Effect of water quality and season on the population dynamics of *Cabomba caroliniana* in subtropical Queensland, Australia

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A B S T R A C T

Cabomba caroliniana is a submersed aquatic macrophyte that originates from the Americas and is currently invading temperate, subtropical, and tropical freshwater habitats around the world. Despite being a nuisance in many countries, little is known about its ecology. We monitored *C. caroliniana* populations in three reservoirs in subtropical Queensland, Australia, over 5.5 years. Although biomass, stem length, and plant density of the *C. caroliniana* stands fluctuated over time, they did not exhibit clear seasonal patterns. Water depth was the most important environmental factor explaining *C. caroliniana* abundance. Plant biomass was greatest at depths from 2–4 m and rooted plants were not found beyond 5 m. Plant density was greatest in shallow water and decreased with depth, most likely as a function of decreasing light and increasing physical stress. We tested the effect of a range of water physico-chemical parameters. The concentration of phosphorus in the water column was the variable that explained most of the variation in *C. caroliniana* population parameters. We found that in subtropical Australia, *C. caroliniana* abundance does not appear to be affected by seasonal conditions but is influenced by other environmental variables such as water depth and nutrient loading. Therefore, further spread will more likely be governed by local habitat rather than climatic conditions.

1. Introduction

Cabomba caroliniana A. Gray (Cabombaceae; fanwort, cabomba) is a fast-growing submerged aquatic macrophyte that originates from South America and the southeastern United States (Ørgaard, 1991). *C. caroliniana* is a popular aquarium species and was introduced to aquatic ecosystems worldwide through disposal of aquarium material and escape from culture. Currently *C. caroliniana* is naturalized in the United States, Canada, Greece, Japan, Malaysia, the Netherlands, Australia, and China (Ørgaard, 1991; Oki, 1992; Les and Mehrhoff, 1999; Zhang et al., 2003; Wilson et al., 2007; Matthews et al., 2013). Once introduced, *C. caroliniana* causes a range of ecological (Mackey and Swarbrick, 1997; Hogsden et al., 2007; Wilson et al., 2007) and socio-economic impacts (Mackey and Swarbrick, 1997; Dugdale et al., 2013).

Cabomba caroliniana was first recorded in Australia in 1967 and is now naturalized in large parts of the country with established populations found from temperate (Victoria, New South Wales) to subtropical (southeast Queensland) and tropical climates (Northern Territory, northern Queensland) (Mackey, 1996; Mackey and Swarbrick, 1997; Ensby, 2004; Schooler and Julien, 2006). Although cultivation and sale of *C. caroliniana* is now prohibited, the plant is increasing its naturalized range and could potentially establish in large parts of Australia with suitable habitat. In Australia, once introduced *C. caroliniana* is difficult to manage due to limited availability of effective control options (Anderson and Diatloff, 1999; Schooler and Julien, 2006; Hogsden et al., 2007). Hence, prevention of further spread is paramount for effective management.

Even though *C. caroliniana* is considered a pest in many countries, little is known about its ecology and population dynamics. While a significant part of the introduced range of *C. caroliniana* lies in subtropical climates (e.g. the majority of *C. caroliniana* infestations in Australia are found in the subtropical climate zone), most research within its introduced range covers temperate climates. Because of the large differences between temperate and subtropical aquatic systems it is not straightforward to extrapolate research findings from temperate regions into subtropical systems affected by *C. caroliniana*. In temperate regions macrophytes tend to exhibit seasonal variations in standing crop biomass. Plant populations usually decline during colder months and plants overwinter

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Table 1
Area, water depth, and water quality in the three reservoirs. Values are means ± SD (maximum for depth). For total N and P the median and the range (in brackets) is presented. Data were collected by the authors between 2005 and 2008 unless indicated otherwise.

	Area (ha)	Depth (m)	Temperature (°C)	Conductivity ($\mu s\,cm^{-1}$)	pH	Secchi depth (m)	Total N (mg L^{-1})	Total P (mg L^{-1})
Ewen Maddock Dam	370	7.7 ± 1.5 (>7 m)[*]	21.6 ± 4.4[#]	126 ± 111[#]	6.8 ± 0.3[#]	1.7 ± 0.4	0.51 (0.28-12.51)[#]	0.02 (0.01-3.44)[#]
Lake Macdonald	260	6.5 ± 0.5 (7.1)[*]	23.2 ± 2.0[#]	106 ± 21[#]	6.7 ± 0.2[#]	1.1 ± 0.2	0.67 (0.00-2.10)[#]	0.02 (0.00-0.12)[#]
Seibs Dam	3.5	(4.0)	23.9 ± 3.3	91 ± 5	6.5 ± 0.7	0.8 ± 0.1	2.74 (2.46-3.03)	0.44 (0.22-0.60)

[*] Data provided by SEQwater.
[#] Data provided by SEQwater, averages from 2005–2008 monthly monitoring.

in the seedbank or as vegetative propagules. In tropical regions, aquatic plant populations are largely shaped by water level variations induced by rainfall patterns. *Cabomba* species show similar variations in growth and biomass depending on geographic location and climate. In the monsoonal climate of Malaysia, *Cabomba furcata* Schultes and Schultes f. (1830) exhibited pronounced seasonal population variations related to high-flow monsoonal rain events (Sharip et al., 2012). In tropical southern Brazil, *C. furcata* populations persist throughout the year, but even though there are no marked high-flow events, there are seasonal fluctuations in productivity that are related to light intensity and availability of organic carbon (Camargo et al., 2006).

