



Elodea mediates juvenile salmon growth by altering physical structure in freshwater habitats

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Abstract Invasive species introductions in high latitudes are accelerating and elevating the need to address questions of their effects on Subarctic and Arctic ecosystems. As a driver of ecosystem function, submerged aquatic vegetation is one of the most deleterious biological invasions to aquatic food webs. The aquatic plant *Elodea* spp. has potential to be a widespread invader to Arctic and Subarctic ecosystems and is already established in 19 waterbodies in Alaska, USA. *Elodea* spp. has been found to alter ecosystem processes through multiple pathways; yet little is known about the impact of *Elodea* spp. on fish life history. A primary concern is the effect of *Elodea* spp. on juvenile Pacific salmon (*Oncorhynchus* spp.), because this invading plant can form dense stands in littoral zones, potentially impacting important

freshwater rearing habitats used by juvenile fish for foraging and refuge from predators. We used a field experiment to test the effect of *Elodea* spp. on juvenile coho salmon (*O. kisutch*) growth in an infested lake near Cordova, Alaska, USA. We found that *Elodea* spp. stands result in reduced growth and a lower trophic position for juvenile coho salmon over the summer compared to habitats dominated by a native assemblage of aquatic plants. While infested sites were not associated with significant changes in water condition or primary productivity compared to sites dominated by native vegetation, zooplankton densities were reduced, and *Elodea* spp. height and vegetation richness increased macroinvertebrate densities. Combined, these results indicate that *Elodea* spp. may alter the flow of energy to juvenile salmon by restructuring space and affecting prey resources for rearing fish. Furthermore, these results suggest that widespread establishment of *Elodea* spp. may

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alter the quality of habitat for juvenile salmon and, by affecting juvenile fish growth, could lead to population-level impacts on salmon returns.

Keywords *Elodea* spp. · Coho salmon · Subarctic lake · Food webs · Fish growth

Introduction

Invasive species introductions to high-latitude (> 60° N) ecosystems are accelerating globally due to warming climate, changing land use, and increasing economic connectivity with temperate regions (Blackburn et al. 2011; Carey et al. 2016; Luizza et al. 2016; Pauchard et al. 2016; Reid et al. 2019). While prevention of invasive species introductions in high-latitude ecosystems is a primary management goal, a number of invasive species have already reached Subarctic and Arctic regions, with a growing list of negative impacts manifesting from these taxa (Wrona et al. 2006; Thiébaud et al. 2007; Chucholl 2013; Huotari and Korpelainen 2013; Carey et al. 2016). With potential to create novel ecosystems that will be difficult to manage, understanding the mechanisms through which invasive species affect aquatic ecosystems is needed to anticipate potential threats and prioritize control and eradication efforts. Exacerbating the management challenge, investigations to date in aquatic invasive species ecology have focused on tropical and temperate ecosystems. High-latitude aquatic systems, however, differ in landscape type (e.g., permafrost), seasonality (e.g., ice cover, daylight), thermal ranges, and composition amongst other factors compared to lower latitude waterbodies. Thus, the degree to which insights from tropical and temperate investigations apply in Subarctic and Arctic waters is unclear, highlighting a need for in situ investigations to advance invasive species ecology and management in high-latitude ecosystems.

In the Subarctic and Arctic region of Alaska USA, *Elodea* spp. (henceforth, ‘*Elodea*’) is the first known aquatic plant to invade Alaskan waters (Carey et al. 2016). Submerged aquatic vegetation, such as *Elodea*, has the potential to impact ecosystems by competing with native plants, forming dense monoculture stands, and changing sediment dynamics, among other stressors (Schultz and Dibble 2012; Fleming and Dibble 2014; Kolada and Kutyla 2016). These processes can

result in the deterioration of abiotic conditions by creating diel fluctuations in dissolved oxygen concentrations, altering pH levels, increasing temperature, and reducing water clarity (Kelly et al. 2015; Carey et al. 2016 and references therein). Submerged aquatic macrophytes subsequently drive changes in primary production and nutrient cycling (Carpenter and Lodge 1986; Kuehne et al. 2016). In some cases, *Elodea* can lead to ecosystem state shifts by creating cycles of algal blooms and internal nutrient loading in infested waterbodies, as observed in a boreal lake in Finland (Sarvala et al. 2020). Furthermore, by altering water quality conditions and nutrients that govern algal periphyton growth, *Elodea* has potential to alter energy flows through aquatic food webs by affecting the link between macrophytes and invertebrates (Kelly et al. 2015 and references therein; Carniatio et al. 2020).

The water quality and physical structure changes resulting from an *Elodea* infestation may affect both prey availability and foraging efficiency for fish (Schultz and Dibble 2012). Specific impacts on fish life history, however, have proved difficult to generalize as existing studies suggest *Elodea* impacts on upper trophic levels may be indirect and mediated by lower-level taxa or multiple abiotic and biotic processes. Indeed, existing field investigations demonstrate the magnitude and direction of *Elodea* impacts on lower food web components can be context dependent. For example, zooplankton abundance decreased with increasing *Elodea* density in a field enclosure experiment in a lake in southern Finland (Kornijow et al. 2005); whereas benthic macroinvertebrate density increased in *Elodea* dominated areas compared to areas of native vegetation in a lake in New Zealand (Kelly and Hawes 2005). Furthermore, *Elodea*’s influence on predator–prey interactions by providing refugia for prey, altering foraging efficiency of fish, or both is expected to be species specific (Schultz and Dibble 2012). As a result, impacts of *Elodea* (or submerged aquatic macrophytes) on specific fish taxa may be difficult to predict without direct in situ investigation.

A primary invasive species concern in Alaska is the potential risk *Elodea* may pose to Pacific salmon (*Oncorhynchus* spp.) populations that support valuable fisheries across the state (Schwoerer et al. 2019; Schwoerer et al. 2020a, b). Coho salmon (*O. kisutch*) are ecologically, culturally, and economically

important throughout their range and their anadromous life history strategies are vulnerable to an *Elodea* infestation. For example, one mechanism by which *Elodea* could affect coho salmon is by altering the freshwater habitats and food webs on which juvenile salmon rely before smolting and migrating to the ocean. Juvenile coho salmon initially emerge from spawning gravel and move to small streams or littoral zones of lakes to forage and seek refuge from predation. Juvenile coho salmon rearing habitat is characterized by low velocity backwaters, floodplains, oxbows, sloughs, beaver ponds, and off-channel habitat often containing large woody debris and vegetative cover (Bradley et al. 2017; Foley et al. 2018). Particularly in watersheds in which coho salmon use lakes as rearing habitat, *Elodea* has the potential to alter prey resources for juvenile coho salmon by changing food webs (Kelly et al. 2015), altering predation refugia for coho salmon, and changing their capture efficiency (Schultz and Dibble 2012). The importance of lakes has been demonstrated for multiple life history strategies of coho salmon and particularly for overwintering habitat (Sethi and Benolkin 2013; Sethi et al. 2021). Thus, an invasion by this submerged aquatic plant could be a driver of coho salmon populations by altering the growth and survival of juveniles.

Overall, *Elodea* can alter physical conditions and food web structure and thus may be a driver of ecosystem function in invaded ecosystems (Luizza et al. 2016; Emery-Butcher et al. 2020); yet, little is known about the ecology of *Elodea* in high-latitude ecosystems and its impact on culturally and economically important fishery resources (Carey et al. 2016). To assess the effect of *Elodea* on fish in high-latitude clines, we implemented an in-situ experiment in a subarctic lake to examine changes in ecosystem process from *Elodea* infestations and to directly measure juvenile coho salmon growth impacts attributable to *Elodea* dominated juvenile fish rearing habitats. We compared primary productivity, consumer abundance, fish trophic position, and fish growth across sites dominated by *Elodea* versus those dominated by native aquatic vegetation. Estimates of growth offer insight into the consequences of individuals' foraging and dietary experiences, providing a tool to examine the influences of *Elodea* on energy transfer to juvenile salmon in lake food webs. Our results suggest that water quality and primary productivity are robust to the presence of *Elodea*, however, *Elodea*

may restructure space in the water column and alter the availability and quality of fish prey, leading to reduced growth and a lower trophic position for juvenile coho salmon.

