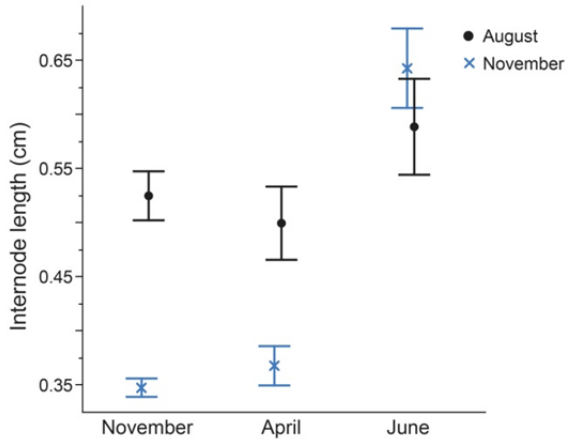
**Figure 2.** Variation (mean  $\pm$  SE) in total *E. canadensis* biomass (mean  $\pm$  1SE g DW pot<sup>-1</sup>; shoot and root weight) among months, from beginning of August (Aug) through to November (Sep: September, Oct: October, Nov) 2013, and also in April (Apr) and June (Jun) 2014, pooling across lakes and transects.

Both internode length (cm) and root-to-shoot weight ratio differed over time and between establishment periods (both  $F_{(1,137)} > 13.5$ ,  $p < 0.005$ ; Figures 3 and 4). The shoots established in November had a shorter internode length and lower root-to-shoot ratio than those established in August at the first two sample dates, but this difference had disappeared by the last sampling date at the beginning of June.

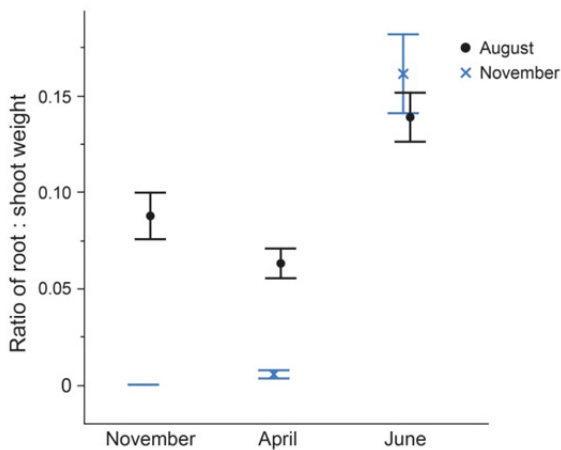
#### Vegetative propagules: relationships with length and lateral shoot production

During autumn (August to November) there were positive relationships between total plant length, the number of lateral shoots and the number of fragmented shoots (i.e. shoots missing their apical buds, which may then act as vegetative propagules) (all  $R^2 > 0.385$ ,  $p < 0.001$ ; Figure 5).





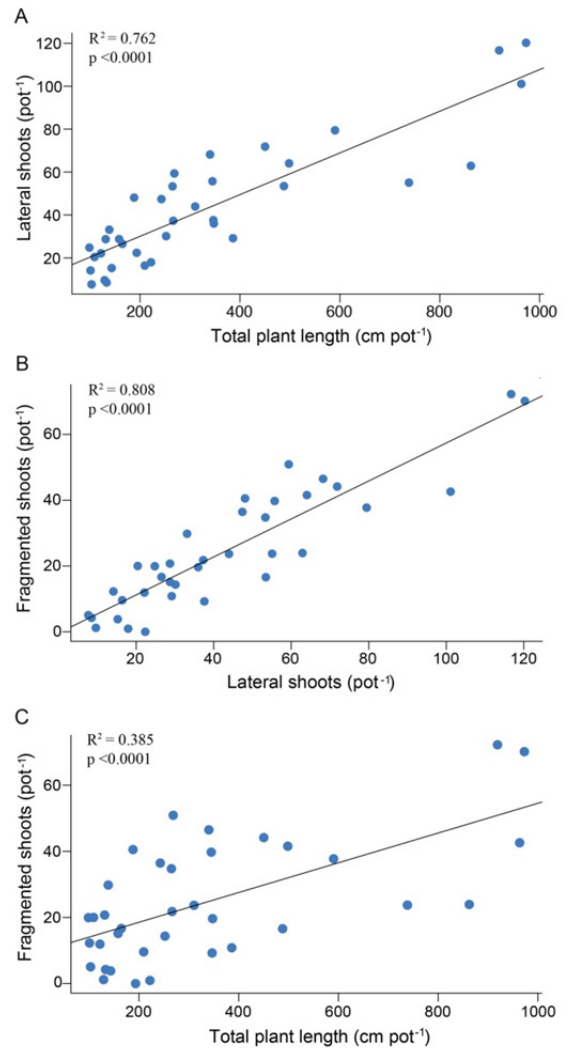
**Figure 3.** Internode length increase of *E. canadensis* propagules (mean  $\pm$  1 SE cm) established in either August (black points) or November (blue points) over the period November 2013 to June 2014, pooling across lakes and transects.