In temperate climates of the continental USA (New Jersey) and Canada there is a seasonal cycle of *C. caroliniana* populations. In spring, *C. caroliniana* grows rapidly toward the water surface and can fill the entire water column (Wilson et al., 2007). Peak biomass of 110–240 g dry mass m^{-2} is reached in the northern hemisphere in late summer to early autumn (August–October) (Noel, 2005; Wilson et al., 2007). Toward the end of the growing season *C. caroliniana* plants fragment, and in spring new shoots emerge from fragments and turion-like structures (Riemer and Ilnicki, 1968; Wilson et al., 2007). While there is currently no information on *C. caroliniana* growth in subtropical climates, it is reasonable to expect that *C. caroliniana* would exhibit seasonal variation in population size similar to those found in temperate climates. However, as temperature fluctuations are less pronounced in subtropical than in temperate aquatic ecosystems, variation in *C. caroliniana* populations might be less pronounced than in temperate climates.

Other environmental factors that are likely to affect subtropical *C. caroliniana* populations are availability of light and nutrients. Even though *C. caroliniana* is a shade tolerant species and can persist in turbid water bodies (Zhang et al., 2003; Lyon and Eastman, 2006), *C. caroliniana* growth is influenced by water turbidity and subsequent light extinction (Schooler, 2008; van Valkenburg et al., 2011). *C. caroliniana* is usually found in shallow water to 3 m, but can grow to 10 m depths in some habitats (Ørgaard, 1991; Mackey and Swarbrick, 1997; Hogsden et al., 2007). In a turbid lake in temperate USA (MA), *C. caroliniana* abundance varied with water depth, with abundance being highest in relative shallow depths (0.5–1.5 m) (Lyon and Eastman, 2006). In its introduced range *C. caroliniana* is able to adapt to a wide range of temperature, water quality and substrate conditions and its distribution is more likely to be determined by dispersal than habitat quality (Sheldon, 1994; Zhang et al., 2003).

Submersed macrophytes such as *C. caroliniana* can satisfy their nutrient requirements either through uptake from the substrate or the water column. *Cabomba caroliniana* thrives in freshwater systems with a wide range of nutrient concentrations, from oligotrophic to eutrophic systems (Oki, 1992; Wilson et al., 2007; van Valkenburg et al., 2011). Elevated nutrient concentrations in the substrate can increase its growth performance (Bickel, 2012). However, we do not know if *C. caroliniana* can be nutrient limited in natural systems or benefits from anthropogenic eutrophication. This lack of knowledge is critical as it prevents projecting future

problems with *C. caroliniana* incursions in the light of increasing anthropogenic eutrophication.

In this paper we present survey results of *C. caroliniana* populations from three infested lakes in South–east Queensland, Australia. We hypothesized that: (1) environmental factors (depth, nutrients and water clarity) affect *C. caroliniana* populations and (2) *C. caroliniana* undergoes seasonal variations in biomass similar to those found in other climates. The knowledge of *C. caroliniana* ecology and population variability in subtropical climates is important to tailor successful management scenarios integrating herbicide and future biological control options (Schooler et al., 2012).

2. Methods

2.1. Fieldwork

Cabomba caroliniana populations were sampled seasonally (approximately every 3–6 months) over 5.5 years from 14 Sept 2004 to 16 March 2010 at three reservoirs in southeast Queensland. The three sites sampled were: Lake Macdonald (26.38549°S, 152.92905°E), Ewen Maddock Dam (26.79658°S, 152.99017°E), and Seibs Dam (26.49354°S, 152.97256°E). The three lakes were all artificially impounded reservoirs that had similar water chemistry with low conductivity and slightly acidic water, but differed in area, depth, and nutrient concentration (Table 1). Lake Macdonald and Ewen Maddock Dam were potable water reservoirs and Seibs Dam was an impounded farm dam that was built for livestock watering, but was not in use during the course of this study (no water was extracted and no livestock were present). Water quality data of Lake Macdonald and Ewen Maddock Dam used in this study was supplied by SEQwater (www.seqwater.com.au), the water supplier of South East Queensland including the greater Brisbane area. The water quality data was collected by SEQwater during their routine monthly monitoring of water quality in these reservoirs (eleven monitoring sites in Ewen Maddock Dam and five sites in Lake Mac-Donald). Water quality data in Seibs Dam was collected by the authors over the course of the study, but this data set was too small to use in a linear regression (see below).

In each lake we selected one focal site for long-term sampling. Each site was randomly selected from a set of pre-defined areas that were accessible and had low potential for management disturbance based on discussions with reservoir managers. Each site was defined as a transect 60 m in length along the shoreline. Permanent stakes were placed at each end of the transect. For each sampling event three points were randomly chosen along the shoreline transect. From each point we ran a transect perpendicular to the shore out into the reservoir and sampled *C. caroliniana* at 1 m depth increments to maximum depth at the site. Sampling was destructive so stakes were placed at the start of each depth transect to prevent sampling the same locations during future sampling events.

Sampling was staged from a boat starting from the shoreline and moving to open water. A weighted measuring tape was used to determine depth. When the desired depth was found, a diver using SCUBA followed the line to the bottom and inserted a three-sided quadrat frame (0.25 m^2) such that the weighed line was positioned

Table 2
Cabomba caroliniana population parameters for the three sampled lakes; colonized depth range, mean plant density, mean stem length, and mean biomass (shoot dry mass). All variables ± SD and range in brackets.