Methods

Field experiment The experimental setup was comprised of juvenile coho salmon feeding in enclosures dominated by native or *Elodea* vegetation. Subsequently, we compare food web structure and composition by assessing aquatic vegetation, abiotic conditions, primary productivity, macroinvertebrate communities, and juvenile coho salmon growth across enclosures. The controlled field experiment was established in McKinley Lake (60.454310°, −145.199505°), Chugach National Forest, AK in 2017 and 2018 using limnocorrals (Curry Industries Ltd., Winnipeg, Manitoba, Canada R2G 1C2). McKinley Lake supports wild populations of rearing coho salmon that contribute to salmon fisheries in Prince William Sound, AK, USA (Pellissier and Somerville 1987) and has a suspected introduction of *Elodea* that occurred prior to 2000 (Carey et al. 2016). The surface area of McKinley Lake is 114 ha, maximum depth is 11 m, and mean depth=5.1 m with annual precipitation of 3.5 m and ice cover lasting 5–7 months (Pellissier and Somerville 1987). It is considered a clear water lake, with turbidity ranging from 0.56 to 1.64 Nephelometric Turbidity Units (as measured in 2017). In June, six limnocorrals (5 m diameter×2 m depth; sidewalls with 4.76 mm mesh) were installed in the littoral zone at a depth of ~1.5 m across three bays of the lake. In each bay, we paired treatment levels with one limnocorral with *Elodea* dominated habitats (henceforth, the '*Elodea* treatment') and one limnocorral with native vegetation dominated habitats (henceforth, the 'native vegetation treatment'). Percent canopy cover of rooted vegetation was visually estimated by a snorkeler at the beginning and end of the experiment. No acceptable locations in the lake for deploying the limnocorrals were completely free of *Elodea*. Furthermore, the limnocorrals were installed at the beginning of the seasonal vegetation growth, thereby increasing the difficulty in predicting the exact amount of vegetation and native species richness within each enclosure, as *Elodea* grows earlier than native species (Thiébaud

2005). Surveying the lake bottom early in the growing season also made it difficult to match native species richness between years (Figure S1). After siting the limnocorrals, all *Elodea* treatments maintained >60% *Elodea* by surface area, and the native vegetation treatments maintained <20% *Elodea* coverage throughout the study (Figure S1). Native species of submerged aquatic vegetation were primarily *Potamogeton richardsonii* and *Myriophyllum sibiricum* and included *Callitriche* sp., *Chara* sp., *Fontinalis antipyretica*, *Hippuris vulgaris*, *Isoetes* sp., *Utricularia macrorhiza*, *Nuphar lutea* ssp. *polysepala*, *P. filiformis*, *P. natans*, *P. pusillus*, *Ranunculus trichophyllus*, *Sparganium hyperboreanum*, and *Zannichellia palustris*.

Once limnocorrals were installed, we set baited minnow traps for 24 h to remove any fish within the enclosures. Subsequently, we collected juvenile coho salmon from McKinley Lake using fyke nets. We measured fork length (mm) and marked their otoliths by immersing fish in 50 ppm alizarin complexone for 4 h following methods of Zimmerman (2005). Marking the fish otoliths with alizarin complexone verified that study fish remained within the limnocorrals throughout the experiment and provided a mark to estimate growth by length specific to the experimental period. To limit further handling stress, we did not measure the mass of each fish. Limnocorrals were then each stocked with 30 individuals (density of 1.53 fish/m²; average fork length (FL) in mm = 58 ± 6 SD; FL range = 47–75 mm) in 2017 and 29 individuals (density of 1.47 fish/m²; average FL in mm = 60 ± 5 SD; FL range = 49–73 mm) in 2018. While no data exist for McKinley Lake, these stocking densities are within the range observed in nearby lentic habitats on the Copper River Delta, AK (0.03–2.11 fish/m²; Lang et al. 2006), where no evidence of density-dependent effects on juvenile coho growth was observed. Fish mortality occurred in all limnocorrals, varying amongst bays but was coinciding across treatment levels within a bay and year (Fig. 1).

Abiotic variables At the start, midpoint, and end of the experiment in 2017 and 2018, we measured temperature (°C), dissolved oxygen (mg/l), specific conductance (µs/cm), and pH using a YSI Professional Plus multiparameter meter (YSI Incorporated, Yellow Springs, OH) recording values at the surface (0.0–0.25 m), mid-depth (0.5–0.75 m), and bottom (1.0–1.5 m) of the limnocorrals for

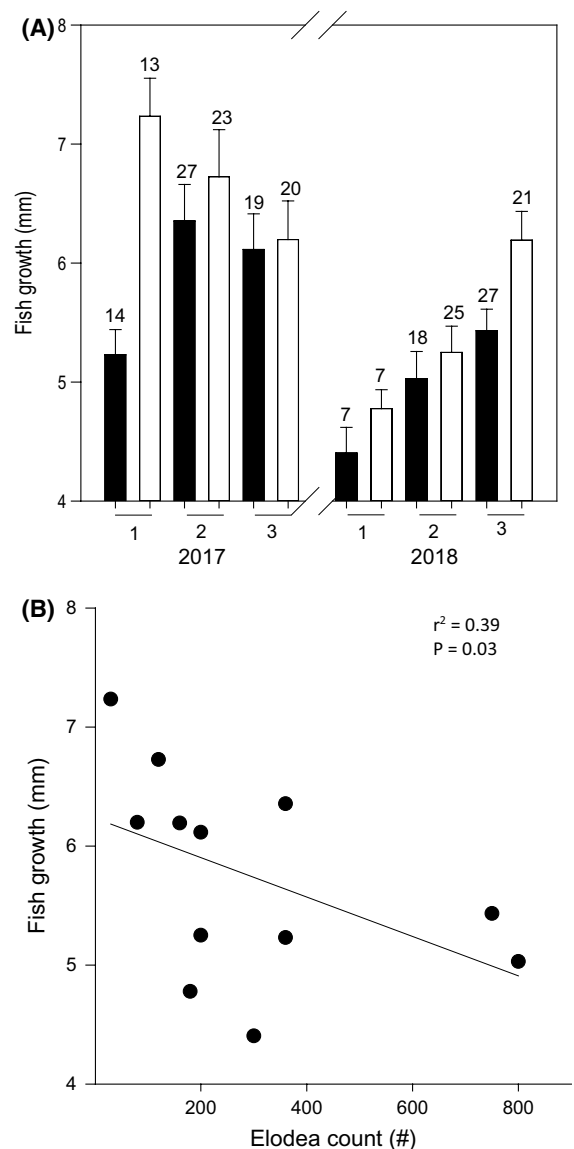


Fig. 1 **A** Differences in fish growth (=/-SE) was observed between the vegetation treatment levels of *Elodea* (filled symbols) and native (open symbols) vegetation accounting for the three bays of the experimental design and years (2017 and 2018) in McKinley Lake, AK. The number of fish collected at the end of the experiment are above each limnocorral. **B** Relationship between fish growth (mm) and *Elodea* stem count across limnocorrals in 2017 and 2018. Plotted line shows univariate normal linear regression fits on log10 transformed data

an average value throughout the water column. Throughout the experiment, water temperature was recorded continuously (every 15 min) using

TidbiT v2 temperature loggers (Onset Computer Corporation). Two temperature loggers were put into each limnocorral with one logger ~0.25 m below the water surface and one logger at ~1 m depth. We assessed the average of the temperature values from both loggers because no difference was observed between temperature loggers at the two depths within each limnocorral. Dissolved oxygen was measured in situ every 10 min with an archival probe (miniDOT® logger, Precision Measurement Engineering Inc., California, USA) at ~0.5 m depth.

