

Multi-trophic impacts of an invasive aquatic plant

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SUMMARY

1. Natural resource agencies are increasingly required to prioritise management of multiple non-native aquatic plants (macrophytes) in freshwater ecosystems. Characterising the consequences of invasions for ecological processes and corresponding ecosystem services is fundamental to this decision-making process, but requires an understanding of impacts across physical, chemical, and biological responses.

2. Accordingly, we evaluated the multi-trophic impacts of the invasive macrophyte *Myriophyllum aquaticum* (Haloragaceae; parrotfeather) along the mainstem Chehalis River, Washington, U.S.A. We examined invertebrate, plant and fish community responses to varying degrees of parrotfeather abundance and simultaneously characterised variation in physical structure and dissolved oxygen (DO) across the dominant native and non-native plant species.

3. DO concentrations were significantly reduced and approached hypoxic levels in areas dominated by parrotfeather compared with native vegetation. Increased structural complexity, volume and biomass of parrotfeather was associated with increased diversity of epiphytic invertebrates.

However, these more diverse invertebrate assemblages were dominated by amphipods, whereas native macrophytes were characterised by cladocerans, chironomids and gastropods. Non-native fishes (primarily centrarchid species) were more strongly associated with sites where parrotfeather was present and diversity of non-native fishes was positively correlated along a gradient of parrotfeather abundance. Native fish associated with parrotfeather areas were those that tend to be tolerant of degraded or lower quality habitats.

4. We saw little evidence of exclusion of other macrophytes; native and non-native plant diversity and abundance were positively correlated with the parrotfeather gradient. This may reflect that analysis was done at a site level, and competitive dominance might be apparent by changes in species richness at smaller (plot) scales or over longer periods. Alternatively, parrotfeather may demonstrate minimal effects on native plant composition.

5. Given the effects observed across multiple habitat characteristics and biota, parrotfeather appears to be a highly impactful invader where it establishes. Many of the changes we observed appear to derive from the emergent leaves and dense mat formation of parrotfeather compared with a submersed structure more typical of the native community. Our results suggest that managers should specifically consider contrasting characteristics between non-native and native physical structure when assessing and prioritising threats of invasive macrophytes.

Keywords: community ecology, fish habitat, habitat complexity, *Myriophyllum aquaticum*, non-native macrophyte

Introduction

Understanding and managing the impacts associated with non-native aquatic plants (macrophytes) has become an increasingly common challenge in freshwater

ecosystems. In rivers, lakes, and wetland ecosystems, macrophytes contribute to fundamental processes such as primary production and nutrient cycling, and influence important aspects of water quality (Caraco & Cole, 2002; Thomaz & Cunha, 2010). Macrophytes also

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provide physical habitat structure that directly and indirectly supports aquatic food webs from algae to fish (Warfe & Barmuta, 2006; Thomaz & Cunha, 2010; Kornijów, Measey & Moss, 2016). Non-native macrophytes therefore have the potential to alter freshwater ecosystems through a variety of physical, chemical, and biological pathways (Ehrenfeld, 2010; Schultz & Dibble, 2012). In conjunction with ecological impacts, non-native macrophytes can compromise many of the ecosystem services that fresh waters provide such as hydropower, fisheries, and recreation (Eviner *et al.*, 2012) and inflict significant economic damages (Lovell, Stone & Fernandez, 2006; Olden & Tamayo, 2014). As a result, considerable efforts in recent decades have been dedicated towards prevention, control, and eradication of non-native macrophytes.

For managers tasked with prioritising limited resources, however, the most appropriate strategy (e.g., a focus on eradication versus containment) is rarely apparent, particularly for new or potential invaders (Vander Zanden & Olden, 2008). Successful outcomes of eradication efforts are highly uncertain (Howell, 2012) and may depend on a host of factors that management agencies cannot control (Pluess *et al.*, 2012). There are considerable costs associated with invasive weed management to be weighed, including not only time and money, but potential impacts to native communities and landscapes (Bergstrom *et al.*, 2009; Parsons *et al.*, 2009). Uncertainty is increased by the possibility that some invasions may result in neutral (or even benign) effects on ecosystems (Thomaz & Cunha, 2010; Schlaepfer, Sax & Olden, 2011). For example, non-native *Lagarosiphon major* and *Elodea canadensis* (Hydrocharitaceae) in an alpine lake in New Zealand were associated with increases in epiphyton, benthic invertebrate diversity and abundance of a native fish (Kelly & Hawes, 2005); *Lagarosiphon major* also appears to provide highly suitable habitat for fish in an altered reservoir system which is largely devoid of native plants (Bickel & Closs, 2009).