	Depth (m)	Shoot dry mass (g m^{-2})	Plant density (N m^{-2})	Stem length (cm)
Ewen Maddock Dam	(1–5)	126 ± 96 (0-472)	18 ± 14 (0-88)	259 ± 120 (20-710)
Lake Macdonald	(1–5)	106 ± 109 (0-671)	15 ± 15 (0-84)	226 ± 98 (41-455)
Seibs Dam	(1–3)	196 ± 152 (0-738)	22 ± 19 (0-116)	219 ± 89 (33-384)

at the diver's left corner. Therefore, sample area was determined at the substrate level (not area at the water surface). The three reservoir sites had silty substrates, which allowed easy removal of plants by pulling from the base (although probably some of the fine root mass was lost during removal and washing). All plants in the plot were collected by pulling roots out of the sediment from plant base, washing at the surface, placing in labeled plastic bags and into coolers, and taken to CSIRO Long Pocket Labs, Indooroopilly, QLD. Samples were refrigerated until measurements were taken (within 5 days of collection).

Measurements included plant stem length, plant density, and dry weight. Each plant was removed from the plastic bag, stretched to full length on a table, and length of longest stem (from stem base) was recorded. Number of entire plants (with a plant defined as all shoots from one common plant base, irrespective of the number of shoots) was counted for each plot. Then roots were cut off at the base and all stems for each plot were placed in a labeled paper bag, dried at 65 °C to constant weight in a drying oven, and weighed to the nearest 0.01 g. Biomass did not include root weight as we could not be sure that all root material was collected using the methods described above.

In 2006, *C. caroliniana* samples were collected from each reservoir to determine N:P tissue content (20 samples in total). Samples were dried at 30 °C and subsequently ground in a tissue grinder. Nitrogen content was determined by combustion using a LECO CNS 2000 combustion analyzer set at 1100 °C. Phosphorus tissue content was obtained by ICPOES following digestion with 5:1 nitric:perchloric acid.

2.2. Statistical analysis

To avoid pseudo-replication averages of the three plots (subsamples) were calculated and used as replicates (one value per depth per sampling event for each lake) in the statistical analysis. Sampling was destructive and each transect represented a new sample area so repeated measures ANOVA was not used to test for differences in temporal patterns. Instead, a three-way ANOVA (depth × season × reservoir) was used to test for significant effects of depth, season and site on *C. caroliniana* populations.

Linear regression was used to examine possible relationships between seasonal averages of water physico-chemical variables (e.g. nutrient concentration; see Table 4 for full list of variables) and seasonal averages of *C. caroliniana* population parameters. Physico-chemical variables were only available on a seasonal basis for Ewen Maddock Dam and Lake Macdonald and the data of these two populations were pooled for this analysis. Data were square root

transformed when necessary to meet the assumptions of parametric tests. Statistical analyzes were carried out in R 3.0.1 (R Core Team, 2013).

3. Results

3.1. Spatio-temporal variation in C. caroliniana population dynamics

Cabomba caroliniana was present from the shoreline to 5 m depth in Ewen Maddock Dam and Lake Macdonald. In Seibs Dam *C. caroliniana* was present to a depth of 3 m. The results of the 3-way ANOVA indicated that mean biomass (shoot dry mass, Table 2) differed significantly between sites and depth (significant site × depth interaction: Table 3) while there was no significant seasonal interaction ($p > 0.05$, Table 3). For plant density and stem length, the statistical relationships were more complex, as there were also significant interactions with season (Table 3). For all three *C. caroliniana* population parameters, depth and site explained the majority of the observed variability in the data while season only contributed little to the plant density and stem length 3-way ANOVA models.

Cabomba caroliniana biomass differed significantly between the three sites (Tukey HSD: $p < 0.02$) with the highest mean dry mass found in Seibs Dam followed by Ewen Maddock Dam and Lake Macdonald (Table 2). Seibs Dam also had the highest *C. caroliniana* density, but the difference was only significant compared to Lake Macdonald (Tukey HSD: $p < 0.00001$). Stem length was significantly lower in Seibs Dam compared to Lake Macdonald (Table 2, Tukey HSD: $p < 0.0001$) but was similar between Seibs Dam and Ewen Maddock Dam (Tukey HSD: $p = 0.60$).

The *C. caroliniana* populations displayed considerable temporal variation in the three lakes (Fig. 1a–c). However, there was no clear seasonal pattern; i.e. biomass maxima occurred in random seasons. Because of the high temporal variability of the *C. caroliniana* stands, there was no statistical difference in biomass between seasons (3-way ANOVA: Table 3). However, plant density and stem length differed significantly between seasons (3-way ANOVA: Table 3). Plant height differed significantly between spring and autumn (Tukey HSD: $p = 0.0245$) and between spring and summer (Tukey HSD: $p = 0.0453$) with highest average biomass occurring in spring. Plant density was significantly higher in spring compared to autumn (Tukey HSD: $p = 0.044$).

Cabomba caroliniana biomass, plant density, and stem length differed significantly between the sampled depths in all three habitats (3-way ANOVA: Table 3). Highest *C. caroliniana* biomass (shoot dry

Table 3
Complete 3-way ANOVA (site × season × depth) table testing statistical differences in spatio-temporal *C. caroliniana* population parameters. Significant differences ($p < 0.05$) are indicated in bold.