Coho salmon To assess whether *Elodea* infestations affected juvenile coho salmon, we measured fish growth and energy density and characterized the trophic position and energy source of study fish using carbon and nitrogen isotopes. At the end of the experiment, stocked juvenile coho salmon were trapped from the limnocorrals using baited minnow traps and cast nets. Fish length (mm) and mass (g) was measured, and fish were immediately frozen. Subsequently, otoliths were removed and one sagittal otolith from each fish was mounted sulcus side down with Crystal Bond 509 on a microscope cover slip attached on one edge to a standard microscope slide. The otolith was then ground with 1200-grit sandpaper in the sagittal plane to the level of the nucleus (Zimmerman 2005). Using a fluorescent light (Leica EL 6000; Leica Microsystems (Switzerland) Limited) images of the otolith were taken with a Leica camera (Model: DMC6200; Leica Microsystems (Switzerland) Limited) mounted on Leica microscope (Model: M60; Leica Microsystems (Switzerland) Limited). Using Image-Pro Premier (Version: 9.2 Build 6156, 64-bit. Media Cybernetics, Inc.), two independent readers measured the distance from the nucleus of the otolith to the alizarin complexone marking and to the edge of the otolith. Aging transects occurred in the dorsal plane of the otolith approximately 135 degrees from the anterior–posterior axis. If consensus of measurements resulted in more than 0.5 mm difference in fish growth estimates, the otolith was remeasured. The proportion of otolith growth that occurred after the alizarin complexone mark (distance between alizarin complexone mark and otolith edge/distance nucleus to otolith edge) was then multiplied by the final fork length (mm) to determine growth (mm) that occurred during the experiment [Experiment Growth = Final FL x (Proportion of otolith growth)].

Prior to analyzing fish growth, we tested the effect of fish density at the end of the experiment by a linear regression of $\log_{10}$ fish growth across $\log_{10}$ final density. Variables here, and throughout the analysis, were $\log_{10}$ transformed to reduce skewness in the experimental data. Next, fish growth assessments encompassed two levels of analyses. First, fish growth was analyzed by Analysis of Variance (ANOVA) with bays nested within year as independent factors to control for potential differences between years and amongst bays. Second, we pooled data across all limnocorrals and analyzed the effect of *Elodea* on fish growth across gradients of stand density (stem count) and stand height, taking advantage of the presence of *Elodea* in all study corrals. Specifically, we implemented linear regressions of $\log_{10}$ fish growth on $\log_{10}$ *Elodea* height and *Elodea* stem count. We used the same steps to analyze fish mass at the end of the experiment with fish density, the *Elodea* and native vegetation treatment, and gradients of *Elodea* height and stem density.

In addition to fish growth and mass, we assessed study fish somatic tissue energy density using bomb calorimetry, an assessment that integrates the entire life span of the fish. Whole fish samples were placed in a freeze dryer (VirTis, Freezemobile 12) at -50°C for 48 h, homogenized with a mortar and pestle and a ≤ 150 mg pellet was pressed from a sub-sample and weighed immediately. A semimicro Parr 1425 calorimeter was used to measure somatic energy following the Parr manual (Parr Instrument Company 1994). Benzoic acid standard and duplicate tissue samples were used to evaluate the precision of the machine. Somatic energy from the calorimeter (cal g $^{-1}$ dry mass) was converted to kJ and reported per unit dry mass (kJ g $^{-1}$ dry mass). Similar to the analysis of fish growth, we tested the influence of density and then compared $\log_{10}$ somatic energy between *Elodea* and native vegetation treatments using ANOVA with bays nested within year as independent factors. Subsequently, we compared individual relationships between $\log_{10}$ *Elodea* height and *Elodea* stem count with log transformed somatic energy using linear regressions.

Fin clips were collected for stable isotope analysis and analyzed at the University of Wyoming Stable Isotope Facility (Laramie, WY USA) to determine carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and C:N ratio values for coho salmon. Fin tissue provides the appropriate

temporal scale of turnover rate (<50 days) to match the duration of the limnocorral experiment (Heady and Moore 2013). Fish tissue C:N ratio values were below 3.5; thus as recommended by Post et al. (2007) for $\delta^{13}\text{C}$ analysis in aquatic animals, we corrected $\delta^{13}\text{C}$ values using the equation $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$. We used separate ANOVAs to test possible differences in $\log_{10} \delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between *Elodea* and native vegetation treatments with bays nested within year as independent factors. We also conducted normal linear regressions to compare individual relationships between $\log_{10}$ *Elodea* height and *Elodea* stem count with $\log_{10} \delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Invertebrate communities Zooplankton and benthic macroinvertebrate communities in the sediment and lower vegetation were collected within limnocorrals at the start, midpoint, and end of the experiment each year to assess potential prey items of juvenile fish. Zooplankton were collected by combining three vertical tows of an 80- μm mesh Wisconsin net. Macroinvertebrates were collected by sweeping a 243- μm mesh D-frame sweep net (Wildco, USA) for 1 min in a 1 m^2 area, minimizing disturbance to the limnocorrals. Zooplankton and macroinvertebrate identification and abundance were completed by Ecoanalyst, Inc. (Moscow, ID, USA). Zooplankton responses of total density and taxa richness were averaged across sampling dates and compared between the *Elodea* and native vegetation treatments using an ANOVA with bays nested within year as independent factors. We did not include the Phylum Rotifera in the zooplankton analysis as rotifers are likely too small to be preferred prey of juvenile coho salmon due to their size selective foraging (Brooks and Dodson 1965). Similarly, we ran ANOVAs including bays nested within year to test macroinvertebrate total density and taxa richness responses between *Elodea* and native vegetation treatments, averaging sample collections across dates to account for the spatial variability in macroinvertebrate distribution. Next, we implemented linear regressions to assess the influence of *Elodea* stem height and *Elodea* stem count on $\log_{10}$ zooplankton and macroinvertebrate responses across limnocorral treatments.

Primary producers Chlorophyll-a and periphyton biomass were used to assess the response of primary producers to our experimental treatment. At the start, midpoint, and end of the experiment, water column

chlorophyll-a was obtained by filtering 500 ml of water onto glass fiber filters (0.7- μm pore size), extracting chlorophyll-a in 90% acetone for 24 h, and then measuring the fluorescence of the sample. At the start of the experiment in 2018, ceramic tiles were suspended at ~0.5 m depth to collect periphyton. At the end of the experiment, the standing periphyton biomass of green algae, diatoms, and cyanobacteria was measured using a portable fluorometer (Benthotech, www.bbe-oldaenke.de). Water column chlorophyll-a averaged across sampling dates was compared between the *Elodea* and native vegetation treatments using ANOVA with bays nested within year. Next, we assessed the association between $\log_{10}$ *Elodea* height and *Elodea* stem count with $\log_{10}$ averaged water column chlorophyll-a using separate normal linear regressions. Biomass of green algae, diatoms, and cyanobacteria at the end of the experiment was compared across *Elodea* and native vegetation treatments in 2018 using ANOVA.