Myriophyllum aquaticum (parrotfeather) is an example of a global aquatic invader for which knowledge of ecological impacts remains low despite establishment in far-reaching temperate and tropical regions. From its native range in South America, parrotfeather (an emergent, floating-mat species) has spread worldwide largely due to its popularity in the aquarium trade and through introductions dating back well over a century ago (Hussner & Champion, 2012). Parrotfeather's ability to regenerate from even small fragments (Hussner, 2009) likely facilitates secondary spread, with boats, equipment, or waterfowl implicated as vectors (Champion,

Clayton & Rowe, 2002; DiTomaso & Healy, 2003). Once established, parrotfeather has proved very difficult to eradicate due to rapid growth rates (Hussner, 2009) and ability to tolerate water fluctuations and even sustained drawdowns (Hussner, Meyer & Busch, 2009; Wersal, Madsen & Gerard, 2013). Uptake and storage of nutrients in stolons may also help facilitate spread, overwintering, and competitive dominance of parrotfeather in areas where it is non-native (Wersal *et al.*, 2011). The potential challenges associated with parrotfeather exemplify the difficulty that managers face in allocating prevention and control efforts, and the need to ascertain the impact of such invaders to support prioritisation and decision-making (Blackburn *et al.*, 2014).

Despite the uncertainty inherent in predicting invasion dynamics, a body of recent research has converged on several key determinants associated with the impacts of non-native aquatic plants. The first of these is examining interactions between non-native species and recipient communities. For example, an invader that has similar morphology to resident native plants may have relatively low impacts (Cunha *et al.*, 2011), whereas an invader possessing a more novel physical structure may outcompete natives (Stiers *et al.*, 2011; Carniatto *et al.*, 2013). Second, possession of certain traits relative to the native community appears to elevate the likelihood of negative effects: these include resource use efficiency and increased growth rates, allelopathy, and phenotypic plasticity (Ren & Zhang, 2009; Schultz & Dibble, 2012). Third, changes in overall habitat complexity due to invasion are implicated in diverse cascading effects that are expressed across invertebrate, plant, and fish communities (Warfe & Barmuta, 2006; Kovalenko, Dibble & Slade, 2010).

These research elements suggest a need for approaches that examine multi-trophic effects of non-native macrophytes, as well as those that describe both the invader and native plant community (Kovalenko *et al.*, 2010; Schultz & Dibble, 2012). Recent literature syntheses reveal that progress in this area of investigation across all invasive species remains limited (Ehrenfeld, 2010; Thomsen *et al.*, 2014). Such approaches, however, offer not only more comprehensive insight into invader impacts, but also allow linkages to be made between ecological processes and ecosystem services, thus supporting managers in evaluating control or eradication priorities (Eviner *et al.*, 2012).

Here, we report on a comprehensive examination of multi-trophic responses to non-native parrotfeather in the Chehalis River, Washington State (U.S.A.). Information related to the biology and distribution of

parrotfeather heavily outweighs that on ecological impacts (but see Stiers *et al.*, 2011). Our objectives were therefore to evaluate the ecological impacts of non-native parrotfeather on local ecosystems by (i) contrasting differences in key abiotic characteristics associated with native and non-native plant species and (ii) assessing invertebrate, plant, and fish community responses to parrotfeather presence and abundance. Results from this study demonstrate the value of investigating the effects of non-native species across multiple levels of biological organisation and use of community approaches to more comprehensively assess the overall impact of aquatic invaders (Ehrenfeld, 2010; Blackburn *et al.*, 2014).

Methods

Study area and site selection

The survey was conducted along the Chehalis River, a 200-km long rainfall-runoff dominated system draining a 2700-km² watershed of forested (74%), developed, wetland, and agricultural land use (5–8% each) in southwest Washington, U.S.A. (Gendaszek, 2011). The river is low-gradient throughout a majority of the basin, and with extensive beaver activity in tributaries and adjacent habitats: as a result, semi- and partially connected habitats such as seasonal wetlands, active or defunct side channels, and backwater sloughs are common features. These areas support diverse populations of commercially and recreationally important fish, including three species of

Pacific salmon as well as Olympic mudminnow (*Novumbra hubbsi*: Esociformes), a highly endemic and state 'Sensitive' species (Kuehne & Olden, 2014). Introduced fish species – largely non-native centrarchids – are also commonly encountered.