	DF	Shoot dry mass	Plant density	Stem length
Site	2	*F = 25.04,* **$p < 0.0001$**	*F = 18.43,* **$p < 0.0001$**	*F = 19.7,* **$p < 0.0001$**
Season	3	*F = 1.73, p = 0.16*	*F = 2.96,* **$p = 0.03$**	*F = 3.54,* **$p = 0.02$**
Depth	4	*F = 38.31,* **$p < 0.0001$**	*F = 104.87,* **$p < 0.0001$**	*F = 69.56,* **$p < n\ 0.0001$**
Site × season	6	*F = 0.88, p = 0.51*	*F = 2.23,* **$p = 0.04$**	*F = 1.037, p = 0.40*
Site × depth	6	*F = 3.50,* **$p = 0.0027$**	*F = 4.87,* **$p = 0.0001$**	*F = 14.98,* **$p < 0.0001$**
Season × depth	12	*F = 0.89, p = 0.56*	*F = 0.95, p = 0.50*	*F = 1.67, p = 0.08*
Site × season × depth	18	*F = 0.85, p = 0.63*	*F = 0.36, p = 0.99*	*F = 0.83, p = 0.67*

Table 4

Linear regression between average seasonal *C. caroliniana* population parameters and average seasonal water physico-chemical properties. Significant R^2 ($p < 0.05$) values are indicated in bold. The mean ($\pm$SD) and range of the seasonal water physic-chemical parameters used in the analysis are presented in the last column.

	Shoot dry mass R^2	Plant density R^2	Stem length R^2	Mean $\pm$ SD (range)
Temperature (C°)	0.00	0.02	0.04	22.8 ± 3.1 (15.8–28.4)
Conductivity (μS cm^{-1})	0.01	0.01	**0.19**	119 ± 25 (65–168)
pH	0.05	0.00	0.01	6.8 ± 0.2 (6.6–7.4)
Secchi depth (m)	0.04	0.00	0.08	1.05 ± 0.17 (0.72–1.40)
Color	0.01	0.07	0.01	47.9 ± 11.3 (29.8–83.3)
Turbidity (NTU)	**0.16**	0.00	0.09	6.1 ± 4.2 (2.1–18.0)
Suspended solids (mg L^{-1})	0.08	0.11	0.08	7.3 ± 7.1 (2.2–28.0)
Dissolved oxygen (mg L^{-1})	0.02	0.04	0.04	5.5 ± 1.2 (3.6–7.8)
Chla (mg L^{-1})	0.00	0.13	0.03	9.1 ± 2.1 (5.1–14.1)
Total N (mg L^{-1})	0.00	0.02	0.00	0.67 ± 0.20 (0.35–1.08)
Total P (mg L^{-1})	**0.20**	**0.43**	**0.19**	0.04 ± 0.03 (0.00–0.16)
NH$_3$-N (mg L^{-1})	**0.19**	0.08	0.11	0.04 ± 0.04 (0.00–0.16)
Soluble reactive P (mg L^{-1})	0.08	**0.17**	**0.22**	0.01 ± 0.01 (0.00–0.04)
Total Mn (mg L^{-1})	0.04	0.04	0.09	0.17 ± 0.16 (0.01–0.56)

mass) was observed in the mid depths from 2–3 m in Ewen Maddock Dam and Lake Macdonald (Fig. 2) and at 2 m for Seibs Dam. The highest biomass was recorded at 738 g m^{-2} in Seibs Dam at 3 m depth (Table 2); the largest samples in Ewen Maddock Dam and Lake Macdonald were recovered at 4 m depth. Biomass tended to be lower in the 1 m depth sampling stations than in the mid depths (not significantly different for Ewen Maddock Dam). The lowest biomass was found in the 5 m depth zone in Ewen Maddock Dam and Lake Macdonald (Seibs Dam did not have *C. caroliniana* beyond 3 m).

Cabomba caroliniana density differed significantly between sampled water depths for all three reservoirs (3-way ANOVA: Table 3). Density was greatest in shallow water (1–2 m) and decreased with increasing depth (Fig. 2). The greatest number of plants, 116 plants m^{-2}, was sampled in Seibs Dam at 1 m water depth (Table 2), the maxima in Lake Macdonald and Ewen Maddock Dam occurred in 1 m depth as well.

Overall, *C. caroliniana* stems grew longer with increasing depth from 1 to 4 m (Fig. 2). Very long plants still occurred at 5 m depth in Ewen Maddock Dam but variability was high. Stem length decreased significantly at 5 m in Lake Macdonald. The plant with the greatest stem length was 7.1 m and was found growing in 3 m of water in Ewen Maddock Dam (Table 2). The longest plants grew in 4 m in Lake Macdonald and 3 m depth in Seibs Dam.

3.2. Effect of physico-chemical parameters on C. caroliniana population dynamics

We performed linear regressions to find potential relationships between seasonal *C. caroliniana* population parameters and water physico-chemical parameters (Table 4). Of the 14 parameters tested, only five (conductivity, turbidity, total P, NH$_3$-N and soluble reactive phosphorus) significantly explained some of the variation of *C. carolinina* populations (Fig. 3 and Table 4), though the relationships were not strong. After removing three outliers (the three largest total P values) from the regression analysis, total phosphorus concentration was the best predictor of *C. caroliniana* populations, in particular plant density ($R^2 = 0.43$; Fig. 3). Turbidity seemed to affect *C. caroliniana* shoot dry mass but had no effect on plant density or stem length (Table 4 and Fig. 3) and there was a small effect of conductivity on stem length.

