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Interactive effects of road salt and sediment disturbance on the productivity of seven common aquatic macrophytes

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Abstract

1. Around the world, freshwater ecosystems are subjected to numerous stressors that can alter community composition in favour of stress-tolerant species. Because combinations of stressors often result in non-additive interactions, elucidating responses to isolated and combined stressors is important to understand the ecological responses to anthropogenic disturbance.
2. In this study, we explored the responses of common macrophyte species to two stressors of increasing concern: elevated salinity from road salt applications and turbidity from human recreational activities and shoreline development. The independent and interactive effects of environmentally relevant salt concentrations and turbidity on macrophyte productivity have received little attention. We hypothesised that both stressors in isolation would reduce macrophyte productivity and that the two stressors combined will lead to a greater (i.e. synergistic) reduction in productivity.
3. To test these hypotheses, we conducted dark- and light-bottle experiments on seven species of native and invasive macrophytes under a factorial combination of three salt concentrations (0, 500 and 3,000 added mg Cl^{-} L^{-1}) and two turbidity conditions (clear and turbid via a disturbance to the sediment).
4. On average, macrophytes exhibited reduced productivity in response to increased salt, but results were highly species-specific. Several species exhibited a unimodal response to elevated salinity, whereas *Elodea canadensis* exhibited a positive response to the high-salt treatment. Similarly, macrophytes exhibited an average reduction in productivity under turbid conditions, but analysis of species-specific responses revealed both neutral and negative responses. Combining the two stresses yielded non-additive responses for some species. Specifically, *Myriophyllum spicatum* appeared to suffer from the combination of salt and turbidity, whereas *Elodea canadensis* and *Ceratophyllum demersum* benefited from the combination.
5. Our results suggest that increased anthropogenic disturbance of freshwater ecosystems can dramatically alter macrophyte species metabolism and might stimulate the growth of some species while deterring the growth of others.

KEYWORDS
Bioturbation, *Ceratophyllum demersum*, Deicer, *Elodea nuttallii*, *Najas flexilis*, *Potamogeton robbinsii*, salinisation

1 | INTRODUCTION

For ecosystems subjected to anthropogenic or natural disturbances, interspecific variation in stress tolerance is an important factor in determining species composition (Lavorel & Garnier, 2002). In the presence of such variation, the loss of one species can be compensated by the growth of one or more tolerant species with similar function (Yachi & Loreau, 1999). As an increasing array of stressors threaten ecosystems, it is imperative to understand how such stressors will affect individual species to improve management efforts and mitigate anthropogenic damage. In addition, it is necessary to explore the effects of isolated and combined stressors because combinations of stressors often interact in non-additive ways that are not predictable from responses to isolated stressors (Côté, Darling, & Brown, 2016; Darling & Côté, 2008). Moreover, the assessment of only a few model species can often underestimate the amount of variation in stress tolerance among species (Kerby, Richards-Hrdlicka, Storfer, & Skelly, 2010). To account for these shortcomings and to provide generality in our conclusions, we need studies that explore the effects of isolated and combined stressors on many species.

Throughout the world, freshwater food webs are responsible for a variety of services (e.g. irrigation, water purification, recreation), yet are among the most disturbed environments (Dodds, Perkin, & Gerken, 2013). At the base of freshwater food webs, primary producers assume several roles that support aquatic communities and the surrounding terrestrial systems. In particular, submerged and emergent macrophytes provide an important energy and nutrient resource for consumers and also provide a three-dimensional shelter for herbivores and detritivores (Brix, 1994; Burks et al., 2006; Carpenter & Lodge, 1986; Jeppesen, Sondergaard, Sondergaard, & Christofferson, 2012). Macrophytes can also alter sediment structure, create substrate for epiphyton growth, adsorb chemical contaminants and increase water clarity by filtering out sediment particles (Brogan & Relyea, 2015, 2017; Jeppesen et al., 2012). Consequently, changes in macrophyte growth or abundance can have substantial bottom-up effects on food webs and buffer them against human-derived disturbances, such as terrestrial erosion, overfishing and chemical pollution (Brix, 1994). The extent to which macrophytes offer these buffering effects will depend on their interspecific tolerance to stressors. Hence, determining their tolerance is an essential step towards improved management and conservation efforts.

Aquatic food webs are increasingly exposed to a diverse array of chemical contaminants (Fleeger, Carman, & Nisbet, 2003; Relyea & Hoverman, 2006; Schwarzenbach et al., 2006). Among northern latitudes, pollution of fresh waters by chloride (Cl^-) salts is becoming an increasing problem due to the use of sodium chloride (NaCl) and other chloride salts as a road de-icing agent during colder months (Findlay & Kelly, 2011). Industrial salt use, groundwater irrigation and wastewater discharge have added to the total Cl^- concentrations in fresh waters, which can reach up to 5,000 mg Cl^- L^{-1} in small wetlands and lakes following extreme storm events (Cañedo-Argüelles et al., 2016; Environment Canada 2001; Findlay & Kelly, 2011; Kaushal, 2016). Biological effects of Cl^- contamination are likely to occur beyond USEPA-mandated chronic and acute thresholds of 230 and 860 mg Cl^- L^-, respectively (USEPA, 1988). Although outflow and dilution often reduce chronic levels of salinity after winter, field surveys have revealed spring and summer Cl^- concentrations up to 500 mg Cl^- L^{-1} in temperate and boreal ponds (Sadowski, 2002; Sriyaraj & Shutes, 2001), and this number is likely to increase with further salt application. Such levels are unlikely to induce plant mortality; field observations indicate that many common macrophytes can survive in waters with up to 4,000 mg soluble salts L^{-1} (Hart et al., 1991). In addition, controlled greenhouse studies have indicated many common macrophytes species can tolerate salinities up to 12,000 mg soluble salts L^{-1} for at least three months (Borgnis & Boyer, 2016; Izzati, 2016; James & Hart, 1993; Wang & Ji, 2007). However, sublethal effects (e.g. reduced growth) are evident at far lower salt concentrations (Hart et al., 1991), likely due to osmotic stress and difficulty in absorbing nutrients (Parida & Das, 2005). Given that such greenhouse studies lack the presence of other natural and anthropogenic stressors, it is likely that combinations of stressors might have synergistic interactions in natural systems.

Elevated turbidity in freshwater systems is an additional stressor of increasing concern that is likely to have a substantial impact on macrophytes (Madsen, Chambers, James, Koch, & Westlake, 2001). This process occurs because of activities that increase the amount of particulate matter in water. For example, the maintenance of shorelines for swimming or fishing can disturb sediments when humans remove plants to clear an area (Strayer & Findlay, 2010). Hardening of shorelines (e.g. building seawalls) and removal of large riparian vegetation can also lead to increased wave energy which increases terrestrial erosion and elevates turbidity. Boat traffic can also have a substantial impact when propellers and anchors disturb sediment, tear apart macrophytes and increase turbidity (Asplund, 2000; Liddle & Scorgie, 1980; Whitfield & Becker, 2014). In at least one macrophyte species (*Vallisneria americana*), light limitation induced by such sediment disturbances is known to negatively interact with elevated salinity to reduce plant productivity (French & Moore, 2003). However, an increase in water turbulence might also increase the concentration of dissolved nutrients. In turn, this could increase macrophyte productivity if the plants are tolerant of short-term shading and elevated salinity, particularly if they can absorb nutrients through leaf tissue (Crossley, Dennison, Williams, & Wearing, 2002; Madsen & Cedergreen, 2002; Volkmann, Halbedel, Voss, & Schubert, 2016). Hence, it is likely that the response of individual macrophyte species will depend on their specific physiology, the severity and duration of the physical disturbance, and the presence of other stressors in the environment.

In this study, we examined the effects of salt contamination and sediment disturbance on the productivity of seven species of native and invasive macrophytes common to the north-eastern USA and spanning taxonomic orders found throughout the world. We hypothesised that elevated turbidity and contamination by NaCl (manipulated as the concentration of $Cl^- L^{-1}$) would reduce macrophyte productivity. We further hypothesised that the combination of the two stressors would lead to a greater reduction in macrophyte productivity than would be expected from either stressor by itself (i.e. the impact on productivity would be synergistic). To test these hypotheses, we conducted dark- and light-bottle experiments on seven different macrophytes species under a factorial combination of three Cl^- concentrations and two turbidity conditions.