Several non-native plants are present in the basin and the subject of varying levels of management and control. These include Brazilian elodea (*Egeria densa*: Hydrocharitaceae), a dense, submersed macrophyte native to South America that was discovered in the Chehalis River approximately the same time as parrotfeather (c. 1994). Brazilian elodea has been the focus of an aggressive removal campaign, however, that has substantially reduced the population extent and was therefore not a suitable candidate for examination of community responses across a gradient of abundance. By contrast, control efforts for non-native parrotfeather have been intermittent since its initial discovery, and infestations ranging from scattered plants to 0.5 hectare areas are found in slow water areas along the mainstem river and adjacent habitats.

We selected slow-water sites with and without parrotfeather along the mainstem and adjacent habitats of the Chehalis River to examine water quality, invertebrate, plant, and fish communities across a gradient of abundance (Fig. 1). We surveyed 22 sites in 2013 and 2014, with sampling conducted once each year in each site between late-July and mid-August. Although our initial goal was to sample sites along a continuous 65 km reach, travel time constraints restricted us to sites within

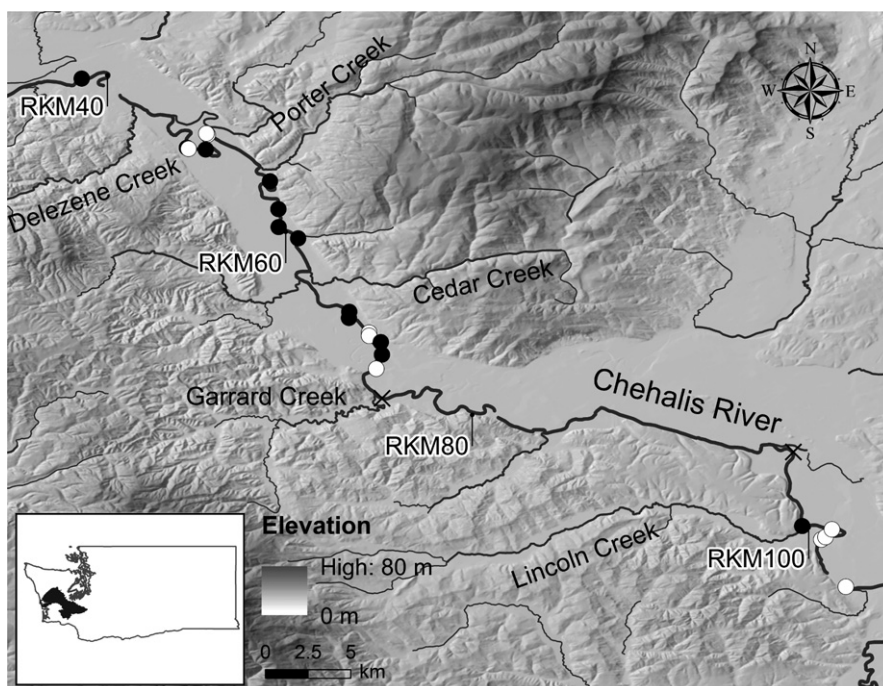


Fig. 1 Area of study with 22 sampling sites along the mainstem Chehalis River and incoming tributaries (stream order >1 depicted). The sites are designated as parrotfeather present (black circles) and not present (white circles). Restricted river access resulted in the exclusion of river kilometer (RKM) 95 to RKM 75 (area shown between × symbols) from survey and sampling. Inset shows the location of the Chehalis River watershed within Washington State.

5 km (upstream and downstream) of boat launches. This resulted in 20 km of river being excluded due to lack of launches (Fig. 1). A subsequent survey of the entire 65-km reach, however, identified very few areas with parrotfeather and no areas that represented a substantial establishment within the 20 km exclusion (L. Kuehne, unpubl. data). As a result, our sampling captured the majority of available sites with parrotfeather along the mainstem.

Selected sampling sites included backwater areas, sloughs, incoming (dammed) creeks, and defunct or dammed side channels. The majority of sites were separated by ≥ 0.5 km along the mainstem (Fig. 1), with the exception of two creeks that were sampled both above and below beaver dams. In each of these cases, two or more beaver dams separated the upstream (i.e., off-channel) site from the downstream (i.e., mainstem-oriented) site. Subsequent analysis showed substantial differences in fish communities between these areas, supporting treatment as independent sites (results not shown).

Between sampling seasons, a subset of sites ($n = 7$) were treated to reduce abundance of parrotfeather. Parrotfeather in these sites was treated with an application of imazapyr in late summer of 2013 (1 month after the first survey). Imazapyr degrades quickly in water and is considered largely non-toxic to aquatic organisms (Stehr *et al.*, 2009; Yahnke *et al.*, 2013). Based on univariate and multivariate comparisons between sampling years, we found no evidence for declines in fish density or differential shifts in fish communities between sites that were treated and those that were not. The single chemical treatment also did not noticeably reduce native or non-native vegetation, both of which were substantially more abundant in 2014 due to warm temperatures and low streamflows; plant community composition in treated sites also did not exhibit unusual shifts between years compared to untreated sites.