Lake reference samples Lake reference samples were compared to samples from limnocorrals with the native vegetation treatment to assess the potential influence of the experimental enclosures on biophysical conditions. Point measurements of temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/l), conductance ($\mu\text{g}/\text{cm}$), and pH were collected at lake reference sites using the same probe and methods as described above and were similar in 2017 and 2018 (Table 1), indicating that the limnocorrals themselves were not affecting physical conditions in the experimental enclosures. Average water temperatures across limnocorrals and lake reference sites were within 1 $^{\circ}\text{C}$ at each sampling point except for lake temperature in the beginning of the experiment in 2018 (Table 1 and see Results). Zooplankton, macroinvertebrates, and chlorophyll-a were also collected in the littoral zone of the lake at ~1.5 m depth following the same procedures as within the limnocorrals. In both years, zooplankton density and macroinvertebrate density of the reference samples were within 1 SD of the limnocorral samples of the native vegetation treatment, which we interpreted as indicating a lack of significant enclosure effect. Chlorophyll-a values were also within 1 SD of the limnocorral samples in both years. In sum, comparisons of biophysical conditions across lake reference samples and limnocorrals suggest the experimental closures themselves did not alter biophysical conditions within study sites.

Table 1 Point samples at the beginning, midpoint, and end of the experiment in 2017 and 2018 for temperature (°C), dissolved oxygen (mg/l), specific conductance (µs/cm), and pH in the experimental levels (*Elodea* vs. native vegetation) and

at a lake reference site outside of the enclosures. Values were averaged (mean ± SD) from readings at the surface (0–0.25 m), mid-depth (0.5–0.75 m), and bottom (1.0–1.5 m)

Year		Temperature (°C)			Dissolved oxygen (mg/l)		
		Begin	Middle	End	Begin	Middle	End
2017	<i>Elodea</i>	15.63 ± 0.1	16.70 ± 0.2	18.20 ± 0.2	10.50 ± 0.4	9.86 ± 0.3	7.48 ± 0.5
	Native	15.64 ± 0.1	16.68 ± 0.2	18.21 ± 0.2	10.47 ± 0.5	10.17 ± 0.2	7.64 ± 0.5
	Lake	15.60 ± 0.0	16.50 ± 0.0	18.07 ± 0.1	10.63 ± 0.1	9.49 ± 0.4	8.67 ± 0.3
2018	<i>Elodea</i>	13.94 ± 1.3	16.49 ± 0.4	15.20 ± 0.7	9.38 ± 0.3	8.55 ± 0.5	7.84 ± 0.9
	Native	13.52 ± 1.7	16.56 ± 0.3	15.23 ± 0.6	9.74 ± 0.6	8.68 ± 0.3	8.17 ± 0.3
	Lake	10.20 ± 1.6	16.00 ± 0.5	14.63 ± 0.9	9.88 ± 0.2	8.80 ± 0.5	9.07 ± 0.2
Year	DOY	Specific conductance (µs/cm)			pH		
		Begin	Middle	End	Begin	Middle	End
2017	<i>Elodea</i>	25.47 ± 0.7	27.30 ± 0.9	29.12 ± 1.1	7.36 ± 0.1	7.42 ± 0.1	7.38 ± 0.2
	Native	25.39 ± 0.8	26.92 ± 1.0	29.00 ± 1.1	7.39 ± 0.2	7.39 ± 0.2	7.41 ± 0.1
	Lake	25.80 ± 0.0	28.23 ± 0.3	29.60 ± 0.0	7.53 ± 0.0	7.49 ± 0.0	7.53 ± 0.1
2018	<i>Elodea</i>	22.69 ± 2.9	24.60 ± 1.1	25.44 ± 1.6	6.30 ± 0.4	6.63 ± 0.2	6.59 ± 0.3
	Native	23.67 ± 2.3	24.58 ± 1.1	25.51 ± 2.1	6.01 ± 0.4	6.60 ± 0.2	6.62 ± 0.2
	Lake	25.53 ± 0.2	25.17 ± 0.4	26.80 ± 0.4	5.91 ± 0.0	7.06 ± 0.4	6.79 ± 0.2

Data Analysis All statistical analyses were conducted using the R statistical programming environment (R Development Core Team, 2021). ANOVAs were conducted using the ‘aov’ package and linear regression analyses utilized the ‘lm’ package. We used a significance level of 0.05 to gauge support for explanatory variables. All data that support the findings of this publication can be found in Carey (2022).

Results

Abiotic variables Point measurements of temperature (°C), dissolved oxygen (mg/l), specific conductance (µs/cm), and pH were similar throughout the water column, across treatments, and remained consistent across all limnocorrals within years, regardless of *Elodea* coverage, suggesting the presence of *Elodea* did not have a meaningful impact on abiotic conditions (Table 1). We observed slightly lower dissolved oxygen in the limnocorrals compared to the lake samples at the end of the experiment both years (Table 1). Water temperatures measured continuously in 2017 ranged between 15.5 and 20 °C, while 2018 was cooler ranging between 13 and 19 °C (Figure S2).

Water temperature temporal patterns throughout the experiment were similar across limnocorrals within bays, with the exception of two limnocorrals in 2018 that started with cooler waters initially, but then mirrored temperature trends across other limnocorrals by the second week of the study. Dissolved oxygen levels remained above 9 mg/l in all limnocorrals throughout the experiment except for 1 point in 2017 (Figure S3). We suspect the logger with a low value got tangled in the sidewall of the limnocorral and did not get an accurate reading as the drop from 9 mg/l in dissolved oxygen occurs abruptly within 10 min. In 2018, the daily average values remained above 7 mg/l throughout the experiment (Figure S3).

Growth of coho salmon Fish growth ($r^2=0.01$, $P=0.80$), somatic energy density ($r^2=0.002$, $P=0.89$), and mass ($r^2=0.13$, $P=0.26$) did not vary significantly across final fish densities (Fig. 1), indicating that density dependent effects did not influence growth outcomes between *Elodea* and native vegetation dominated food webs. We found evidence that both physical conditions and macrophyte habitats affected fish growth outcomes. Growth of coho salmon was higher in limnocorrals dominated by native macrophytes compared to those infested with

Elodea (ANOVA Treatment: $F_{1,7}=6.69$; $P=0.036$; Year $F_{1,7}=22.35$; $P=0.002$; Nested Bay $F_{2,7}=5.23$; $P=0.04$; Fig. 1A). In the warmer year (2018), fish growth averaged 6.3 mm, while in the cooler year (2017) fish growth averaged 5.2 mm, suggesting temperature was a primary determinant of growth that was modified by the vegetation treatment. An a-posterior analysis of $\log_{10}$ transformed data found a positive relationship between fish growth and warmer average daily water temperatures ($r^2=0.45$, $P=0.017$) pooling data across limnocorrals. Consistent with our comparison of fish growth across treatment levels, we found a negative relationship between higher *Elodea* stem count and individual fish growth (Fig. 1B), indicating denser *Elodea* stands were associated with lower fish growth. No relationship, however, was observed between *Elodea* height and fish growth.

While juvenile coho salmon growth differed across vegetation treatment levels, study fish maintained comparable somatic energy density (ANOVA Treatment: $F_{1,7}=0.21$; $P=0.66$; Year $F_{1,7}=3.20$; $P=0.12$; Nested Bay $F_{2,7}=0.93$; $P=0.44$). Analyses across treatment levels or pooling across limnocorrals failed to support association between coho salmon energy density and treatment level, *Elodea* height ($r^2=0.004$, $P=0.84$), or *Elodea* stem count ($r^2=0.004$, $P=0.84$). Similarly, no patterns were observed across vegetation treatment levels for fish mass (ANOVA Treatment: $F_{1,7}=0.07$; $P=0.79$; Year $F_{1,7}=3.11$; $P=0.12$; Nested Bay $F_{2,7}=0.11$; $P=0.89$) or between fish mass and *Elodea* height ($r^2=0.02$, $P=0.64$) or *Elodea* stem count ($r^2=0.10$, $P=0.32$).