2 | METHODS

2.1 | Macrophyte species

We conducted experiments on seven macrophyte species that are common to freshwater lakes in the north-eastern USA. *Potamogeton robbinsii* (Robbin's pondweed) is commonly found in muddy areas of wetlands and is considered highly intolerant of anthropogenic disturbances (Beck, Hatch, Vondracek, & Valley, 2010). A field survey of Canadian lakes rarely found it in waters with concentrations greater than 3 mg $Cl^- L^{-1}$ (Pip, 1987). *Stuckenia pectinata* (sago pondweed) is a cosmopolitan plant found in both lentic and lotic systems. Given that this species has been documented in both fresh and brackish waters, *S. pectinata* is considered tolerant to moderate amounts of anthropogenic disturbance (Davis & Brinson, 1980; Tiner, 2009), although it appears to exhibit reduced growth rates above a salinity of 5 g salt L^{-1} (Borgnis & Boyer, 2016). *Myriophyllum spicatum* (Eurasian watermilfoil) is also cosmopolitan and is classified as highly invasive, particularly in North America. *Myriophyllum spicatum* is more tolerant to salt than many other freshwater macrophyte species (Beck et al., 2010), although it also exhibits reduced growth with elevated salinity (Haller, Sutton, & Barlowe, 1974; Wang & Ji, 2007). *Elodea canadensis* (Canadian waterweed) and *Elodea nuttallii* (American waterweed) are both widespread throughout much of North America and can survive in fresh and brackish waters. Little is known regarding the effects of physical or chemical disturbance on *E. nuttallii*. *Elodea canadensis* is considered moderately tolerant to disturbances, although it is known to reduce photosynthetic rates above 100 mg $Cl^- L^{-1}$ (Beck et al., 2010). *Najas flexilis* (slender naiad) can be found in both fresh and brackish water and is considered moderately tolerant to anthropogenic disturbances (Beck et al., 2010; Davis & Brinson, 1980). *Ceratophyllum demersum* (American coontail) is found throughout North American ponds and lakes, is found in disturbed conditions (Davis & Brinson, 1980) and is tolerant up to a salinity of 5 ppt (Izzati, 2016). Unlike the other macrophytes species in our study, *C. demersum* is not rooted, although it can anchor itself to substrate via leaf tissue. All other species are rooted but can absorb nutrients through both roots and shoots, with the possible exception of *N. flexilis* (Carignan & Kalff, 1980).

2.2 | Experimental design

We collected stems of each macrophyte species in summer 2016 immediately prior to beginning the trial on that species (i.e. no more than 48 hr prior to the starting time; Table 1). The locations of collection are listed in Table 1. All specimens came from eutrophic lakes according to nitrogen and phosphorus measurements of surface water conducted by the New York Citizen Statewide Lake Assessment Program (Collin's Lake: 0.020 mg P L^{-1}, 0.460 mg N L^{-1}; Burden Lake: 0.014 mg P L^{-1}, 0.358 mg N L^{-1}; Snyder's Lake: 0.029 mg P L^{-1}, 0.520 mg N L^{-1}). We collected all specimens within 10 m of the shoreline. All collection sites were in developed areas that experience substantial boat traffic, and therefore likely to experience turbid conditions. We collected stems with their roots by gently pulling the stem from the base or scooping the soil under the shoot. We immediately placed stems in a bucket with water from their collection lake and transported them back to the laboratory, where we held them in outdoor plastic wading pools filled with off-gassed tap water until they were used in the experiment.

We conducted our experiment at the Rensselaer Aquatic Facility in Troy, NY. Our experimental design included a fully factorial combination of three added NaCl treatments (0, 500, and 3,000 mg $Cl^- L^{-1}$, which corresponds to salinities of 0, 0.8 and 5.0 ppt, respectively), and two turbidity treatments (turbid and non-turbid) for each plant species. Because our goal was to calculate gross primary productivity (GPP), we accounted for both net primary productivity (NPP) and respiration by crossing all treatments with both a light and dark treatment, for a total of 12 treatments for each macrophyte species. We replicated each treatment five times for a total of 60 experimental units per species. Each experimental unit consisted of a 1-L glass jar filled to overflowing with water containing the appropriate Cl^- concentration. We conducted separate experiments on the seven macrophyte species over 51 days between the beginning of July and the end of August, for a total of 420 experimental units. For each experiment, we also created an additional set of no-macrophyte controls for each treatment to account for background NPP and respiration. We replicated each control twice, which established an additional 24 experimental units per experiment (i.e. an additional 168 experimental units) for a grand total of 588 experimental units.

To avoid the potential introduction of macroorganisms other than macrophytes, we thoroughly rinsed all shoots and roots prior to their introduction into glass jars. After rinsing, we placed a single plant shoot into a single jar along with 120 ml of sandy-loam soil, which was enough to cover the roots. Chemical analysis from a separate experiment indicates that the addition of soil elevated the nutrient content of the water to 51 μg total phosphorus L^{-1} and 350 μg total nitrogen L^{-1} (K. Coldsnow, *personal communication*). We used the same soil for each experiment and homogenised all soil prior to placing it in the jar, so that the chemical composition of the soil should not have affected the relative responses of plants within and among experiments. We then filled each jar to the top with water containing either ambient levels of Cl^- (25 mg $Cl^- L^{-1}$; herein referred to as low-NaCl) or amended with NaCl (Solar Salt, Morton Salt) to 500 mg $Cl^- L^{-1}$ or 3000 mg $Cl^- L^{-1}$ (herein referred to as intermediate- and high-NaCl, respectively). To minimise sediment disturbance, we gently filled all jars using a siphon from a bucket

TABLE 1 Species name, common name, collection location, planting date and trial date for the seven macrophytes species tested in this study. The planting date refers to the date that we planted macrophytes shoots in jars and began the acclimation period; the trial date refers to the date that we conducted light- and dark-bottle trials

Species name	Common name	Collection location	Collection coordinates	Planting date	Trial date
Potamogeton robbinsii	Robbin's pondweed	Crooked Lake	42.613182, −73.525656	20 July	27 July
Stuckenia pectinata	Sago pondweed	Collin's Lake	42.825488, −73.955714	9 August	16 August
Myriophyllum spicatum	Eurasian watermilfoil	Snyder's Lake	42.663387, −73.634193	19 August	26 August
Elodea canadensis	Canadian waterweed	Collin's Lake	42.825488, −73.955714	4 August	11 August
Elodea nuttallii	American waterweed	Burden Lake	42.597563, −73.567569	29 June	6 July
Najas flexilis	Slender naiad	Snyder's Lake	42.663387, −73.634193	15 August	23 August
Ceratophyllum demersum	American coontail	Snyder's Lake	42.663387, −73.634193	6 July	13 July

containing water with the appropriate Cl^- concentration. We filled all no-macrophyte control jars in the same manner. Because the process of filling all jars required a substantial amount of time (~8 hr per trial), we randomised the order in which we filled the jars. After filling, we placed all jars into outdoor, plastic wading pools filled with water to buffer temperature variability over time. We placed *c.* 20 jars in a single pool and added them in the order that they were filled to ensure random placement of replicates across all pools. The water level outside of the jars was maintained *c.* 2 cm below the top of the jars so that no water from the pool entered the jars.