The *C. caroliniana* tissue nutrient content appeared unrelated to the water column nutrient concentration in the respective reservoirs (Tables 1 and 5). While the nitrogen loading in the water column varied considerably in the three habitats (Table 1; total N = 0.51–2.74 mg L^{-1}), nitrogen tissue content differed little (Table 5; N% dry wt = 2.64–2.89). Similarly, there was no clear pattern between the phosphorus loading of the water column (Table 1; total P = 0.02–0.44 mg L^{-1}) and the phosphorus tissue content (Table 5; P% dry wt = 0.14–0.24). For example, Seibs Dam had a much higher P loading compared to the other two reservoirs, but *C. caroliniana* tissue samples from Lake Macdonald had the highest P content. The N:P ratios of the *C. caroliniana* tissue samples were similar between Ewen Maddock Dam and Seibs Dam (N:P = 20.6 and 18.1), but were lower in Lake Macdonald (Table 5; N:P = 12.3).

4. Discussion

Cabomba caroliniana populations were highly variable over time and among reservoirs. However, while the biomass, density, and stem length of the *C. caroliniana* plants fluctuated over time, there were no discernible seasonal patterns. One reason for this might be that the climate in Queensland is favorable for *C. caroliniana* growth year-round and that other external factors affect the extent of *C. caroliniana* stands in the sampled lakes. The water temperatures found in the three lakes fall within the optimum temperature range reported in the literature (Ørgaard, 1991; Mackey and Swarbrick, 1997) throughout the year. The optimum growing conditions regarding temperature and water chemistry also explain the much higher maximum biomass (472–740 g m^{-2}) and a similar average biomass (126–196 g m^{-2}) that was measured in these subtropical lakes compared to peak biomass (110–240 g m^{-2}) observed in temperate Canadian lakes (Noel, 2005; Hogsden et al., 2007). In fact, average biomass in all three of the Queensland lakes were year-round on a similar level compared to the peak biomass attained in the temperate lakes.

The subtropical *C. caroliniana* populations in Queensland did not exhibit similar seasonal variations as observed in tropical populations of *C. furcata* in Brazil and Malaysia (Camargo et al., 2006; Sharip et al., 2012). Both of these *C. furcata* populations occurred in areas with a monsoonal climate and plant biomass varied with monsoonal flow events. The subtropical *C. caroliniana* populations

Table 5

Mean N and P tissue content $\pm$ SD (with range in brackets) of *C. caroliniana* collected from the three reservoirs in 2006 and the N:P ratio.

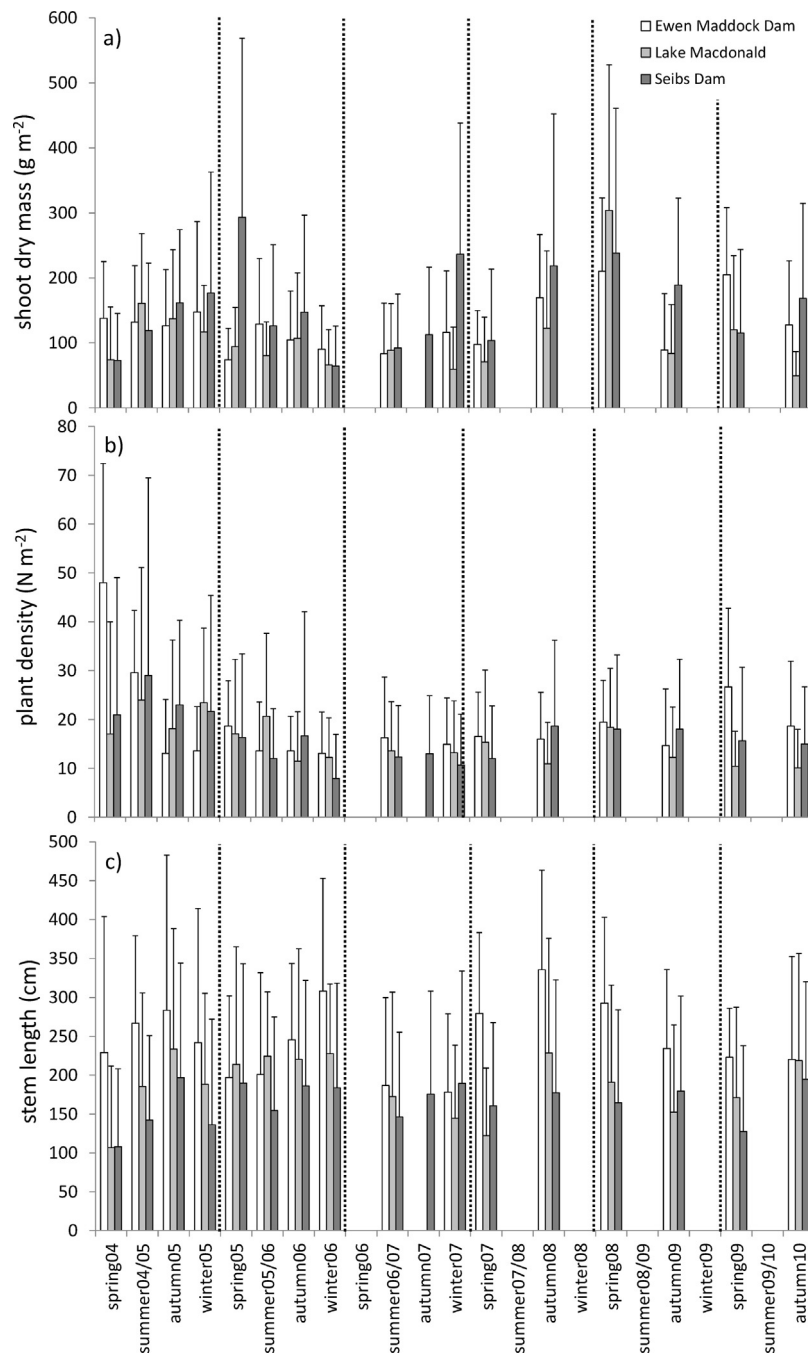|	N (% dry wt)	P (% dry wt)	N:P
Ewen Maddock Dam	2.69 ± 0.38 (2.07–3.03)	0.14 ± 0.14 (0.07–0.16)	20.6 ± 4.1 (17.0–27.7)
Lake Macdonald	2.89 ± 0.19 (2.60–3.11)	0.24 ± 0.04 (0.17–0.28)	12.3 ± 1.6 (10.7–15.8)
Seibs Dam	2.64 ± 0.54 (2.07–3.13)	0.15 ± 0.04 (0.11–0.17)	18.1 ± 1.6 (16.4–19.6)