Trophic position of coho salmon Overall, isotope results indicated that the *Elodea* treatment influenced the trophic position of coho salmon, with both nitrogen and carbon signatures indicating a shift in trophic level and source energy flows compared to native vegetation treatment corrals. Differences in trophic position were indicated by the ANOVA on $\delta^{15}\text{N}$ (ANOVA Treatment: $F_{1,7}=6.64$; $P=0.037$; Year $F_{1,7}=22.71$; $P=0.002$; Nested Bay $F_{2,7}=17.387$; $P=0.002$). Fish in the native vegetation treatment had higher $\delta^{15}\text{N}$ values than the *Elodea* treatment in 2017 and 2018 when individually comparing each bay (Table 2). *Elodea* characteristics (stem density, stem count) were not significantly associated with $\delta^{15}\text{N}$. No relationship was found for $\delta^{13}\text{C}$ across the vegetation treatment (ANOVA Treatment: $F_{1,7}=1.50$; $P=0.26$;

Table 2 Average nitrogen isotopes ($\delta^{15}\text{N} \pm \text{SE}$) of coho salmon (*Oncorhynchus kisutch*) fin tissue from the experimental enclosures placed in three separate bays of McKinley Lake, AK with final fish densities and sample size (n) of fish with $\delta^{15}\text{N}$ values in 2017 and 2018

Year	Bay	Treatment	$\delta^{15}\text{N}$	($\pm \text{SE}$)	N
2017	1	<i>Elodea</i>	8.89	(± 0.17)	14
	1	Native	9.03	(± 0.16)	13
	2	<i>Elodea</i>	8.86	(± 0.13)	27
	2	Native	9.18	(± 0.17)	23
	3	<i>Elodea</i>	9.00	(± 0.16)	19
	3	Native	9.03	(± 0.15)	20
2018	1	<i>Elodea</i>	8.91	(± 0.16)	7
	1	Native	9.00	(± 0.24)	7
	2	<i>Elodea</i>	9.24	(± 0.13)	18
	2	Native	9.31	(± 0.10)	25
	3	<i>Elodea</i>	9.40	(± 0.11)	27
	3	Native	9.44	(± 0.12)	21

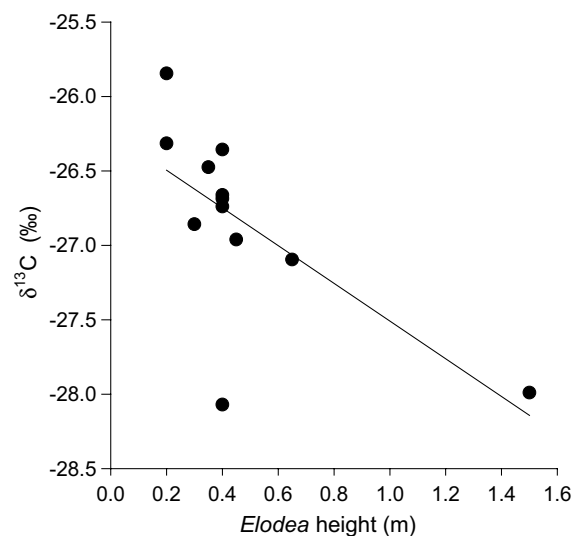


Fig. 2 Average carbon ($\delta^{13}\text{C}$) values of coho salmon (*Oncorhynchus kisutch*) fin tissue from the experimental enclosures plotted against average *Elodea* height (m) in each enclosure across 2017 and 2018. Plotted line shows univariate normal linear regression fits with on $\log_{10}$ transformed data

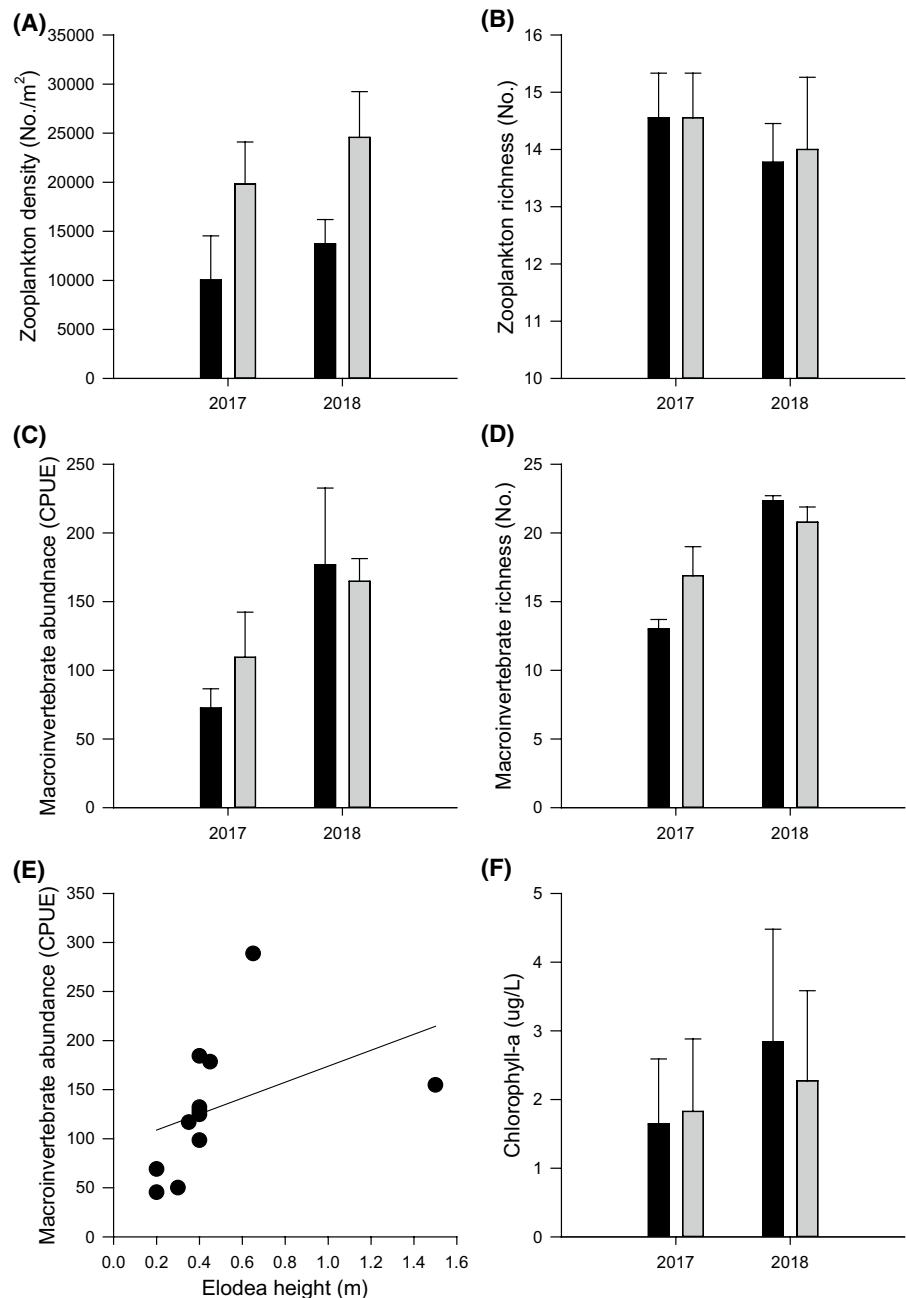
Year $F_{1,7}=0.74$; $P=0.42$; Nested Bay $F_{2,7}=1.14$; $P=0.37$). We did, however, observe a strong relationship between *Elodea* height and $\delta^{13}\text{C}$ ($r^2=0.54$, $P=0.007$; Fig. 2), where increasing *Elodea* height was associated with depleted $\delta^{13}\text{C}$ signatures. These

results indicate that taller *Elodea* stands may be associated with a relative shift in juvenile coho salmon diet sources from a littoral food web to a more pelagic food web pathway.