Following the addition of all macrophytes, we allowed them to acclimate. After 24 hr, we gently shook the leaves (to remove any sediment). After an additional 24 hr, we disturbed all turbid treatments (including turbid no-macrophyte controls) using a stirring rod. We standardised this disturbance by driving the rod into the soil on two edges of the jar and pushing the rod back and forth five times. Following these back-and-forth disturbances, we also gently swirled the water in the turbid treatments to suspend the lighter sediment particles. Although this represented a major sediment disturbance, water was clear after approximately 24 hr. Moreover, our method of disturbing the sediment did not noticeably damage the macrophytes shoots. Preliminary sampling and analysis of water immediately following a disturbance indicated that this method generated a consistent sediment concentration in the water column. After 24 hr following the sediment disturbance, we gently tapped each macrophyte shoot to dislodge any sediment particles that settled on the plant surface. This procedure simulated gentle wave action in natural systems that would normally remove settled sediment. Three days after this first sediment disturbance, we disturbed all turbid treatments a second time (i.e. 6 days after initial macrophyte introduction). Immediately following each disturbance, we replaced any water that overflowed the jar by adding water containing the appropriate Cl^- concentration. Other than the two brief sediment disturbances, there was no other source of water movement within jars during the acclimation period.

One day after the second soil disturbance (i.e. 7 days after initial macrophyte introduction), we conducted light-bottle dark-bottle trials over 4 hr. We measured the initial dissolved oxygen (DO) and temperature in each jar using a benchtop DO meter with a connected stir paddle (YSI 5000, Yellow Spring, FL). We read the initial DO at the same time of the day for each experiment. To minimise the disturbance which the paddle might cause to macrophyte shoots, we placed the probe and paddle inside a small cup with the bottom cut off and replaced with 1-mm mesh screening. The screening allowed the free flow of water but provided a buffer to absorb some of the kinetic energy from the paddle. The mesh screen also pressed down the macrophyte shoot and allowed the paddle to stir water without interference. We also used this mesh screen in the no-macrophyte controls. We recorded the exact time that we measured the initial DO. Immediately following the initial DO reading of a single replicate, we replaced any water that overflowed the jar and immediately sealed all jars with parafilm secured by rubber bands. We visually inspected each seal to ensure that no air bubbles were below the parafilm. Preliminary laboratory testing demonstrated that this seal prevented liquid from leaving the jar. We completely covered all dark-bottle jars with aluminium foil. After sealing the jars, we put them back into the wading pools. After 4 hr, we unsealed the jars, read the final DO, recorded the time and extracted the macrophyte with its root. We dried all macrophytes at 60°C for a minimum of 24 hr to obtain dry mass.

We calculated the DO uptake of each jar per minute of incubation and per dry g macrophyte tissue. We also corrected the uptake of each jar for background uptake, using the average value of each set of controls (see Supporting Information for background NPP and GPP values). We used the value of O_2 production in the light jars as a measure of NPP. We calculated GPP as NPP + respiration, where respiration is equal to the amount of O_2 consumed under dark conditions. We assumed that the amount of respiration under light conditions is equivalent to the amount of respiration under dark conditions. Because we did not a priori pair light- and dark-bottle replicates in our experimental design, we determined values of GPP as all possible combinations of NPP and respiration within a treatment. We then analysed these data using bootstrapping techniques (see below).

2.3 | Statistical analyses

To demonstrate the variability in NPP across macrophyte species in the absence of the NaCl and turbidity stressors, we conducted a one-way analysis of variance (ANOVA) with a data set that excluded all turbid and added NaCl treatments (i.e. intermediate- and high-NaCl treatments). To demonstrate the independent and interactive effects of species, NaCl and turbidity on NPP, we conducted a three-way analysis of variance (ANOVA) with a model that all possible main effects and interaction terms. Upon finding a significant (i.e. $p < .05$) three-way interaction, we then conducted two-way ANOVAs for each macrophyte species with models that included NaCl treatment, turbidity treatment and their interaction. We conducted Tukey's post hoc tests to assess treatment differences among salt concentrations. Prior to all analyses, we verified that our data met the assumptions of ANOVA by examining the linearity of residual values and homoscedasticity of error variances with Q–Q and scale-location plots, respectively.

Like our analysis on NPP, we first demonstrated the variability in GPP across macrophyte species used in our study by conducting a one-way analysis of variance (ANOVA) with a data set that excluded all turbid and added NaCl treatments (i.e. intermediate- and high-NaCl treatments). We then analysed the effect of species, NaCl and turbidity on GPP. We first calculated the GPP of all possible light- and dark-bottle replicate combinations within each treatment. Subsequently, we employed a bootstrapping approach with 10,000 iterations to generate means and 90% confidence intervals. We calculated bootstrapped means and confidence intervals for GPP values of each plant species regarding both turbidity and NaCl treatment (i.e. 48 total treatments). We conducted all bootstrapping in R (version 3.1.2, The R Foundation for Statistical Computing) using the package *boot* (Canty & Ripley, 2017).

To test for differences in bootstrapped GPP treatment means, we conducted a three-way analysis of variance (ANOVA) with a similar model as that used to assess NPP. We included all possible GPP values in this analysis, but adjusted the denominator degrees of freedom for the actual number of treatments. Similar to our analysis of NPP, we conducted two-way ANOVAs for each macrophytes species with models that included NaCl treatment, turbidity treatment and their interaction. Again, we included all possible GPP values in this analysis, but adjusted the denominator degrees of freedom for the actual number of treatments. We considered GPP to be different between treatments when there was no overlap between confidence intervals (Payton, Greenstone, & Schenker, 2003). We conducted all ANOVAs in R using the package *car* (Fox, Weisberg, & Bates, 2018) with type II sums of squares.

3 | RESULTS

3.1 | NPP

When considering the effect of macrophyte species in the absence of both turbidity and elevated NaCl, we found more than a 10-fold difference in NPP among species ($F_{6,27} = 91.6$, $p < .001$; Figure 1a). *Potamogeton robbinsii* exhibited between 275% and 1,904% greater NPP than all other species ($p < .001$). *Elodea nuttallii* and *S. pectinata* exhibited 332% and 434% greater NPP, respectively, than *N. flexilis* ($p \le .045$).

When considering all treatments, we found significant effects of species, NaCl, turbidity and all interactions on NPP (Table 2). Moreover, when examining effects on individual species, we consistently found significant or nearly significant (i.e. $.05 < p \le .1$) interactive effects of NaCl and turbidity (Table 3a, Figure 2). A detailed description of NPP responses for each species can be found in the Appendix S1.

Three species (*P. robbinsii*, *E. nuttallii* and *N. flexilis*) exhibited a negative response to increasing NaCl treatments under both clear and turbid conditions. In clear conditions, *P. robbinsii* and *N. flexilis* exhibited a reduction in NPP only in the high-NaCl treatment, whereas *E. nuttallii* exhibited a reduction in NPP in both the intermediate- and high-NaCl treatments. Among turbid treatments, *P. robbinsii* and *N. flexilis* both exhibited a continuous reduction in NPP with increasing NaCl treatments, whereas *E. nuttallii* exhibited a sharp reduction in NPP at the intermediate- and high-NaCl treatments. Three other species (*C. demersum*, *M. spicatum* and *S. pectinata*) exhibited a unimodal response to elevated NaCl under clear