**Figure 4.** Change in root:shoot weight ratio (mean  $\pm$  1 SE) of *E. canadensis* propagules established in either August (black points) or November (blue points) over the period November 2013 to June 2014, pooling across lakes and transects.

## Discussion

Our study aimed to investigate the dynamics of *Elodea canadensis* growth and dieback in Swedish boreal lakes. This included investigation of how the abiotic environment and a key biotic factor, ambient *E. canadensis* coverage, affected the growth and morphology of propagules established at different times of year, and the occurrence of the species relative to the native flora early in the spring. Our growth experiment revealed that *E. canadensis* grows significantly in boreal lakes during cooler periods of the



**Figure 5.** Total plant (main stem and lateral shoots combined) length (cm pot<sup>-1</sup>) plotted against the number of lateral shoots (pot<sup>-1</sup>) (A); Number of lateral shoots (pot<sup>-1</sup>) plotted against number of fragmented shoots (pot<sup>-1</sup>) (B); Total plant length (cm pot<sup>-1</sup>) plotted against the number fragmented shoots (pot<sup>-1</sup>) (C). Data points are based on mean variable per transect per month, August to November.

year, including very late in the autumn, which has been less studied in the field than the main summer growth period. Furthermore, in our early spring macrophyte survey, *E. canadensis* was observed much more frequently than all native species, except for the overwintering bryophyte *F. antipyretica*. Intriguingly, growth of *E. canadensis* was positively related to local population size, quantified as coverage of *E. canadensis* in August. The continuous growth of *E. canadensis* during autumn and re-growth in early spring, along with the apparently self-reinforcing



effect of increasing densities on population growth, might give the species a significant “head start” over native macrophytes as it continues to spread north into boreal and subarctic biomes.

*Effects of the abiotic environment and ambient population cover on growth, morphology, and vegetative propagule production*

We observed a positive relationship between *E. canadensis* cover and the growth of shoots in our pots, suggesting intraspecific facilitation of biomass accrual (McKie et al. 2009). Similar results were observed by Barrat-Segretain (2005) in a laboratory experiment, who showed that *E. canadensis* grows best in monocultures or when it is aggregated, compared to mixed stands with the closely related species *Elodea nuttallii*. Such monocultures might allow the species to better control resources (light, nutrients etc.) or modify the environment in a beneficial way (McCreary 1991; Gaston 1999; McKie et al. 2009; Jiang et al. 2010). It is possible that the formation of dense intraspecific aggregations of *E. canadensis* has the benefit of protecting individual shoots from grazing pressure (not quantified in our study) or other forms of environmental exposure. In particular, the long fetch lengths of some of our transects are probably associated with periods of high wave action, which is less likely to impact individual shoots within a dense stand. *Elodea canadensis* also produces allelopathic chemicals against periphyton and competitors (Erhard and Gross 2006). Such allelopathic effects have been more difficult to observe in open lake environments *in situ* compared with laboratory microcosms (Lurling et al. 2006; Lombardo et al. 2013), but are likely to be most effective in dense aggregations where multiple shoots have the potential to build up a critical mass of allelopathic chemicals at local scales.