Zooplankton density and richness The infestation of *Elodea* reduced the density of zooplankton available and, thereby, the forage base of juvenile coho salmon. Consistent in both years, zooplankton

density differed between the *Elodea* and native vegetation treatments (ANOVA Treatment: $F_{1,7}=6.34$; $P=0.040$; Year $F_{1,7}=1.62$; $P=0.24$; Nested Bay $F_{2,7}=1.29$; $P=0.33$), with more zooplankton density found in the native vegetation treatment (Fig. 3A). While higher amounts of *Elodea* reduced zooplankton density, we did not find evidence of an *Elodea* effect on zooplankton richness (ANOVA Treatment:

Fig. 3 Effect of *Elodea* spp. on zooplankton and macroinvertebrate communities in experimental enclosures. Zooplankton density (A), zooplankton richness (B), macroinvertebrate catch per unit effort (CPUE; C), macroinvertebrate richness (D), and Chlorophyll-a (E) comparing *Elodea* (black bars) and native treatment (gray bars) levels inside of limnocorrals in McKinley Lake, AK in 2017 and 2018. Barplots (A–D, F) represent mean values ($\pm$ SE) from measurements pooled across study years. The scatter plot and univariate linear regression line in (E) show the relationship between macroinvertebrate abundance (CPUE) and *Elodea* height in limnocorrals combining data from 2017 and 2018



$F_{1,7}=2.11$; $P=0.19$; Year $F_{1,7}=0.54$; $P=0.49$; Nested Bay $F_{2,7}=2.70$; $P=0.14$; Fig. 3B). In both years, Cyclopoida copepodites, Chydoridae, *Bosmina longirostris*, and Copepoda nauplii were the numerically dominant taxa across the limnocorrals. Furthermore, *Elodea* stand characteristics (stand height, stem count) were not strongly associated with zooplankton density or richness, apart from a weakly supported association between increasing *Elodea* stem count and lower zooplankton density ($r^2=0.26$, $P=0.09$).

Benthic macroinvertebrate abundance and richness Field collections indicate a complex relationship between benthic macroinvertebrates and aquatic vegetation within the limnocorrals. A large difference between years for macroinvertebrate abundance and richness was also observed confirming temporal variability in macroinvertebrate communities (Fig. 3C, D). Due to the complexity and temporal variability, the analysis steps did not find statistical support for a relationship between the vegetation treatment (ANOVA Treatment: $F_{1,7}=0.73$; $P=0.42$; Year $F_{1,7}=12.03$; $P=0.01$; Nested Bay $F_{2,7}=4.08$; $P=0.07$; Fig. 3C) or *Elodea* stem count with macroinvertebrate abundance ($r^2=0.001$, $P=0.92$). Moreover, no patterns were found across treatments by the ANOVA for macroinvertebrate richness (ANOVA Treatment: $F_{1,7}=0.84$; $P=0.39$; Year $F_{1,7}=15.93$; $P=0.005$; Nested Bay $F_{2,7}=0.17$; $P=0.85$) indicating the amount of *Elodea* did not alter the macroinvertebrate assemblage (Fig. 3D). While macroinvertebrate richness was different between years, similar taxa were found in both treatments, with snails (*Menetus* spp.) and clams (*Musculium* spp., *Sphaerium* spp., and *Pisidium* spp.) being the numerically dominant taxa in 14 out of 21 sample dates in 2017 and 18 out of 21 in 2018. *Elodea* stand height, however, was positively associated with macroinvertebrate abundance ($r^2=0.46$; $P=0.02$; Fig. 3E) indicating the abundance of macroinvertebrates is the primary difference in the macroinvertebrate community.

Primary producers Assessments of chlorophyll-a and periphyton indicated that *Elodea* infestations did not affect primary productivity within the limnocorrals. Chlorophyll-a concentrations were comparable between *Elodea* and native vegetation treatments. Chlorophyll-a measured in the water column began at similar values for both the *Elodea* and native treatments and increased from the start to the end of the experiment in 2017 and 2018 (Fig. 3F). The

ANOVA results indicated differences between years, but no relationship between the vegetation treatment and chlorophyll-a (ANOVA Treatment: $F_{1,7}=18.17$; $P=0.004$; Year $F_{1,7}=0.76$; $P=0.41$; Nested Bay $F_{2,7}=0.39$; $P=0.79$). Similar to the ANOVA analysis of the treatment, *Elodea* height and stem count did not predict chlorophyll-a concentration in the water column. Finally, periphyton analysis in 2018 indicated no difference in green algae, blue-green algae, diatoms, or total cell count (cells/mm²) across treatments.

Discussion

Elodea negatively impacted fish growth in our subarctic lake study system. Juvenile coho salmon rearing in *Elodea* dominated enclosures grew 8% less in total length during the experiment than their counterparts in habitats comprised of native aquatic vegetation. However, fish from both types of enclosures had comparable somatic energy density and mass, suggesting less energy net of base metabolic needs was available for allocation to growth for juveniles rearing in *Elodea* dominated habitats. This pattern could reflect either higher energy expenditures or lower energy intake in the invasive dominated habitats for coho salmon. The negative effect of this invasive aquatic plant is concerning for juvenile coho salmon as poor growth would have consequences across life stages. By decreasing growth, *Elodea* may indirectly affect juvenile coho salmon survival by reducing size refugia from predation in freshwater and upon entering saltwater. Furthermore, poorer growth outcomes achieved during what could be a productive summer season may lead to lower overwinter survival and may delay the ability to smolt, thereby increasing the number of years spent rearing in freshwater as opposed to benefitting from higher growth rates foraging in the ocean food web (Beamish and Mahnken 2001).

By implementing a controlled field experiment, results provide insights into the potential mechanisms through which *Elodea* may mediate juvenile coho salmon growth in Subarctic lakes. Our expectation that *Elodea* would affect salmon growth by reducing water quality was not supported, as abiotic conditions were comparable throughout the study across both native vegetation and *Elodea* dominated habitats, and at reference sites outside of the limnocorrals.

Large diel fluctuations in dissolved oxygen driven by photosynthesis and respiration have been observed in lakes with dense stands of *Elodea*, yielding daily minimum concentrations harmful to fish and other aquatic organisms (1–2 mg/l) (Ondok et al. 1984; Mjelde et al. 2012). Low dissolved oxygen concentrations just above the substrate (e.g., within 5 cm, Spicer and Catling 1988) could have indirect effects on food webs. For instance, *Elodea* reduced a crayfish population in a Norwegian lake due in part to low dissolved oxygen (Hessen et al. 2004). In our study system, however, dissolved oxygen values were similar between *Elodea* and native vegetation treatments throughout the experiment and did not reach levels that would cause stress to coho salmon, as values were above 9 mg/l in 2017 and above 7 mg/l in 2018. Future studies should consider *Elodea* senescence, as low dissolved oxygen can result from decomposing *Elodea* perturbing the entire lake ecosystem (Barko and James 1998; Burks et al. 2001; Diehl et al. 1998; Jeppesen et al. 1998). While respiration can also alter pH levels, no differences in point samples of pH or conductance were found between treatments, with little temporal change in these conditions throughout the experiment.