Fig. 1. Measures of *C. caroliniana* abundance over time including: (a) *C. caroliniana* biomass (shoot dry mass), (b) plant density, and (c) stem length in three reservoirs in southeast Queensland over the course of the study. No sampling took place in spring 2006, summer 2007/08, winter 2008, summer 2008/09, winter 2009 and summer 2009/10. Missing bars in autumn 2007 indicate zero values.

in Queensland are situated in a similar monsoonal climate but did not show any seasonal patterns. The reason for this might be the high inter-annual variability of rainfall in Queensland. During the study periods, the climate in Queensland was in a dry cycle and there were no major flooding events. Therefore, the lack of a seasonal pattern that was found in these *C. caroliniana* populations might be the result of the absence of flood events during the survey time period. Also, the studied populations are situated in drinking water reservoirs (Ewen Maddock Dam Lake Macdonald) and a farm dam (Seibs Dam), which likely experience lower fluctuations in water levels as compared to the *C. furcata* populations studied in a natural flood plain environment in Brazil (Camargo et al., 2006). The water level of Ewen Maddock Dam for example fluctuated only

by a maximum of 1.4 m during the study period (data supplied by SEQwater). Also, both studies of *C. furcata* populations were limited to a single seasonal cycle (Camargo et al., 2006; Sharip et al., 2012), while the present survey was conducted over 5.5 years. Therefore, it is possible that the seasonal patterns that were found in the *C. furcata* populations might not occur during all years in these populations.

While there was no clear temporal pattern for the studied *C. caroliniana* populations, there were clear differences in *C. caroliniana* biomass, stem length, and density between the three reservoirs. This can partly be explained by differences in the habitat qualities of the reservoirs. The two deeper reservoirs, Ewen Maddock Dam and Lake Macdonald, allowed stems to grow longer than in Seibs Dam.
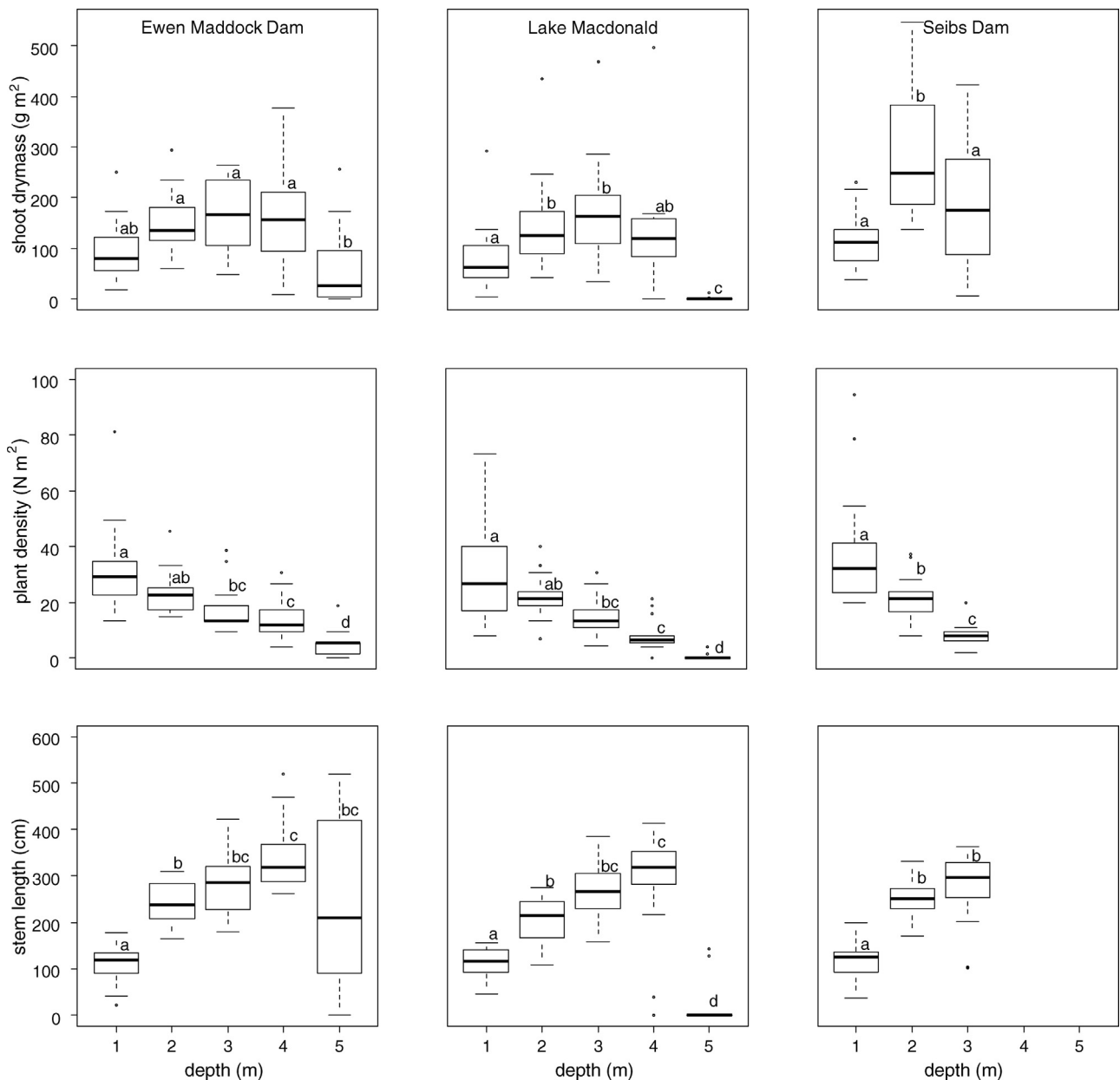
Fig. 2. Relationship between depth and plant biomass (shoot dry mass), depth and plant density, and depth and stem length (vertical) for the three reservoirs (horizontal). Letters indicate significant differences at the $p < 0.05$ level.