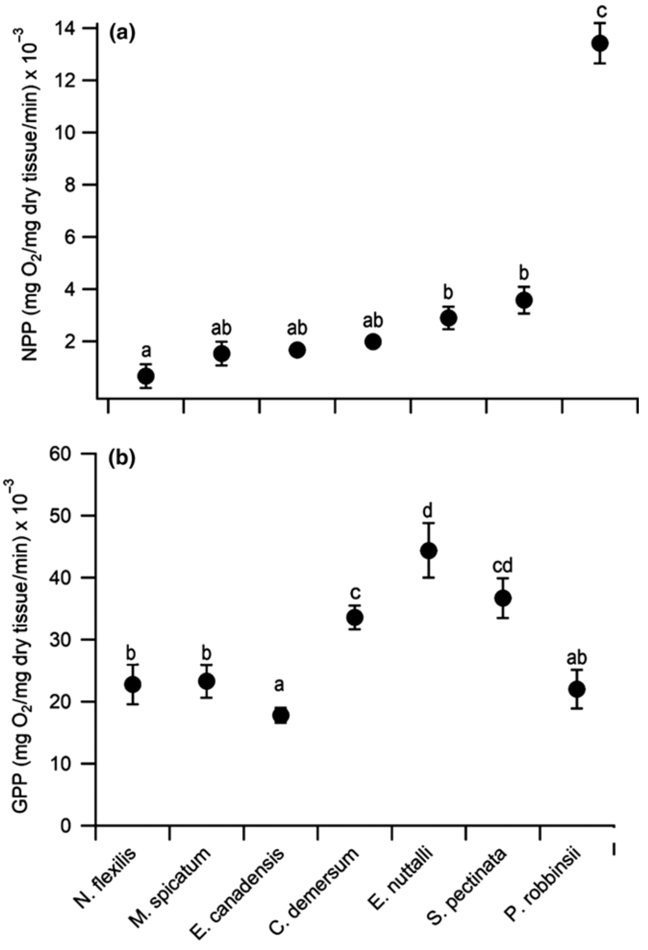

FIGURE 1 Average NPP (a) and GPP (b) of individual macrophytes species in the absence of NaCl or turbidity. For NPP, values represent actual means and bars represent ±1 *SE*. For GPP, values represent bootstrapped means and error bars represent ±95% bootstrapped CIs. All values are standardised by mg dry macrophyte tissue and by minute

TABLE 2 Results from the three-way ANOVA on macrophyte NPP and GPP. Data included all possible combinations of light- and dark-bottle replicates within treatments. We adjusted the denominator degrees of freedom to appropriately represent the true number of replicates within each treatment. Subscripts represent numerator and denominator degrees of freedom, respectively. Bold *p*-values are significant at $p \leq .05$

	NPP		GPP	
Factor	*F*	*p*	*F*	*p*
Species	$264.3_{6,164}$	**<.001**	$22.9_{6,159}$	**<.001**
Salt	$71.1_{2,164}$	**<.001**	$7.8_{2,159}$	**<.001**
Turbidity	$20.8_{1,164}$	**<.001**	$10.2_{1,159}$	**.002**
Salt × Turbidity	$13.5_{2,164}$	**<.001**	$6.7_{2,159}$	**.002**
Species × Turbidity	$11.4_{6,164}$	**<.001**	$2.7_{6,159}$	**.017**
Species × Salt	$41.9_{12,164}$	**<.001**	$25.6_{12,159}$	**<.001**
Species × Salt × Turbidity	$6.8_{12,164}$	**<.001**	$5.6_{12,159}$	**<.001**

GPP, gross primary productivity; NPP, net primary productivity.

conditions. Under turbid conditions, we observed a similar response for *S. pectinata* whereas *C. demersum* and *M. spicatum* exhibited consistently positive and negative responses to elevated NaCl, respectively. In contrast to all other species, *E. canadensis* exhibited a positive response to high NaCl under both clear and turbid conditions.

Regarding effects of turbidity within NaCl treatments, we found variable effects among species. Turbidity consistently reduced NPP of *P. robbinsii* at all levels of NaCl, whereas it only reduced NPP of *E. nuttallii* in the intermediate-NaCl treatment and of *S. pectinata* in the high-NaCl treatment. In contrast, turbidity increased NPP of *C. demersum* and *N. flexilis*, but only in the high- and low-NaCl treatments, respectively. *Elodea canadensis* and *M. spicatum* exhibited mixed effects of turbidity within NaCl treatments; *E. canadensis* exhibited an increase in NPP in the high-NaCl treatment and a decrease in the intermediate-NaCl treatment, whereas *M. spicatum* exhibited an increase in NPP in the low-NaCl treatment and a decrease in the high-NaCl treatment.

3.2 | GPP

When considering the effect of macrophytes species in the absence of both turbidity and elevated NaCl, we found a substantial difference in GPP among macrophyte species ($F_{6,28} = 6.2$, $p < .001$). The order of responses differed from the order of responses for NPP (Figure 1b). *Elodea nuttallii* exhibited 32%–149% greater GPP than all species except *S. pectinata*. *Ceratophyllum demersum* and *S. pectinata* exhibited 44%–52% greater GPP than *M. spicatum*, *N. flexilis*, *P. robbinsii*, and *E. canadensis*. *Najas flexilis* and *M. spicatum* exhibited 28% and 24% greater GPP, respectively, than *E. canadensis*.

When considering all treatments, we found significant effects of species, NaCl, turbidity and all interactions on macrophyte GPP (Table 2). Moreover, when examining effects on individual species, we found significant or nearly significant interactive effects of NaCl and turbidity on all species except *P. robbinsii* and *S. pectinata* (Table 3b, Figure 3). A full description of GPP responses can be found in the Appendix S1.

Among treatments, patterns of GPP for five of the macrophyte species (*E. canadensis*, *M. spicatum*, *N. flexilis* and *S. pectinata*) paralleled their NPP responses. For *P. robbinsii*, the pattern of GPP was reverse that of NPP; specifically, GPP increased with increasing salinity under both clear and turbid conditions. For *C. demersum*,

TABLE 3 Results from the two-way ANOVAs for each macrophytes species. Data included all possible combinations of light- and dark-bottle replicates within treatments. We adjusted the denominator degrees of freedom to appropriately represent the true number of replicates within each treatment. Subscripts represent numerator and denominator degrees of freedom, respectively. Bold *p*-values are significant at $p \leq .05$; italicised values are significant at $p \leq .1$

	Salt		Turbidity		Salt × Turbidity	
	F	*p*	*F*	*p*	*F*	*p*
(a) NPP						
Potamogeton robbinsii	$152.5_{2,24}$	**<.001**	$58.6_{1,24}$	**<.001**	$4.2_{2,24}$	**.027**
Stuckenia pectinata	$28.4_{2,24}$	**<.001**	$14.7_{1,24}$	**<.001**	$3.6_{2,24}$	**.043**
Myriophyllum spicatum	$24.8_{2,24}$	**<.001**	$0.1_{1,24}$	.795	$30.0_{2,24}$	**<.001**
Elodea canadensis	$28.5_{2,24}$	**<.001**	$0.1_{1,24}$	.781	$5.5_{2,24}$	**.011**
Elodea nuttallii	$23.2_{2,21}$	**<.001**	$0.8_{1,21}$	.385	$2.9_{2,21}$	*.079*
Najas flexilis	$20.9_{2,24}$	**<.001**	$2.2_{1,24}$	.152	$4.7_{2,24}$	**.019**
Ceratophyllum demersum	$19.5_{2,23}$	**<.001**	$0.9_{1,23}$	.344	$2.7_{2,23}$	*.090*
(b) GPP						
Potamogeton robbinsii	$58.7_{2,24}$	**<.001**	$<0.1_{1,24}$	.902	$2.1_{2,24}$	.139
Stuckenia pectinata	$18.3_{2,23}$	**<.001**	$25.7_{1,24}$	**<.001**	$1.1_{2,24}$	.337
Myriophyllum spicatum	$15.9_{2,24}$	**<.001**	$0.3_{1,24}$	.564	$21.9_{2,24}$	**<.001**
Elodea canadensis	$55.2_{2,24}$	**<.001**	$0.4_{1,24}$	.550	$5.4_{2,24}$	**.012**
Elodea nuttallii	$5.2_{2,18}$	**.017**	$1.8_{1,18}$	.196	$3.0_{2,18}$	*.074*
Najas flexilis	$11.7_{2,23}$	**.001**	$1.4_{1,23}$	.248	$2.9_{2,23}$	*.077*
Ceratophyllum demersum	$17.1_{2,23}$	**<.001**	$2.0_{1,23}$	.652	$5.4_{2,23}$	**.012**