Water temperature is an important environmental factor that affects fish growth (Magnuson et al. 1990) and the field experimental design allowed us to control for temperature by pairing enclosures in bays. Yet, similar to patterns of dissolved oxygen, we found no systematic differences in water temperatures across the *Elodea* and native vegetation treatments or at reference sites outside of the enclosures, supporting the conclusion that water quality is not driving the differences observed in fish growth among macrophyte treatments. Temperatures were not likely warm enough or cold enough to cause stress to study fish. Water temperatures in limnocorrals were often close to the 14–17 °C optimal temperature range for rearing juvenile coho salmon as determined in other latitudes of their distribution (Pacific Northwest, U.S.A.: Richter and Kolmes 2005 and references therein; California: Lusardi et al. 2020). Overall, water temperatures were warmer in 2017 and resulted in higher fish growth across all study enclosures compared to 2018, however the growth deficit for fish rearing in *Elodea* dominated enclosures was apparent in both study years. As all measured water conditions were consistent across both treatments, we suspect juvenile coho

salmon in *Elodea* dominated enclosures had lower energy intake through the food web, and not necessarily higher energy costs due to water quality, compared to their native vegetation treatment counterparts.

Differences in nitrogen isotopes ($\delta^{15}\text{N}$) between treatments supported that an *Elodea* dominated habitat can affect juvenile coho salmon growth by altering the food web. Coho salmon in enclosures dominated by *Elodea* had lower $\delta^{15}\text{N}$ values, indicating a lower trophic position, compared to fish rearing in enclosures dominated by native vegetation. The lower trophic positioning of juvenile coho salmon in *Elodea* dominated enclosures is likely driven by characteristics of the submerged aquatic vegetation harboring different types or abundances of prey (Fig. 4). Submerged aquatic vegetation has been found to alter the quality of prey resources, thereby influencing trophic positions of fish in other ecosystems (Thomaz and Cunha 2010; Carniatto et al. 2020). We suspect prey in *Elodea* dominated habitats is lower in quality due to lower energy density, higher handling time, or both, and trophic position, which reduces the $\delta^{15}\text{N}$ values and ultimately growth of juvenile coho salmon. In addition, there was also a strong relationship between *Elodea* height and fish carbon isotopes ($\delta^{13}\text{C}$), indicating *Elodea* stand space architecture may influence the diet source for juvenile coho salmon by altering prey availability and foraging selectivity (Fig. 4).

To further examine the influence of *Elodea* on coho growth, trophic position, and diet source, we assessed different food web components starting with primary producers. As with abiotic variables, however, we found no evidence that *Elodea* infestations altered primary productivity in experimental enclosures compared to plots dominated by native vegetation. Phytoplankton biomass, inferred from chlorophyll-a in the water column, was similar across the treatments as was the periphyton biomass observed at the end of the experiment. The lack of effects of *Elodea* on primary producers in our study system differs from studies of other invaded waterbodies which found that *Elodea* reduced productivity of lakes by increasing sedimentation, shading algae, and outcompeting algae for phosphorus (Perkins and Underwood 2002; Kornijow et al. 2005). However, these *Elodea* studies in the United Kingdom and southern Finland occurred in smaller and shallower waterbodies compared to our experimental lake (McKinley Lake, AK); we suspect lake depth is an important factor

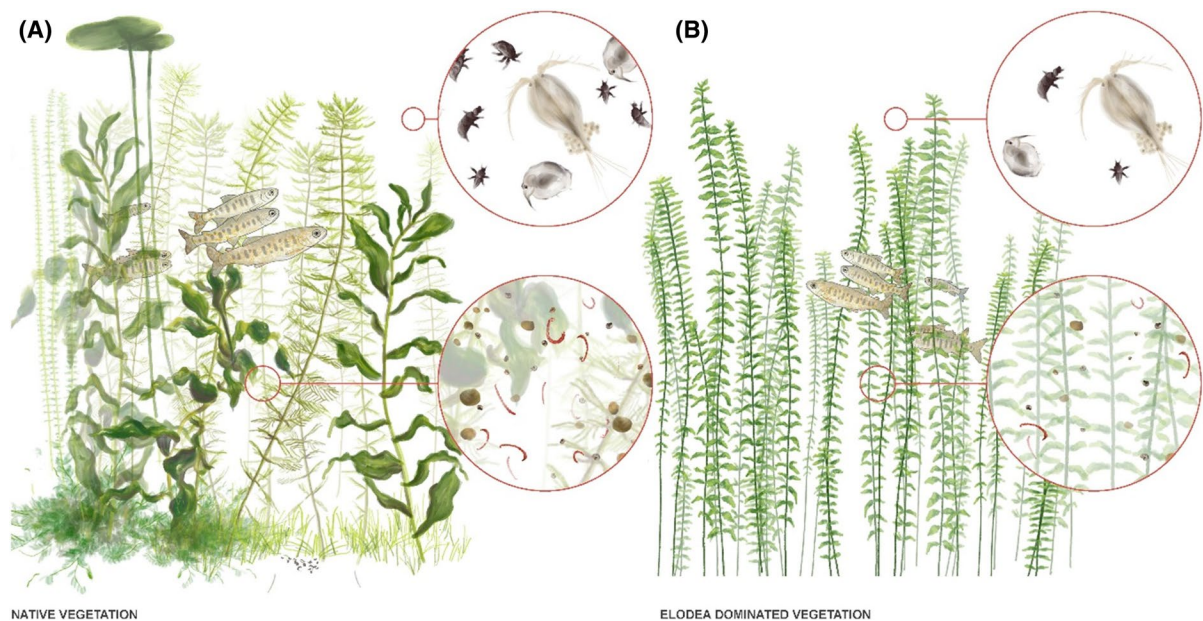


Fig. 4 Conceptual figure demonstrating mechanisms of how *Elodea* stand architecture may alter space in the water column and affect the availability of zooplankton (upper bubbles) and macroinvertebrates (lower bubbles), thereby altering prey access by juvenile coho salmon (*Oncorhynchus kisutch*). Native dominated habitat (A) and *Elodea* dominated habitat (B) are contrasted with more zooplankton in native dominated

habitat and more macroinvertebrates with higher vegetation taxa richness. Unaffected by the experimental treatment are abiotic variables and local primary productivity. Combined, the altered architectural space suggests energy flow away from coho salmon in *Elodea* dominated food webs resulting in lower growth and lower position in food web. Figure design and illustration by Cecil Howell

to consider in evaluating the importance of *Elodea* on the pelagic food web. Experiment duration might play an important role as well. For example, the negative effect of *Elodea* on phytoplankton biomass noted by Lürig et al. (2021) in a mesocosm experiment in Switzerland occurred over a longer duration than our experiment could be conducted, suggesting longer-term studies would be valuable in understanding *Elodea* effects on Subarctic food webs. Longer-term studies at the spatial scale of lakes could address how the decomposition of *Elodea* contributes to internal nutrient loading, cycles of algal blooms, and eutrophication (Thiébaud et al. 2007; Di Nino et al. 2005; Heikkinen et al. 2009; Sarvala et al. 2020).