Biological surveys for fish and plants

Fish communities were surveyed using baited Gee minnow traps (23 × 44 cm, 2.5 cm opening, 0.6 cm mesh) set overnight. Traps were deployed in transects perpendicular to shore 5 m apart and with 3 m between individual traps, creating an unbiased grid for sampling fish and plant communities in each site. All sites had little to no flow and areas of shallow vegetation, but varied considerably in size (range: 150–12 500 m²) due to differing habitat type (i.e., backwater, side channel, or incoming tributaries) and presence of beaver dams. To account for

differences in size, the number of traps was scaled according to total area, with a minimum of 10 traps deployed in the smallest sites up to a maximum of 30 traps per site. Five sites were too large (>2500 m²) to be completely surveyed by 30 traps (without increasing space between traps), so a representative portion of these sites was subsampled. All fish species in the traps were identified and counts recorded.

We attempted to set hoop nets (76 cm diameter, 1 cm mesh) as an alternative gear type to capture larger-bodied species, but logistical problems (sinking substrates, insufficient or excess depths) prevented successful deployment in all sites. In the 13 sites with hoop net catch data, there were no species captured in hoop nets that were not also captured in minnow traps; we therefore relied on the more comprehensive minnow trap data for community analyses.

Aquatic plant communities were characterised through visual observations as well as collection of vegetation samples to determine relative abundance of species' biomass. At each trap, the dominant, secondary, and tertiary plant species were visually identified. Plant biomass samples were collected at odd-numbered traps (i.e., half of the traps deployed) using a standardised vertical rake turn method. This rapid method results in species detection rates that are comparable to diver-quadrat sampling, making it suitable for large-scale ecological surveys (Johnson & Newman, 2011). Rakes can oversample canopy-forming species, however, thereby biasing biomass estimates (Johnson & Newman, 2011). To account for this, we used the relative abundance of biomass collected in statistical analyses, thereby correcting for systematic collection biases. All plant samples were rinsed, sorted to species, and frozen for storage. Samples were subsequently dried to a constant weight at 80 °C to obtain species-specific dry weights.

Invertebrate sampling

To compare invertebrate diversity and communities associated with the most common native and non-native macrophytes, we identified monospecific stands within sites to collect sweep samples of epiphytic invertebrates. Ideally, all invertebrate samples associated with macrophyte species would have been collected from within the same site to reduce potential for inter-site variation; however, we found that sites tended to contain large monospecific stands of only 1–2 species. For example, a site might contain large extents of common waterweed (*Elodea canadensis*) and parrotfeather, but not narrow leaf bur-reed (*Sparganium angustifolium*) which favours the

same depth. We collected replicate samples for each plant species ($n = 2$) opportunistically as monospecific stands were encountered across sites (each replicate was comprised of two separately collected subsamples to check for within-site variation).

Using a standard *D*-frame net (mesh size = 0.5 mm), invertebrate samples were collected by sweeping the vegetation in the lower middle to upper water column within a 0.5 m² area for 60 s (Turner & Trexler, 1997). The three native plant species sampled for invertebrates were waterweed, narrow leaf bur-reed, and Richardson's pondweed (*Potamogeton richardsonii*). The non-native aquatic plants sampled were parrotfeather and Brazilian elodea. We attempted to collect samples for hornwort (*Ceratophyllum demersum*) – a dominant native species – but as hornwort is rootless and favours deeper water (≥ 0.6 m), sweep sampling was not feasible. Invertebrate samples were preserved in 90% ethanol in the field, and subsequently processed in the laboratory in accordance with USEPA Bioassessment Macroinvertebrate Protocols (Barbour *et al.*, 1999). Based on preliminary processing of samples, we developed a curve to estimate the number of individuals required to detect all morphospecies ($200 \pm 10\%$). Each sample was sieved at 0.5 mm and subsampled until the target number of individuals was reached. Invertebrates were identified to the lowest practical taxonomic level, typically sub-class or order using a dissecting microscope ($\times 80$). Counts from subsamples were averaged, resulting in two replicates per macrophyte species for comparison.