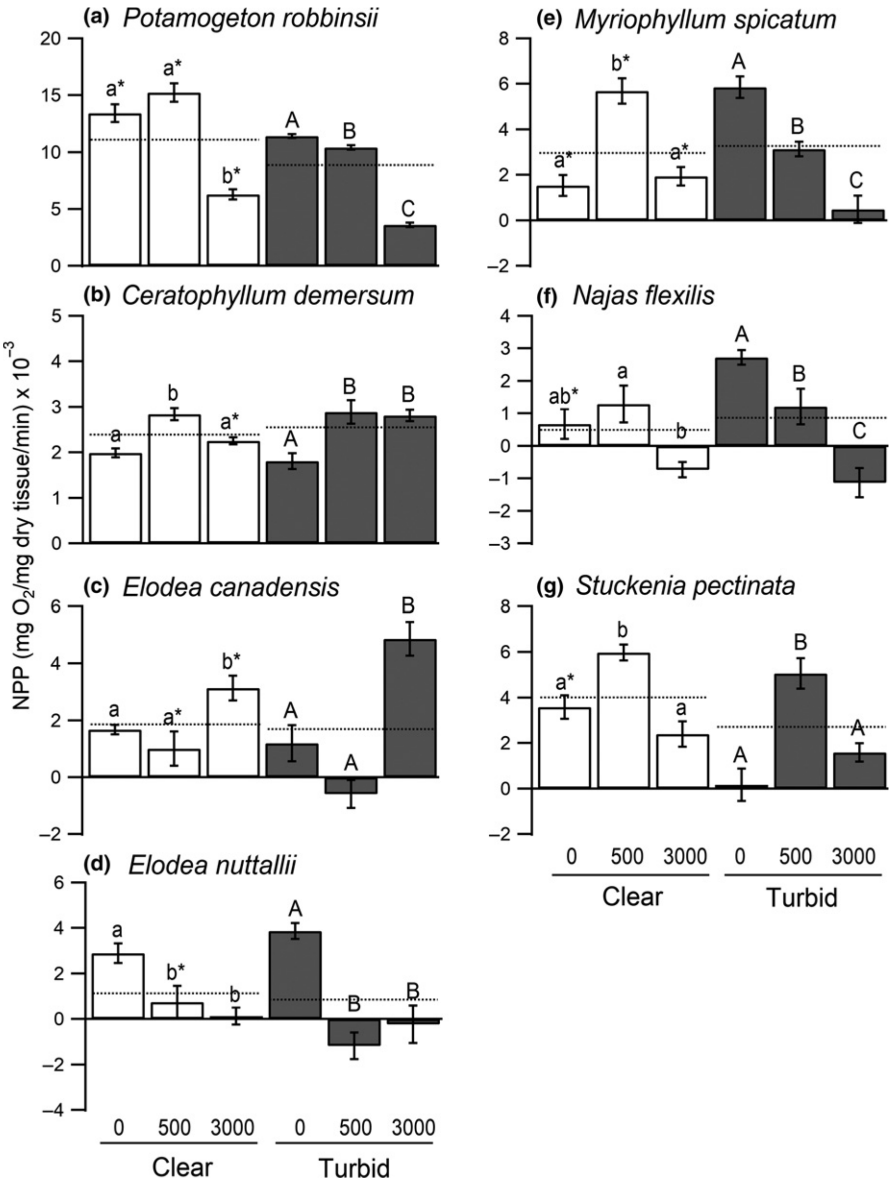

FIGURE 2 Average NPP of all NaCl treatments within both clear (white bars) and turbid conditions (grey bars) for (a) *Potamogeton robbinsii*, (b) *Ceratophyllum demersum*, (c) *Elodea canadensis*, (d) *Elodea nuttallii*, (e) *Myriophyllum spicatum*, (f) *Najas flexilis* and (g) *Stuckenia pectinata*. All values are standardised by mg dry macrophyte tissue and by minute. Dotted lines represent averages across salt treatments within clear and turbid treatments. Letters above bars indicate differences among treatments within either clear (lowercase letters) or turbid conditions (capital letters). Asterisks next to letters indicate differences between clear and turbid conditions within NaCl treatments. Error bars represent ±1 *SE*

there was an increase in GPP with elevated Cl^- concentrations under clear conditions that plateaued at the intermediate-NaCl treatment. In contrast, there was a continuous increase in GPP at each elevated NaCl treatment under turbid conditions. For *E. nuttallii*, we saw a similar trend in NPP and GPP under clear conditions, whereas we saw a sharp increase in GPP in the high NaCl under turbid conditions.

4 | DISCUSSION

Our study examined the independent and interactive effects of NaCl contamination and turbidity on the productivity of seven macrophyte species under semi-controlled conditions. When considering both NPP and GPP, we found substantial interspecific variation to elevated NaCl levels including positive, negative and unimodal responses. Although average effects of turbidity were often subtle, we generally found neutral or negative responses on NPP. However, we found myriad interactions between NaCl treatments and turbidity. Moreover, we found that the combination of stressors can interact to produce non-additive effects on productivity. This finding is important, since these two disturbances often co-occur in nature, particularly in regions where stormwater run-off is the predominant vehicle that transports salt contaminants to freshwater systems.

4.1 | Effect of NaCl under clear conditions

We hypothesised that elevated NaCl should generally reduce the productivity of freshwater macrophytes. Fully submerged plants must maintain turgor pressure within cells, which becomes increasingly difficult at high salt levels that draw water out of cell vacuoles (Parida & Das, 2005). Excess Na^+ can also disrupt physiological processes (e.g. enzyme activity; Hart et al., 1991). In partial support of this hypothesis, we found that both *P. robbinsii* and *E. nuttallii*