Contrary to this, the higher nutrient concentrations could account for the higher *C. caroliniana* biomass encountered in Seibs Dam for example through a more compact and denser growth form. In fact, we found a positive linear relationship between total phosphorus and *C. caroliniana* growth. The smaller area of Seibs Dam may also result in lower mechanical disturbance on the *C. caroliniana* stems due to the lower effective fetch, therefore allowing *C. caroliniana* to accumulate a higher biomass.

Not surprisingly, water depth was the main environmental variable associated with variation in *C. caroliniana* biomass, density, and stem length. *C. caroliniana* grew to depths of 5 m in Ewen Maddock Dam and Lake Macdonald, but biomass was greatest in mid depths of 2–4 m. The higher biomass in the mid depths is possibly the result of the increasing stem length with increasing depth. In deeper water *C. caroliniana* stems elongate to reach the higher light intensities of surface waters, and subsequently standing crop biomass increases with depth. However, in deeper water beyond 4 m (in Ewen Maddock Dam and Lake Macdonald), *C. caroliniana*

biomass became highly variable. This is most likely a result of a combination of light attenuation and physical stress.

The availability of light for photosynthesis is one of the most important environmental factors regulating aquatic plant growth (Sand-Jensen, 1989; Bornette and Puijalon, 2011) and water clarity frequently shapes species composition in macrophyte communities (Hawes et al., 2003). Due to the reduced light availability in deeper water, depths greater than 4 m are marginal habitat for *C. caroliniana*. In Seibs Dam low water clarity is likely responsible for *C. caroliniana* being restricted to less than 4 m depth (see also: Schooler and Julien, 2006).

Plant density was greatest at shallow depths in all three habitats. This may be due to broken fragments lodging near the shore and then taking root. Plants in water greater than 1 m depth tended to be solitary with root clumps separated from other plants, whereas plants in less than 1 m depth tended to have roots that grew together and formed a mat. Shallow habitats also have relatively higher light availability and allow increased plant density, com-
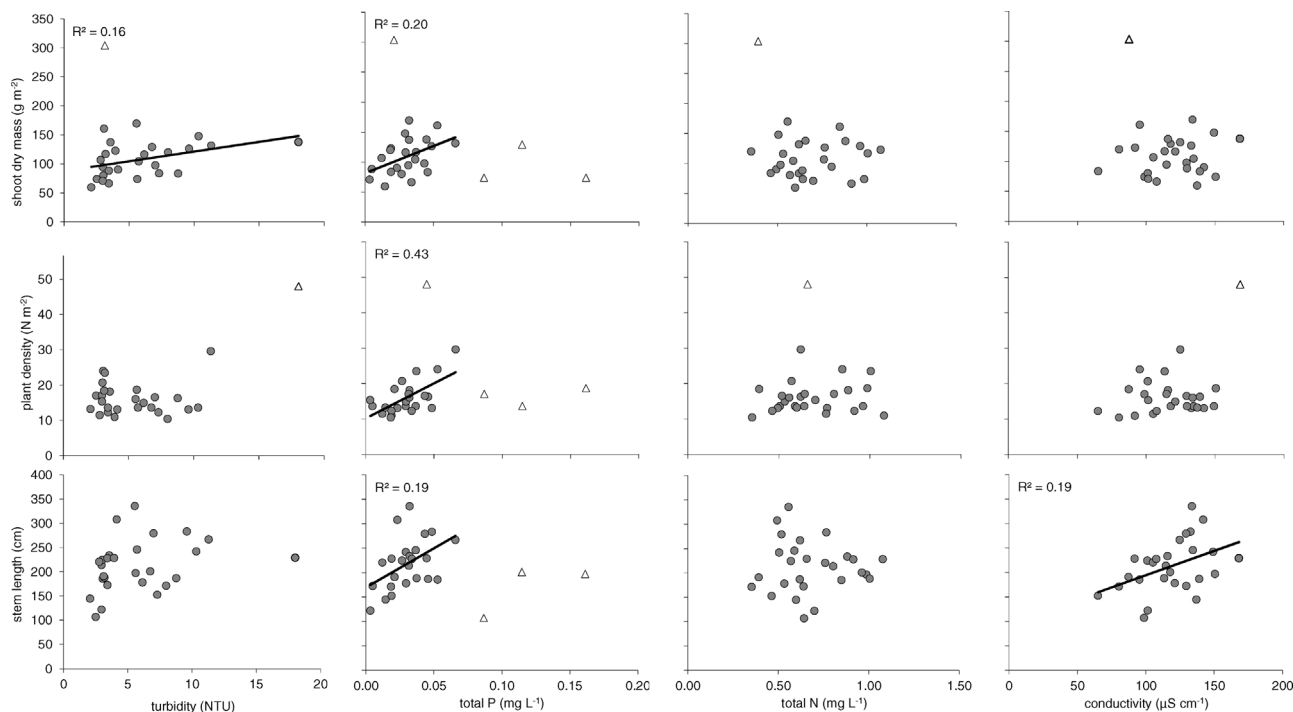
Fig. 3. Linear regression between seasonal averages of water physico-chemical parameters and *C. caroliniana* population parameters. Outliers that were removed from the regression analysis are plotted as triangles. Significant R^2 ($p < 0.05$) values are displayed in the plots.