Dissolved oxygen measurements

To characterise the dissolved oxygen (DO) concentrations associated with different plant species, in 2014 we measured DO at each trap using a handheld water quality meter (YSI Model Pro2030, galvanic DO sensor calibrated daily). All point measurements were at a depth of 20 cm, and prior to vegetation and fish sampling to minimise disturbance. It was not possible to strictly control the time of day for DO measurements due to differing travel and collection time required at sites; however, all sites were surveyed between the hours of 10:00 and 15:00 hours. To supplement point sampling and assess diel changes in DO, a single battery operated sonde was deployed in one site to contrast DO fluctuations in areas with open water compared to the dominant native waterweed and non-native parrotfeather (see Supplemental Methods for more information). DO fluctuated most in the early mornings and late afternoons, and was relatively stable during the day, giving us greater

confidence in the comparability of daytime point samples to contrast DO concentrations associated with native and non-native aquatic plants.

Physical structure and complexity of native and non-native plants

We conducted a supplemental set of laboratory measurements to characterise differences in the physical structure and complexity of native and non-native macrophytes, and examine associations with invertebrate diversity. Using specimens of individual plants collected in the field, we calculated three metrics related to physical shape and structure: fractal dimension, plant volume, and dry weight biomass. Fractal dimension (*D*) is a ratio that reflects similarity of geometric patterns when measured at varying scales; higher *D* indicates more complex physical shape or structure (Dibble & Thomaz, 2009). The volume of plants (PV) when immersed in water is also an indicator of physical plant biomass and structure. Both of these metrics have been shown to correspond with abundance and diversity of macroinvertebrates and together represent a robust way to characterise and compare surface and whole-plant structural attributes (Warfe, Barmuta & Wotherspoon, 2008; Dibble & Thomaz, 2009). Finally, dry weight biomass is a measure of plant density and is frequently used to characterise occurrence and dominance in aquatic plant surveys (Duarte & Kalff, 1990).

Individual plant specimens ($n = 4$) were collected in August 2014 for the same native and non-native species as were sampled for invertebrates: native waterweed, narrow-leaf bur-reed, and Richardson's pondweed, and non-native parrotfeather and Brazilian elodea. We also collected specimens of native hornwort for which invertebrates were not sampled (see above). Plants were collected and stored in plastic bags with water for transport to the laboratory. In order to compare structure and biomass across emergent and submersed species, the emergent portions were removed from parrotfeather and narrow leaf bur-reed.

Plant specimens were individually staged in a 38-L aquarium, using small weights to anchor plants to the bottom and simulate natural shapes in the water, enabling us to measure fractal *D*. An SLR digital camera was used to capture a 25 cm \times 30 cm area of the plant specimen. As all specimens exceeded 30 cm in height, separate photos were taken of the upper 30 cm (i.e., surface) and lower 30 cm (i.e., root) areas; four replicate photos of each were taken and subsequently processed.

PV was measured for each specimen by displacement in water; specimens were then dried to a constant weight at 80 °C to obtain an individual dry weight.

The photographs for fractal D were converted to black and white silhouette in Adobe Photoshop, allowing analysis of the 'edge' or boundary fractals, which is considered to better reflect characteristic differences in plant architecture (Thomaz & Cunha, 2010). D was calculated by the box counting method in the free software Fractop v0.3b, using grid divisions of 2, 4, 6, 8, 12, 16, 32, 64, 128, and 256. The average D from upper and lower water column photographs was used to compare physical complexity for each species.

Statistical analyses

Physical structure and effects on dissolved oxygen and invertebrate assemblage. Differences between species' physical structure (fractal D , volume, and dry weight) were contrasted using ANOVA and Tukey's *post hoc* tests following log or square root transformations as needed to meet criteria for normality and heteroscedascity.

To compare DO concentrations associated with native and non-native plants, we grouped the point samples measured at each quadrat or trap based on the dominant species identified in that quadrat (or open water if no vegetation was present). Because some species were more common than others, sample sizes were unequal and criteria for normality and heteroscedascity were not met. We therefore utilised the Welch test on ranked data to test for overall significance and the Ryan–Elinot–Gabriel–Welsch (REGWQ) test for pairwise comparisons; both of these tests have been shown to control Type I error rates and maximise power when distributions are skewed and variances are unequal (Cribbie *et al.*, 2007).