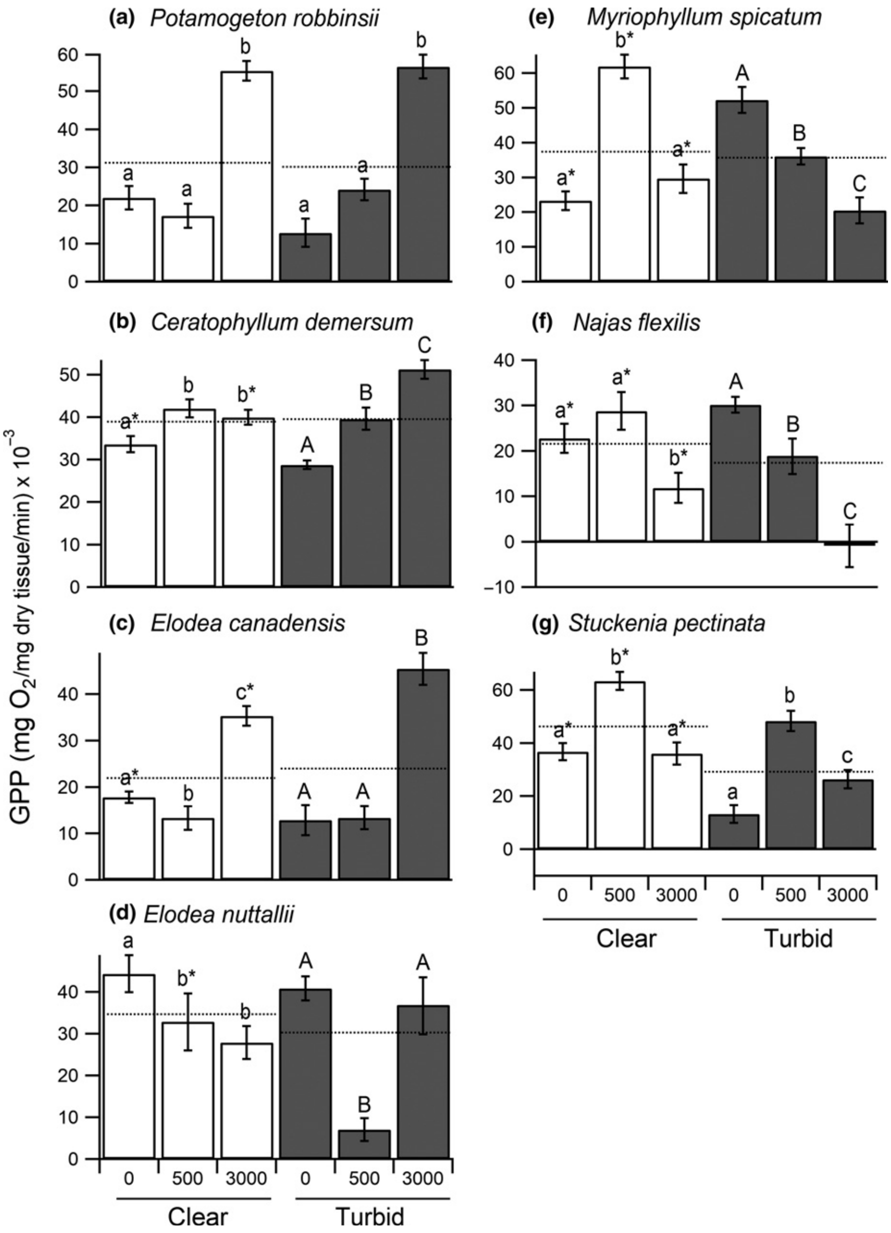

FIGURE 3 Average GPP of all NaCl treatments within both clear (white bars) and turbid conditions (grey bars) for (a) *Potamogeton robbinsii*, (b) *Ceratophyllum demersum*, (c) *Elodea canadensis*, (d) *Elodea nuttallii*, (e) *Myriophyllum spicatum*, (f) *Najas flexilis* and (g) *Stuckenia pectinata*. Values represent bootstrapped means from all possible combinations of light- and dark-bottle responses within treatments. Interpretation of dotted lines, letters and symbols is as in Figure 2. Error bars represent ±95% bootstrapped CIs. Note that we did not detect any interaction between NaCl and turbidity for *P. robbinsii* or *S. pectinata*, and we have only separated the treatments for ease of interpretation

exhibited a sharp decline in NPP with increasing Cl^- concentration. For *P. robbinsii*, this decline was associated with a concurrent increase in GPP, indicating that the bulk of energy produced was used for cell maintenance under stressful conditions. Surveys indicate that this species is highly sensitive to anthropogenic presence and is rarely found in waters with Cl^- content greater than 3 mg Cl^- L^{-1} (Pip, 1987). In contrast, surveys indicate that *E. nuttallii* is highly resistant to eutrophication and turbidity (Thiébaut & Muller, 1999), although no study has directly assessed the effects of elevated salinity on this species. One possible explanation for the decline of *E. nuttallii* NPP at elevated NaCl might be that the plant slows growth when it is stressed. Indeed, our observation of a concurrent decline in GPP indicates that both energy acquisition and usage declined with elevated NaCl. Further experimentation could investigate this possibility by removing *E. nuttallii* from salinity stress and observing subsequent productivity.

Under clear conditions, the remaining macrophyte species exhibited either a positive or unimodal response in which NPP and GPP both peaked at the intermediate-NaCl treatment. This contrasts with our hypothesis, yet it is important to note that nearly all past assessments of macrophyte tolerance to elevated salinity have only examined the effects of Cl^- concentrations >1,000 mg/L. Although these studies collectively indicate that salt contamination reduces macrophyte growth, it is possible that low amounts of Na^+ and Cl^- can benefit some plants. Haller et al. (1974) demonstrated that some macrophyte species exhibit an increase in growth up to 3 g NaCl L^{-1} (1.8 g Cl^- L^{-1}). Indeed, Cl^- is an essential ion needed for photoreduction of oxygen in plants (Bollard & Butler, 1966). Alternatively, plants exposed to non-lethal amounts of Cl^- might increase energy production to compensate for energetic losses due to salt-induced damage. Parida and Das (2005) detail the numerous biochemical pathways involved in allowing macrophytes to cope with elevated salinity, including mechanisms that facilitate water retention, protect chloroplast function and maintain ion homeostasis. The salinity level at which a plant can no longer produce sufficient energy for cellular maintenance and subsequently begins to die will likely depend on the species as well as the duration of exposure.

4.2 | Effect of turbidity and interaction with NaCl

We found that turbidity induced negative, positive and neutral effects on both GPP and NPP of individual macrophyte species. Turbidity significantly reduced NPP of *P. robbinsii* at all NaCl levels and of *S. pectinata* at the low-NaCl level. One likely explanation for this result is a reduction in photosynthesis following light limitation from sediment in the water column and particles that temporarily settled on leaf surfaces. Turbidity also induced a reduction in the GPP of *S. pectinata*, indicating declining productivity and growth. Given that this species has a relatively shallow maximum depth (*c.* 3 m; Sheldon & Boylen, 1977), *S. pectinata* is likely to be strongly affected by light limitation induced by turbid conditions. In contrast, *P. robbinsii* has a relatively deep maximum depth and is more likely to tolerate temporary or extended reductions in light availability through lower growth rates. In support of this, we found no effect of turbidity on GPP for this species.

In contrast to the responses of *P. robbinsii* and *S. pectinata*, we found that both NPP and GPP increased for *M. spicatum* and *N. flexilis* under turbid and low-NaCl conditions. Both of these species have relatively deep maximum depths and are likely able to absorb sufficient light for growth at these depths. *Myriophyllum spicatum* is particularly well known for tolerating turbid conditions and can form tall, underwater monocultures. Indeed, the tolerance of *M. spicatum* to turbidity might provide one explanation for how it has established itself as a prolific invader in many human-impacted freshwater systems. In addition, storm events, wave action, run-off and wind that generate small amounts of turbidity can benefit CO_2 and nutrient uptake of some species by generating movement around the leaf surface and reducing the boundary layer through which gases must diffuse to the leaf surface (Madsen et al., 2001). Future work that separates the effects of light limitation, nutrient limitation, and water movement is needed to fully determine the mechanism underlying the effects of physical disturbance on macrophyte productivity.

When we combined turbid conditions with elevated NaCl, *P. robbinsii*, *E. nuttallii*, *M. spicatum*, *N. flexilis* and *S. pectinata* exhibited either no effect or at least one instance of reduced NPP relative to clear conditions. We observed concurrent increases in GPP for *P. robbinsii*, *C. demersum* and *E. nuttallii*, suggesting that the plants shifted allocation of energy to cellular maintenance (Parida & Das, 2005). It is likely that a sufficient shift of energy towards cellular maintenance will eventually lead to plant death. For both *M. spicatum* and *N. flexilis*, the high-NaCl treatment induced a further decline in NPP and GPP relative to intermediate-NaCl treatments, which suggests that energy production and use has stagnated or the plant stems had died. Rapid plant death is likely to promote microbial decomposition, which would lead to a sharp increase in apparent respiration and apparent GPP, as was observed with *E. nuttallii*. Although the salt tolerance of many species is mainly anecdotal and reliant on survey data, there is evidence that most of the species in our study can survive in brackish water, with the possible exception of *P. robbinsii* (Beck et al., 2010; Borgnis & Boyer, 2016; Davis & Brinson, 1980; Pip, 1987). Hence, our study demonstrates that the combination of turbidity and salt stress can act synergistically to reduce the productivity of some macrophyte species.

Not all species in our study exhibited a synergistic response to the combination of stressors. Specifically, *C. demersum* and *E. canadensis* exhibited increased NPP and GPP when placed in turbid conditions with elevated NaCl. Both species are highly tolerant to elevated salinity and are capable of absorbing nutrients through both shoots and roots (Borgnis & Boyer, 2016; Davis & Brinson, 1980; Izzati, 2016). Incubation trials revealed that *C. demersum* is tolerant of salinity up to 5 ppt (i.e. 5 g soluble salt L^{-1}; Izzati, 2016) and is relatively tolerant to low-light conditions (Davis & Brinson, 1980). *Elodea canadensis* is among the most rapidly spreading macrophyte species in Europe, is often considered a nuisance species in its native ranges due to immense biomass accumulation and can grow faster in brown, carbon-rich water relative to clear water (Mormul, Ahlgren, Ekvall, Hansson, & Brönmark, 2012; Nichols & Shaw, 1986). It is important to note that *M. spicatum* exhibits the same characteristics as *E. canadensis*, yet *M. spicatum* exhibited an entirely opposite response to the combination of stressors. Indeed, previous studies have found that *M. spicatum* exhibits vigorous growth at 20 g NaCl L^{-1} (12.1 g Cl^{-} L^{-1}) and can withstand tidal fluctuations (Mataraza, Terrell, Munson, & Canfield, 1999; Nichols & Shaw, 1986). One possible reason for the difference in response between *E. canadensis* and *M. spicatum* might be the fragility of the latter's leaves and their susceptibility to breakage. Dispersal of *M. spicatum* is predominantly through the spread of vegetative fragments, such as those that adhere to boats. Bruckerhoff, Havel, and Knight (2015) demonstrated that small fragments have a low tolerance to desiccation stress relative to full stems; small fragments might be similarly unable to tolerate salt stress. We did observe a greater number of *M. spicatum* fragments in turbid jars relative to other macrophytes species. Further work must be done to determine whether stem fragility is a trait that determines the response of macrophytes to multiple stressors.