We additionally observed that internode lengths increased most strongly when ambient *E. canadensis* cover was greater, and both PO<sub>4</sub> and TOC concentrations were higher. This result is suggestive of a response to low light environments. Formation of a dense *E. canadensis* canopy in a monospecific stand might restrict light availability for conspecifics, and an increase in internode length pushes apical florescences towards the light in these conditions. Higher TOC levels similarly alter the light environment (Søndergaard et al. 2012), though we are unable to assess whether the relationship between internode length and the environmental axis is more strongly driven by TOC or PO<sub>4</sub> due to the strong correlation between these two variables. Overall, field results presented in this paper, together with experi-

mental observations by Mormul et al. (2012), point towards a degree of flexibility in the responses of *E. canadensis* to variable environmental conditions.

Population growth of an invasive macrophyte such as *Elodea canadensis* is greatly facilitated by its capacity to re-sprout from vegetative propagules fragmented from existing shoots. In our study, the tendency of propagules, in the form of apical stem buds, to fragment was affected by *E. canadensis* cover, overall length of the plant and the number of lateral shoots produced. Specifically, where the coverage of *E. canadensis* was greater, shoots grew longer. These larger plants also tended to fragment more (lose their apical buds), particularly nearer to the water surface. As a result, not only the length but also the total number of apical buds increased with increasing coverage of *E. canadensis*. These field results are in line with laboratory observations which showed that fragmentation stimulates formation of lateral shoots and affects total plant length (Mielecki and Pieczynska 2005). In addition, the potential for lentic submerged macrophytes to disperse by fragmentation is dependent on the mechanical action of waves and/or ice-breaking in the littoral zone. The degree of this mechanical stress determines the fragmentation potential, where greater mechanical stress creates more fragments (Jupp and Spence 1977; Chambers 1987; Coops et al. 1994). We did not quantify the extent to which differences in wave or ice action affected the tendency of our shoots to fragment, and then stimulate further growth, but this would be a worthy topic for further research.

*Timing of propagule establishment and growth at low temperatures: Outcomes for spring regrowth*

We found that the spring regrowth of propagules established the previous November was slower than that of propagules established the previous summer, though both propagule groups ultimately attained similar regrowth by June. The initial superior performance of the older propagules is likely to reflect the extended period for growth of these shoots prior to winter dieback, enabling them to invest more in dormant apices for subsequent spring regrowth, and also possibly reduced winter die back under the ice. Notably, Madsen and Brix (1997) observed that at 5 °C *E. canadensis* allocated only 1.5% of its growth to root formation. Our propagules established in November showed a similar response, with barely any roots observed at the beginning of April. However, later in the spring, propagules from both establishment periods converged in internode length and in root-to-shoot ratios, indicating that during May the propagules established the previous November increased

in root production and foliar growth. These results demonstrate that vegetative propagules of *E. canadensis* have a high potential for regrowth from dormant apices, even when established very late in the autumn. From an invasion perspective this is an important finding: propagules introduced even during less climactically suitable periods of the year also have a high potential for establishing and contributing to population growth, and potentially even founding new populations.

Overall, our results show that *Elodea canadensis* has the potential to grow at temperatures as low as 5 °C in lakes. A previous experiment found that growth of *E. canadensis* almost ceases at 5 °C (Madsen and Brix 1997), but this was based on transplants of propagules from warmer (8 °C) water in a homothermic stream to colder aquaria maintained in the laboratory, whereas we studied the regrowth of shoots that had overwintered *in situ* as water temperatures warmed in the early spring. Results from both our spring field survey and the growth experiment show that these warming conditions trigger regrowth of *E. canadensis* quite soon after spring snowmelt. This indicates that *E. canadensis* may be able to establish in even very strongly seasonal climates further north in the boreal zone. Indeed, based on our observations, *E. canadensis* has a longer growing season than those reported for the majority of native macrophytes in Sweden (Mossberg and Stenberg 2003).