We calculated the invertebrate diversity associated with each plant species using the Shannon–Wiener diversity index (H'), and tested for significant differences between plant species using the Welch test and REGWQ for *post hoc* comparisons to accommodate heteroscedastic data. Invertebrate counts were also converted to relative abundances of dominant taxa to more easily compare invertebrate communities associated with different aquatic plants. Dominant taxa categories were determined based on prevalence across all plant species as well as consideration of importance in fish diets: these were Amphipoda, Chironomidae, Cladocera, Copepoda, Gastropoda, and large-bodied insects (Odonata, Ephemeroptera, and Hemiptera). Preliminary multivariate examination confirmed that invertebrate communities

were differentiated based on aquatic plant species identity rather than the site or depth where the sample was collected. All one-way and pairwise testing were conducted in R using the stats (R Core Team, 2015) and mutoss (MuToss Coding Team *et al.*, 2015) packages; diversity indices were calculated using the vegan package (Oksanen *et al.*, 2015).

Fish and plant community responses to parrotfeather abundance. Community composition of aquatic plants and fish with respect to parrotfeather presence were explored using non-metric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity coefficient; the accuracy of the NMDS ordination is interpreted by 'stress' values (Kruskal, 1964). Raw counts of fish species and biomass of aquatic plant species (minus parrotfeather) at each site were log-transformed to reduce the influence of highly abundant species and standardised to relative abundance to account for differences in sampling effort across sites of varying size. Plant and fish communities were analysed separately for each sampling year. As rare species can disproportionately affect multivariate analysis, species that were present in only one site were removed from the NMDS analysis for that year.

We also examined plant and fish responses across a gradient of parrotfeather abundance. Abundance of all aquatic vegetation varied between 2013 and 2014 due to substantial differences in streamflows and air temperature between the 2 years. To create a parrotfeather gradient that respected interannual and site-level variation, we conducted a principal component analysis (PCA) on five attributes that reflected the extent of parrotfeather in each of the 12 sites where it was present. These attributes were: (i) percent of shoreline with parrotfeather, (ii) visual assessment (scale of 1–5) of the extent of parrotfeather, (iii) total parrotfeather biomass collected at the site and normalised by the number of traps, (iv) the proportion of traps where parrotfeather was present, and (v) the proportion of traps where parrotfeather was the dominant plant species.

The PCA was conducted separately for each sampling year, and the scores from the first principal component (PC1, i.e., the parrotfeather gradient) were extracted for correlation with plant and fish diversity and abundance indices. For both plants and fish, we calculated the Shannon–Wiener diversity index (H') separately for native and non-native species in each year. Plant and fish abundance were calculated for each site as the native or non-native biomass (plants) and native or non-

native counts (fish) normalised by the number of traps. Linear correlations of these metrics with the degree of parrotfeather abundance (PC1 scores) were examined using Pearson product-moment correlation coefficients. All analyses of biological community data were conducted using the vegan package in R (Oksanen *et al.*, 2015).

Given the potential for spatial proximity to confound analysis of communities across sites and longitudinal extent, we tested the plant and fish data for evidence of spatial autocorrelation (i.e., sites that are closer together have more similar composition) using Mantel tests on geographic distance and community composition matrices for plants and fish in each year. We also tested for a specific type of autocorrelation in terms of longitudinal (upstream to downstream) trends by examining correlations of NMDS axes (for plants and fish) and PC axes (for parrotfeather) with river kilometer (RKM). Mantel tests resulted in very low evidence of spatial autocorrelation in either year for plants (Mantel $R < 0.20$, $P > 0.06$) and fish (Mantel $R < 0.09$, $P > 0.18$). Correlations with RKM were non-significant ($R < 0.35$, $P > 0.12$) with the exception of a negative correlation of NMDS axis 2 for plant communities in 2014 only ($R = 0.69$, $P < 0.01$). Overall, tests indicated little to no evidence of spatial autocorrelation that would confound interpretation of results.

Results

Physical structure of native and non-native plant species

Complexity of native and non-native plant species as measured by fractal D in the laboratory ranged from 1.57 to 1.82 and varied significantly between species (Fig. 2a; ANOVA $F_{5,18} = 10$, $P < 0.01$). Complexity of both non-native parrotfeather and Brazilian elodea were high compared to native plants (surpassed only by native narrow-leaf bur-reed), but were significantly different only compared with native hornwort (Tukey's, $P < 0.01$). Differences between non-native parrotfeather and Brazilian elodea and the native plant community were more strongly apparent in comparisons of plant volume and dry weight biomass (Fig. 2b; ANOVA $F_{5,18} = 10.23$ and 17.07 , $P < 0.001$). Volumes of both non-native species were significantly greater than two native species (waterweed and Richardson's pondweed) (Tukey's, $P < 0.01$), and dry weight biomass was significantly greater than three native species (waterweed, Richardson's pondweed, and narrow-leaf bur-reed) (Tukey's, $P < 0.01$).