5 | CONCLUSIONS

Our study demonstrates that combinations of anthropogenic disturbances, including both physical and chemical stressors, can have positive and negative effects on the productivity of common macrophytes species. These results reiterate the necessity of conducting studies that examine the range of species responses to both isolated and combined stressors. In contrast to most theory purporting that invasive species are likely to be those that thrive in disturbed systems, we found that two native species exhibited the greatest productivity in treatments with turbid conditions and high NaCl. Hence, human activity might aid management efforts to eradicate invasive species, yet it is also likely to generate a large biomass of native species that are of equal nuisance to landowners, given that it lowers the recreational value of a lake. Moreover, local efforts to lower native or invasive macrophyte biomass often include activities that further increase turbidity (e.g. raking, handcutting, dredging and spraying of herbicides that leads to increase phytoplankton biomass). Our results suggest that such efforts might generate a positive feedback loop which exacerbates macrophyte growth.

As with any study, applicability of the results is limited by a choice of treatments and experimental venue. It is important to note that our experimental design limited intraspecific variation within macrophyte species using shoots from the same lake. Intraspecific variation in stress tolerance can be ecologically relevant, and future studies should question the magnitude of this effect (Hester, Mendelssohn, & McKee, 1998). The Cl^- concentrations that we used in our study represent the high end of the contamination spectrum among natural wetlands and lakes. However, the unimodal results observed in our study suggest that the effects of Cl^- might not be linear and that low concentrations can have sublethal effects on productivity. Further research in artificial mesocosms or natural ecosystems at a wider range of salt concentrations is needed to fully understand the interaction between Cl^- contamination and turbidity. It is also imperative that future studies explore the effects of alternative de-icing salt formulations (e.g. $MgCl_2$), which are becoming more prevalent due to their greater effectiveness at lower air temperatures. Although most alternative salts share a common anion (i.e. Cl^-), recent work suggests that they can have very different effects on aquatic organisms due to difference in cations (Schuler et al., 2017). Moreover, there is increasing evidence that aquatic plants and animals might evolve tolerance to chronic salt contamination that is characteristic of many freshwater systems near roadways and other human development (Coldsnow, Mattes, Hintz, & Relyea, 2017; Daley, Potter, & McDowell, 2009; James, Cant, & Ryan 2003). Further research that examines the response of macrophytes under extended exposure to salt contamination is likely to provide a greater understanding for how aquatic communities have changed and will continue to change in the future.

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REFERENCES

Asplund, T. R. (2000). *The effects of motorized watercraft on aquatic ecosystems*. Madison, WI: Wisconsin Department of Natural Resources, Bureau of Integrated Science Services.

Beck, M. W., Hatch, L. K., Vondracek, B., & Valley, R. D. (2010). Development of a macrophyte-based index of biotic integrity for Minnesota lakes. *Ecological Indicators*, *10*(5), 968–979. https://doi.org/10.1016/j.ecolind.2010.02.006

Bollard, E. G., & Butler, G. W. (1966). Mineral nutrition of plants. *Annual Review of Plant Physiology*, *17*(1), 77–112. https://doi.org/10.1146/annurev.pp.17.060166.000453

Borgnis, E., & Boyer, K. E. (2016). Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the Upper San Francisco Estuary. *Estuaries and Coasts*, *39*(3), 707–717. https://doi.org/10.1007/s12237-015-0033-5

Brix, H. (1994). Functions of macrophytes in constructed wetlands. *Water Science and Technology*, *29*(4), 71–78.

Brogan, W. R. III, & Relyea, R. A. (2015). Submerged macrophytes mitigate direct and indirect insecticide effects in freshwater communities. *PLoS ONE*, *10*(5), e0126677. https://doi.org/10.1371/journal.pone.0126677

Brogan, W. R. III, & Relyea, R. A. (2017). Multiple mitigation mechanisms: Effects of submerged plants on the toxicity of nine insecticides to aquatic animals. *Environmental Pollution*, *220*, 688–695. https://doi.org/10.1016/j.envpol.2016.10.030

Bruckerhoff, L., Havel, J., & Knight, S. (2015). Survival of invasive aquatic plants after air exposure and implications for dispersal by recreational boats. *Hydrobiologia*, *746*(1), 113–121. https://doi.org/10.1007/s10750-014-1947-9

Burks, R. L., Mulderij, G., Gross, E., Jones, I., Jacobsen, L., Jeppesen, E., & Van Donk, E. (2006). Center stage: The crucial role of macrophytes in regulating trophic interactions in shallow lake wetlands. In R. Bobbink, B. Beltman, J. T. A. Verhoeven, & D. F. Whigham (Eds.), *Wetlands: Functioning, biodiversity conservation, and restoration* (pp. 37–59). Berlin and Heidelberg: Springer. https://doi.org/10.1007/978-3-540-33189-6

Cañedo-Argüelles, M., Hawkins, C. P., Kefford, B. J., Schäfer, R. B., Dyack, B. J., Brucet, S., . . . Coring, E. (2016). Saving freshwater from salts. *Science*, *351*(6276), 914–916. https://doi.org/10.1126/science.aad3488

Canty, A., & Ripley, B. (2017). *boot: Bootstrap R (S-Plus) Functions*. R package version 1.3-18.

Carignan, R., & Kalff, J. (1980). Phosphorus sources for aquatic weeds: Water or sediments? *Science*, *207*(4434), 987–989. https://doi.org/10.1126/science.207.4434.987

Carpenter, S. R., & Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic botany*, *26*, 341–370. https://doi.org/10.1016/0304-3770(86)90031-8

Coldsnow, K. D., Mattes, B. M., Hintz, W. D., & Relyea, R. A. (2017). Rapid evolution of tolerance to road salt in zooplankton. *Environmental Pollution*, *222*, 367–373. https://doi.org/10.1016/j.envpol.2016.12.024

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1824), 20152592.

Crossley, M. N., Dennison, W. C., Williams, R. R., & Wearing, A. H. (2002). The interaction of water flow and nutrients on aquatic plant growth. *Hydrobiologia*, *489*(1), 63–70. https://doi.org/10.1023/A:1023298302557

Daley, M. L., Potter, J. D., & McDowell, W. H. (2009). Salinization of urbanizing New Hampshire streams and groundwater: Effects of road salt and hydrologic variability. *Journal of the North American Benthological Society*, *28*(4), 929–940. https://doi.org/10.1899/09-052.1

Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology letters*, *11*(12), 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x

Davis, G. J., & Brinson, M. M. (1980). Responses of submersed vascular plant communities to environmental change. No. 79/33. US Fish and Wildlife Service.

Dodds, W. K., Perkin, J. S., & Gerken, J. E. (2013). Human impact on freshwater ecosystem services: A global perspective. *Environmental Science & Technology*, *47*(16), 9061–9068. https://doi.org/10.1021/es4021052

Environment Canada (2001). Priority substances list assessment report. Road salts. Environment Canada, Gatineau, Canada. Retrieved from http://www.hc-sc.gc.ca/ewh-semt/pubs/contaminants/psl2-lsp2/road_salt_sels_voirie/index-eng.php

Findlay, S. E. G., & Kelly, V. R. (2011). Emerging indirect and long-term road salt effects on ecosystems. *Annals of the New York Academy of Sciences*, *1223*(1), 58–68. https://doi.org/10.1111/j.1749-6632.2010.05942.x

Fleeger, J. W., Carman, K. R., & Nisbet, R. M. (2003). Indirect effects of contaminants in aquatic ecosystems. *Science of the Total Environment*, *317*(1), 207–233. https://doi.org/10.1016/S0048-9697(03)00141-4

Fox, J., Weisberg, S., & Bates, D. (2018). *car: Companion to Applied Regression*. R package version 2.0-2.