pared to deeper areas where *C. caroliniana* stands exhibit reduced plant density, but each plant tends to produce more stems with greater stem length in order to maximize light acquisition. *C. caroliniana* populations in temperate USA (MA) and Canadian lakes exhibit similar patterns in depth distribution as found here, with *C. caroliniana* being limited to comparatively shallow depths, either as a result of high turbidity (Lyon and Eastman, 2006) or because of the more sheltered aspect of shallow bays that allow prolific *C. caroliniana* growth (Hogsden et al., 2007).

When testing for effects of water physico-chemical parameters on *C. caroliniana* populations, we found few significant relationships and these were not strong. We expected that measures of water transparency (Secchi depth, turbidity and water color) would affect *C. caroliniana*. However, we only found a significant linear relationship between turbidity and shoot dry mass. The lack of a strong effect of water transparency on *C. caroliniana* growth can be explained by a combination of the low light requirements of *C. caroliniana* (Zhang et al., 2003; Lyon and Eastman, 2006), the shallow habitats that were part of this study and the comparatively high water transparency in general; i.e. in the studied systems *C. caroliniana* is not limited by light and therefore we were unable to find any significant relationships. More research is clearly needed to accurately measure the light requirements of *C. caroliniana* in the future. *Cabomba caroliniana* growth is reduced at a higher pH (Bickel, 2012Bickel, 2012 Mackey and Swarbrick, 1997; Ørgaard, 1991), therefore we expected to find a relationship between the pH and *C. caroliniana* populations. However, we did not find any evidence of such a relationship in this study. The reason for this is most likely that the three reservoirs have a pH conducive to *C. caroliniana* growth and the sampled pH range was too narrow to be able to detect a meaningful relationship.

We also anticipated that nutrient concentrations in the water column would influence *C. caroliniana* growth. While nitrogen concentration in the water column did not show any effect on *C. caroliniana*, we found a positive relationship between phosphorus concentrations and *C. caroliniana* population parameters. This would mean that *C. caroliniana* is potentially limited by phosphorus

in the studied systems, while nitrogen is not limiting. Considering the concentration of macro-nutrients in the water column, all three of the systems could be described as eutrophic (Table 1), with high availability of nitrogen and phosphorus. While macrophytes are commonly able to satisfy their nutrient requirements from the water column (e.g. Madsen and Cedergreen, 2002), there seems to be no consistent relationship between nutrient concentrations in the water column and growth parameters in the literature. Some studies find a lack of relationship between nutrient loading and macrophyte growth (Madsen and Cedergreen, 2002) while other report such a relationship (Wersal and Madsen, 2011; O'Hare et al., 2010). The reason for this might be that the available nutrients satisfy the nutrient requirements for maximum growth and therefore additional nutrients do not result in higher growth rates (Madsen and Cedergreen, 2002).

The tissue nutrient concentrations found in *C. caroliniana* were similar to those found in other macrophytes (Duarte, 1992; James et al., 2006). However, the water column nutrient concentration in the three reservoirs did not correspond with the nutrient content in *C. caroliniana* tissue. Again, there are no consistent findings from the literature. Some researchers found a relationship (James et al., 2006), while others did not (Güswell et al., 2003). It has also been suggested that N:P ratios might be more indicative of nutrient limitations than nutrient tissue content itself (Güswell and Koerselman, 2002) and that N:P ratios >20 indicate a phosphorus limitation (Güswell et al., 2003). The N:P ratios found in Ewen Maddock Dam (20.6) and Seibs Dam (18.1) were higher or close to the suggested threshold of 20. This means that *C. caroliniana* might be limited by phosphorus in these systems, corroborating the findings from the regression analysis.

This study indicates that in warm subtropical areas *C. caroliniana* growth patterns are more likely regulated by local habitat variables than seasonal conditions. Therefore, future spread of this plant will be more restricted by habitat conditions than climatic aspects. Currently we do not know if the depth limitation of *C. caroliniana* that was found here was solely due to light attenuation and physical stress or other environmental variables. We expect that pH will be

one of the most important factors determining *C. caroliniana* spread. As *C. caroliniana* does not tolerate pH > 7.5 (Bickel, 2012Bickel, 2012 Mackey and Swarbrick, 1997; Ørgaard, 1991), establishment will be primarily determined by the pH of the recipient water. Apart from abiotic factors, human transport of fragments will largely determine the future spread of this species in Australia (Bickel, 2015). *C. caroliniana* rarely produces viable seeds in its introduced range and therefore depends primarily on humans to disperse vegetative propagules to new watersheds.

Acknowledgements

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