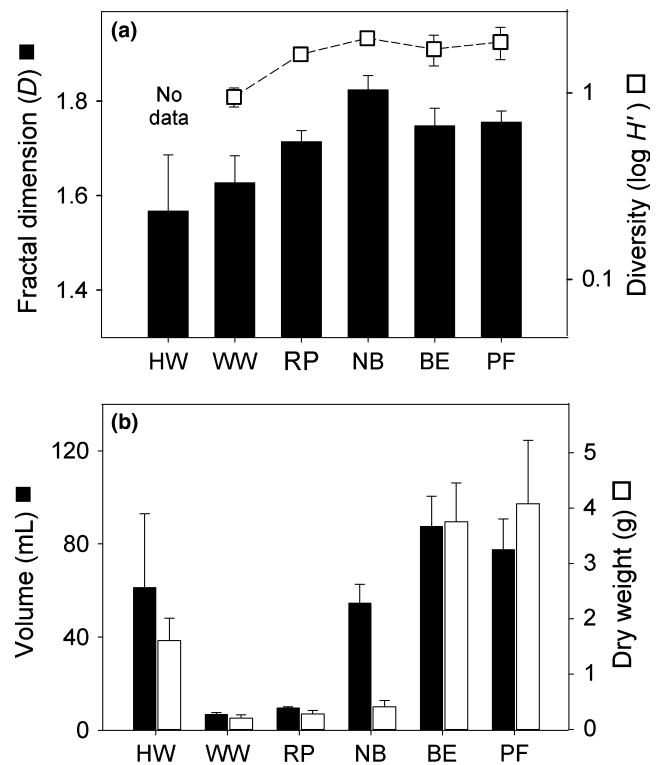


Fig. 2 (a) Mean \pm SE of fractal D (bar graph, $n = 4$) and Shannon's H' for invertebrate diversity (\square , $n = 2$) associated with dominant native and non-native plant species and (b) mean \pm SE plant volume (black bars) and dry weight (white bars) for individual plant specimens measured previously for fractal D ($n = 4$). Species codes are: HW = hornwort, WW = waterweed, RP = Richardson's pondweed, NB = narrow-leaf bur-reed, BE = Brazilian elodea, PF = parrotfeather. [Note: invertebrates were not collected for HW].

Effects of plant characteristics on invertebrate assemblages and dissolved oxygen

Diversity of invertebrates (H') collected from plant species was closely associated with fractal D , and was therefore relatively high for both parrotfeather and Brazilian elodea (Fig. 2a). However, differences in H' were significant only between waterweed and parrotfeather and waterweed and narrow-leaf bur-reed (Welch ANOVA, $F_{4,2} = 256.6$, $P < 0.01$; REGWQ, $P < 0.05$). Comparisons of dominant invertebrate taxa revealed substantial differences in community composition between native and non-native macrophyte species (Fig. 3). Cladocera, chironomids, and gastropods distinguished the communities associated with native plants, while amphipods (and copepods to a lesser extent) were prevalent in parrotfeather and Brazilian elodea. Large-bodied insects (Odonata + Ephemeroptera + Hemiptera) were a strong component in only one native species (narrow-leaf bur-reed), but overall were better

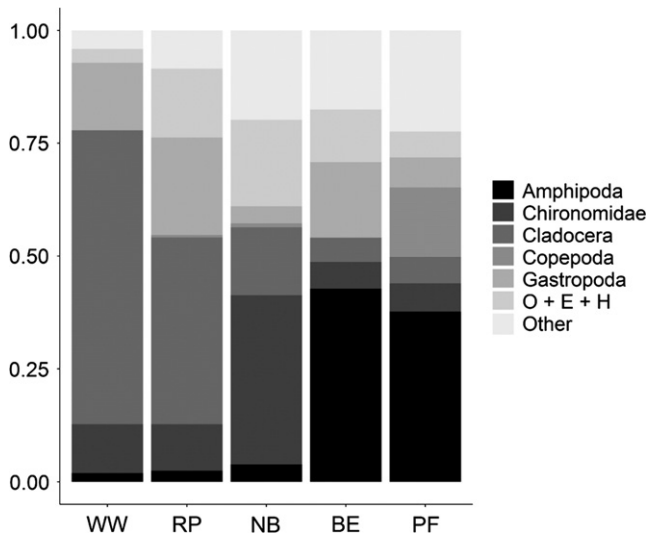


Fig. 3 Relative abundance of dominant invertebrate taxa found in native (WW, RP, NB) and non-native (BE, PF) aquatic plant species. 'O+E+H' = Odonata, Ephemeroptera, and Hemiptera. Aquatic plant species codes are: WW = waterweed, RP = Richardson's pondweed, NB = narrow-leaf bur-reed, BE = Brazilian elodea, PF = parrotfeather.

represented in native macrophytes compared to parrotfeather and Brazilian elodea.