French, G. T., & Moore, K. A. (2003). Interactive effects of light and salinity stress on the growth, reproduction, and photosynthetic capabilities of *Vallisneria americana* (wild celery). *Estuaries*, *26*(5), 1255–1268. https://doi.org/10.1007/BF02803628

Haller, W. T., Sutton, D. L., & Barlowe, W. C. (1974). Effects of salinity on growth of several aquatic macrophytes. *Ecology*, *55*(4), 891–894. https://doi.org/10.2307/1934427

Hart, B. T., Bailey, P., Edwards, R., Hortle, K., James, K., McMahon, A., . . . Swadling, K. (1991). A review of the salt sensitivity of the Australian freshwater biota. *Hydrobiologia*, *210*(1–2), 105–144. https://doi.org/10.1007/BF00014327

Hester, M. W., Mendelssohn, I. A., & McKee, K. L. (1998). Intraspecific variation in salt tolerance and morphology in *Panicum hemitomon* and *Spartina alterniflora* (Poaceae). *International Journal of Plant Sciences*, *159*(1), 127–138. https://doi.org/10.1086/297530

Izzati, M. (2016). Salt Tolerance of Several Aquatic Plants. *Proceeding International Conference on Global Resource Conservation*, *6*(1), 154–157.

James, K. R., & Hart, B. T. (1993). Effect of salinity on four freshwater macrophytes. *Marine and Freshwater Research*, *44*(5), 769–777. https://doi.org/10.1071/MF9930769

James, K. R., Cant, B., & Ryan, T. (2003). Responses of freshwater biota to rising salinity levels and implications for saline water management: A review. *Australian Journal of Botany*, *51*, 703–713. https://doi.org/10.1071/BT02110

Jeppesen, E., Sondergaard, E., Sondergaard, M., & Christofferson, K. (2012). *The structuring role of submerged macrophytes in lakes*, *Volume 131 of Ecological Studies Series*. New York, NY: Springer Science & Business Media.

Kaushal, S. S. (2016). Increased salinization decreases safe drinking water. *Environmental Science & Technology*, *50*, 2765–2766. https://doi.org/10.1021/acs.est.6b00679

Kerby, J. L., Richards-Hrdlicka, K. L., Storfer, A., & Skelly, D. K. (2010). An examination of amphibian sensitivity to environmental contaminants: Are amphibians poor canaries? *Ecology letters*, *13*(1), 60–67. https://doi.org/10.1111/j.1461-0248.2009.01399.x

Lavorel, S., & Garnier, É. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Liddle, M. J., & Scorgie, H. R. A. (1980). The effects of recreation on freshwater plants and animals: A review. *Biological conservation*, *17*(3), 183–206. https://doi.org/10.1016/0006-3207(80)90055-5

Madsen, T. V., & Cedergreen, N. (2002). Sources of nutrients to rooted submerged macrophytes growing in a nutrient-rich stream. *Freshwater Biology*, *47*(2), 283–291. https://doi.org/10.1046/j.1365-2427.2002.00802.x

Madsen, J. D., Chambers, P. A., James, W. F., Koch, E. W., & Westlake, D. F. (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia*, *444*(1), 71–84. https://doi.org/10.1023/A:1017520800568

Mataraza, L. K., Terrell, J. B., Munson, A. B., & Canfield, D. E. Jr (1999). Changes in submersed macrophytes in relation to tidal storm surges. *Journal of Aquatic Plant Management*, *37*, 3–12.

Mormul, R. P., Ahlgren, J., Ekvall, M. K., Hansson, L., & Brönmark, C. (2012). Water brownification may increase the invasibility of a submerged non-native macrophyte. *Biological Invasions*, *14*(10), 2091–2099. https://doi.org/10.1007/s10530-012-0216-y

Nichols, S. A., & Shaw, B. H. (1986). Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. *Hydrobiologia*, *131*(1), 3–21. https://doi.org/10.1007/BF00008319

Parida, A. K., & Das, A. B. (2005). Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety*, *60*(3), 324–349. https://doi.org/10.1016/j.ecoenv.2004.06.010

Payton, M. E., Greenstone, M. H., & Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science*, *3*(1), 34.

Pip, E. (1987). Species richness of aquatic macrophyte communites in Central Canada. *Aquatic Ecology*, *21*(2), 159–165.

Relyea, R., & Hoverman, J. (2006). Assessing the ecology in ecotoxicology: A review and synthesis in freshwater systems. *Ecology Letters*, *9*(10), 1157–1171. https://doi.org/10.1111/j.1461-0248.2006.00966.x

Sadowski, E. (2002). The impacts of chloride concentrations on wetlands and amphibian distribution in the Toronto region. *Prairie Perspectives*, *5*, 144–162.

Schuler, M. S., Hintz, W. D., Jones, D. K., Lind, L. A., Mattes, B. M., Stoler, A. B., . . . Relyea, R. A. (2017). How common road salts and organic additives alter freshwater food webs: In search of safer alternatives. *Journal of Applied Ecology*, *54*(5), 1353–1361. https://doi.org/10.1111/1365-2664.12877

Schwarzenbach, R. P., Escher, B. I., Fenner, K., Hofstetter, T. B., Johnson, C. A., von Guntin, U., & Wehrli, B. (2006). The challenge of micropollutants in aquatic systems. *Science*, *313*, 1072–1077. https://doi.org/10.1126/science.1127291

Sheldon, R. B., & Boylen, C. W. (1977). Maximum depth inhabited by aquatic vascular plants. *American Midland Naturalist*, *97*(1), 248–254. https://doi.org/10.2307/2424706

Sriyaraj, K., & Shutes, R. B. E. (2001). An assessment of the impact of motorway runoff on a pond, wetland and stream. *Environment International*, *26*(5), 433–439. https://doi.org/10.1016/S0160-4120(01)00024-1

Strayer, D. L., & Findlay, S. E. G. (2010). Ecology of freshwater shore zones. *Aquatic Sciences*, *72*(2), 127–163. https://doi.org/10.1007/s00027-010-0128-9

Thiébaut, G., & Muller, S. (1999). A macrophyte communities sequence as an indicator of eutrophication and acidification levels in weakly mineralised streams in north-eastern France. *Developments in Hydrobiology*, *Man and River Systems* (pp. 17–24). Dordrecht, The Netherlands: Springer.

Tiner, R. W. (2009). *Field guide to tidal wetland plants of the northeastern United States and neighboring Canada: Vegetation of beaches, tidal flats, rocky shores, marshes, swamps, and coastal ponds*. Amherst, MA: University of Massachusetts Press.

U.S. E.P.A. (1988). *Office of Water, Regulations, and Standards, Criteria and Standards Division*. Ambient Water Quality Criteria for Chloride. EPA Pub. No. 440588001. Environmental Protection Agency, Washington, DC, USA.

Volkmann, C., Halbedel, S., Voss, M., & Schubert, H. (2016). The role of dissolved organic and inorganic nitrogen for growth of macrophytes in coastal waters of the Baltic Sea. *Journal of Experimental Marine Biology and Ecology*, *477*, 23–30. https://doi.org/10.1016/j.jembe.2016.01.005

Wang, W. H., & Ji, M. (2007). Comparison on salt tolerance of nine submerged macrophytes". *Journal of Agro-Environmental Science*, *26*(4), 1259–1263.

Whitfield, A. K., & Becker, A. (2014). Impacts of recreational motorboats on fishes: A review. *Marine pollution bulletin*, *83*(1), 24–31. https://doi.org/10.1016/j.marpolbul.2014.03.055

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, *96* (4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

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