While we did not find evidence that *Elodea* infestation affected primary productivity in experimental enclosures, our results demonstrated lower zooplankton density in the *Elodea* dominated sites. The influence of *Elodea* on zooplankton has been observed in other controlled field enclosure experiments, such as the decrease in zooplankton density that accompanied an increase in *Elodea* density, documented by

Kornijow et al. (2005). While we observed a strong effect on zooplankton density, we did not observe a difference in the abundance of macroinvertebrates and observed a high amount of variability across treatment levels. Spatial and temporal variability is often observed in macroinvertebrate communities with or without invasive submerged aquatic vegetation. Yet, we were surprised no effect was detected in macroinvertebrates as an *Elodea* invasion has led to different macroinvertebrate communities in other lakes albeit in different directions for the change in abundances (Kelly and Hawes 2005; Kelly et al. 2015). While there could be differences in the macroinvertebrate assemblage with fewer taxa responding to *Elodea*, we suspect that the native submerged aquatic vegetation in our study system is architecturally complex enough to offset a positive effect from the introduction of *Elodea* as observed by Kelly and Hawes (2005) in a New Zealand lake. Further considering gradients of architectural complexity, our *Elodea* treatment is likely not dominated enough by *Elodea* to have reduced the architectural complexity of

the littoral zone vegetation similar to the pattern seen by Kelly et al. (2015) in a lake in Northern Ireland. The combination of an architecturally complex native assemblage with the level of *Elodea* infestation tested in this experiment results in the more nuanced effect.

While *Elodea* treatments as a group were not associated with higher macroinvertebrate abundance, pooling across all experimental enclosures, *Elodea* stand architecture is associated with positive macroinvertebrate abundance. Specifically, *Elodea* height was indicated as a driver of macroinvertebrate abundance with higher *Elodea* stands in the system leading to more macroinvertebrates. We explored the positive relationship between *Elodea* height and macroinvertebrate density a-posteriori and found that taller *Elodea* was related to higher native vegetation richness ($r^2=0.35$, $P=0.04$), supporting our conclusion above on the positive effects of native community complexity. Higher vegetation richness was found to be related to higher macroinvertebrate abundance (linear regression and blocking between years—Vegetation taxa richness: $r^2=0.7$, $P=0.004$). Higher native aquatic vegetation has been documented supporting a larger macroinvertebrate community (Carpenter and Lodge 1986). Combined, when the *Elodea* stand is taller, it is primarily at a low stem count with a few very tall stems surrounded by diverse native vegetation. These few *Elodea* stems likely got an early start growing in the summer, but do not numerically dominate the vegetation community with a low relative species abundance. The few taller *Elodea* stems and higher richness of native vegetation led to more abundant macroinvertebrates. The importance of vegetation characteristics has been documented for other invasive macrophytes (e.g., *Hydrilla verticillate*) and shows different submerged aquatic vegetation can have similar richness and diversity of invertebrate taxa, but higher invertebrate density (Carniatto et al. 2020).

This pattern of *Elodea* height and macroinvertebrate abundance is further complicated by the zooplankton response in that *Elodea* height reduced fish $\delta^{13}\text{C}$ values, indicating a larger contribution from the pelagic food web than littoral food web. We suspect that in food webs with higher native richness and taller *Elodea* height, fish have the same diet source, albeit with more benthic macroinvertebrates, that diet source is supplemented by much more zooplankton reflecting a relatively larger pelagic carbon

isotope signature. A future research question is to consider indirect consequences of foraging on pelagic resources such as potential for exposure to avian predation from increased time spent in the water column rather than benthic habitat. Understanding of how *Elodea* invasions may affect predator refugia for juvenile fish as they alter foraging behavior in response to changing architecture of submerged aquatic vegetation is an important research avenue moving forward to inform the mechanisms through which invasive waterweeds could drive population-level impacts on salmon.

Our results establish that *Elodea* affects zooplankton density and macroinvertebrate abundance, but the mechanisms through which this invasive aquatic plant affects juvenile coho growth are complex. We found no changes to water quality or primary productivity at the base of the food webs in experimental enclosures, nor the composition of consumer trophic levels, attributable to *Elodea*. Thus, we suspect the space architecture of *Elodea* stands alters the access to and quality of forage for juvenile coho salmon, altering the flow of energy to juvenile salmon as evidenced by their lower food web position and slower growth in *Elodea* dominated habitats, along with diet source differences across *Elodea* height (Fig. 4). Future studies to investigate whether *Elodea* stand architecture mediates top-down processes that affect macroinvertebrate communities by changing predation refugia dynamics, or whether *Elodea* stand architecture affects bottom-up processes driving macroinvertebrate communities by influencing the availability or quality of macrophyte habitat for primary producers, are needed to further elucidate the processes through which stand space alteration may affect fish growth. Furthermore, there is a need to better understand prey selectivity of juvenile coho salmon in this Subarctic, littoral food web, while also considering somatic energy of prey type, foraging efficiency, and density dependence. Higher densities of coho salmon would exacerbate prey resource differences between native and *Elodea* infested food webs and we suspect fish foraging and growth would respond more quickly than our experiment. Interspecific competition is another mechanism that could alter the effect size of *Elodea* on fish growth and the time in which effects manifest as a fish response.

Given its potential for rapid expansion, studies exploring direct and indirect impacts of *Elodea*, and

other aquatic invasive plants, on ecosystem processes are needed to support invasive species management in the increasingly connected and sensitive Subarctic and Arctic clines (Strayer 2010; Emery-butcher et al. 2020). In situ experiments, such as the limnocorral trials employed here, are a powerful tool to discern mechanisms through which invasive species impact aquatic food webs and ultimately species with economic and cultural value such as coho salmon. In some respects, controlled treatments were conservative in that the *Elodea* treatments still contained a small percentage of native macrophyte species, although we think this is representative of submerged aquatic vegetation in other colonized waterbodies in the region. There are, however, lakes in the Subarctic in which the submerged aquatic vegetation has been almost completely homogenized with *Elodea* (see examples in Carey et al. 2016; Sethi et al. 2017). We suspect that the effect of *Elodea* density scales with the amount of *Elodea* present in the system (Carniatto et al. 2020).

This study reiterates that submerged aquatic vegetation drives fundamental ecosystem processes and, therefore, invasive submerged aquatic vegetation can dominate an ecosystem (Kuehne et al. 2016). Moreover, *Elodea* is likely to affect other commercially important species (e.g., Sockeye salmon *O. nerka*) as well as other species that are important components of food webs (Schwoerer et al. 2019; Schwoerer et al. 2020a, b). Sockeye salmon may be particularly vulnerable to *Elodea* invasions as juveniles rear in lakes for 1–2 years during which time changes to prey resources could alter their growth rates similarly to coho salmon. Long-term impacts of *Elodea* in aquatic ecosystems of Alaska need to be assessed along with preventing further spread. As more *Elodea* populations establish in Alaska, the risk of dispersal throughout the state increases rapidly (Schwoerer et al. 2020a, b; Schwoerer et al. 2022). Prevention of *Elodea* introductions altogether would be the best management strategy, considering the exacerbated challenges of combatting an invader in a remote setting (Carey et al. 2016) and the difficulty and expense of eradicating such an invader (Sethi et al. 2017). However, many vectors, including floatplanes, boats, trailers, anglers, hunters, and hikers, increase the chance for spread from infested waters into the waterways of Alaska (Schwoerer et al. 2020a, b; Schwoerer et al. 2022) and fragments of *Elodea* have high

survival rates allowing them to be dispersed over long distances. Thus, there is a need to both prevent and understand its impacts in different contexts, as environmental controls may prove to be important. An important next step is understanding how temperature differences could alter the invasive effect of *Elodea*, especially in a region experiencing rapid warming such as the Subarctic (Post et al. 2019).

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Author contributions All authors contributed to the study conception and design. Data collection was performed by MC, GR, TT, and CZ. Data analysis was conducted by MC and SS. The first draft of the manuscript was written by MC and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request and available at Carey MP (2023) Determining how *Elodea* spp. impact fish performance in Subarctic food webs. U.S. Geological Survey data release, <https://doi.org/10.5066/P9GXS8G8>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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