#### *Implications and further research needs*

A central finding from our study is that the growth of *E. canadensis* shoots is enhanced as the ambient cover of its conspecifics increases. Further research is required to assess the generality of this finding, given our study was conducted in only three lakes which were specifically chosen to be representative of Sweden's Uppland region, where water nutrient concentrations, light levels, and alkalinity are overall favorable for the growth of *E. canadensis* (Larson and Willén 2006). Conspecific densities might be less important for the performance of *E. canadensis* relative to these and other environmental factors under more extreme conditions, or where other biotic factors (e.g. grazing pressure) are intense. More research is similarly needed into whether the underlying cause of the positive relationship between intraspecific density and *E. canadensis* growth primarily reflects enhanced allelopathy against periphyton, or other benefits arising from growth in dense aggregation (e.g. shelter, control of resources).

Regardless of the underlying mechanism, it is unlikely that the reinforcing effect of intraspecific density on population growth will continue indefi-

nately. Indeed, this species is known to go through a cycle of intensive growth followed by a population crash, indicating that there comes a point when further expansion of population cover is associated with negative outcomes, possibly arising from intense density-dependent competition for nutrients, space and light (Rørslett et al. 1986; Simpson 1990; Strand and Weisner 2001; Simberloff and Gibbons 2004). However, such crashes rarely result in the disappearance of *E. canadensis* from the local species pool. Furthermore, during the period of maximum population density, numerous individual shoots have the potential to produce even more vegetative propagules, reinforcing its potential to disperse to other suitable habitats through river-lake networks, or via other vectors (e.g. attached to boats or dispersing birds). Quantification of these cycles, including their pervasiveness, duration, and driving factors remains poor, and requires research conducted over longer time periods than the duration of our growth experiment.

Our results suggest that *Elodea canadensis* is unlikely to be overly limited by temperature (see also Riis et al. 2012; Mormul et al. 2012), or long winters. Rather, in common with other aquatic invasive macrophytes, *E. canadensis* is a versatile species that can grow under variable conditions and spread rapidly in river-lake networks, and is suited to degraded and artificial habitats, including agricultural ditches and artificial ponds (Nichols and Shaw 1986; Josefsson and Andersson 2001; Larson and Willén 2006; Riis et al. 2012). This suggests that ongoing climate change will favor the further spread of *E. canadensis* northwards into suitable boreal and subarctic ecosystems, particularly if human activity also increases in these regions, pressuring freshwater habitats further (e.g. Carey et al. 2016). Worryingly, its spread into northern latitudes may also be facilitated by the trend for increasing concentrations of dissolved organic carbon in boreal regions known as "brownification", which appears to suppress native macrophytes while favouring *E. canadensis*, reflecting its capacity for growing in low-light environments (Mormul et al. 2012). Alternatively, the preponderance of soft, low alkalinity water in many boreal lakes might ultimately limit the performance of the species in boreal regions (Sand-Jensen and Gordon 1986). These contrasting scenarios highlight the need for more research into how different abiotic and biotic factors (including competition with other native and invasive species, and herbivory) interact to regulate not only its spread but also level of impact (Barrat-Segretain 2005; Netten 2011).

*Elodea canadensis* is increasingly regarded as a less important invasive threat on the European continent, in part reflecting its long history in the region,

and also recent evidence pointing to a limited impact on native biodiversity (Boiché et al. 2010; Kolada and Kutyla 2016). We suggest that the risk for *E. canadensis* and other invasive macrophytes to not only spread but also cause significant ecological and economic damage in un-invaded boreal, subarctic and alpine regions requires urgent assessment, particularly in those countries straddling the northern edge of the species' current distribution range.

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## Supplementary material

The following supplementary material is available for this article:

**Appendix 1.** Chemical analysis procedures.

**Appendix 2.** Supplementary tables.

**Appendix 3.** Supplementary figures.

This material is available as part of online article from:

[http://www.aquaticinvasions.net/2017/Supplements/AI\\_2017\\_Tattersdill\\_etal\\_Appendix\\_1.pdf](http://www.aquaticinvasions.net/2017/Supplements/AI_2017_Tattersdill_etal_Appendix_1.pdf)

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