Dissolved oxygen concentrations varied significantly depending on the associated aquatic plant species (Welch ANOVA, $F_{5,104} = 12.30$, $P < 0.001$). Quadrats where native plant species were dominant were similar to or had higher DO than areas with no vegetation (Fig. 4). The lowest DO concentrations were observed in quadrats dominated by parrotfeather (mean = $3.7 \text{ mg O}_2 \text{ L}^{-1}$, $SD = 2.2$), and were significantly lower than was observed for all native species or open areas (REGWQ, $P < 0.05$). Diel comparison of DO concentrations between waterweed and parrotfeather within a single site supported the point samples comparison, with typically lower (but more fluctuating) DO concentrations observed in the parrotfeather patch over a 24-h period (Fig. S1).

Plant and fish assemblages

In each year, there were 12 sites where parrotfeather was present and 10 sites without parrotfeather (reference sites); these sites were consistent between both sampling years (Fig. 1). Macrophyte surveys documented 16 native and 5 non-native species (Table 1). The three most common native species recorded in visual surveys were waterweed, hornwort, and narrow leaf bur-reed; parrotfeather was the most common and

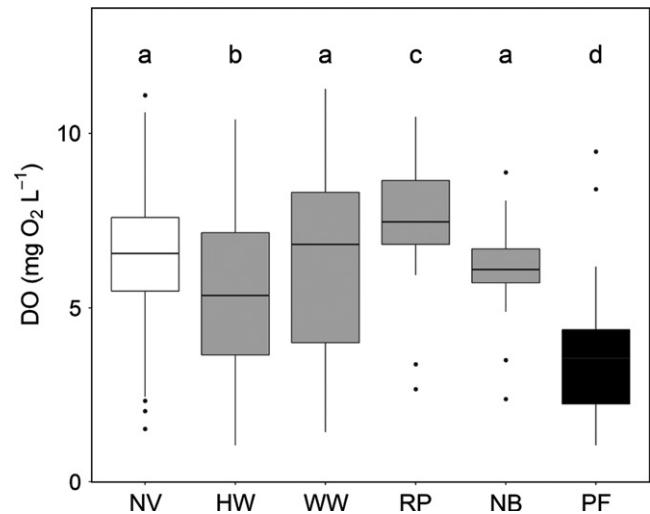


Fig. 4 Dissolved oxygen (DO) concentrations associated with traps or quadrats where no vegetation (white), native (grey) and non-native (black) macrophyte species were identified as dominant. Aquatic plant species codes and samples sizes (n) are as follows: NV = No vegetation (88), HW = hornwort (82), WW = waterweed (108), RP = Richardson's pondweed (31), NB = narrow-leaf bur-reed (29), PF = parrotfeather (22). Letters indicate significant differences between groups as determined by Ryan-Elninot-Gabriel-Welsch (REGWQ) test for pairwise comparisons. Growth forms for the different macrophyte species are: submersed (HW, WW, RP) and emergent (NB, PF).

abundant non-native species based on both visual surveys and biomass collected. With few exceptions, more biomass was collected for species in 2014 than in 2013 (Table 1).

Plant community composition based on collected biomass was consistent between years (Fig. 5), and associated to some extent with presence of parrotfeather. Three distinct native communities – dominated separately by waterweed, Richardson's pondweed, and narrow leaf bur-reed – are apparent (Fig. 5); of these, waterweed has some association with parrotfeather sites. A fourth native community – comprised of hornwort, floating-leaved pondweed (*Potamogeton natans*), and mild waterpepper (*Polygonum hydropiperoides*) – is largely associated with sites where parrotfeather is present. Parrotfeather sites are more tightly clustered in ordination space compared to non-parrotfeather sites, indicating greater similarity or homogeneity in plant community composition (Fig. 5).

In fish surveys, we captured >5800 individuals representing 10 native and 10 non-native species. The northern pikeminnow (*Ptychocheilus oregonensis*: Cyprinidae) and three-spined stickleback (*Gasterosteus aculeatus*: Gasterosteidae) were the most abundant and widespread native fishes, occurring in >95% of sites when both

Table 1 Total biomass of macrophytes collected across all sites in each year ($n = 211$ rake samples) and representation in visual surveys of dominant, secondary, and tertiary species. The proportion of total visual observations where the species was present is 'Obs (%)' and the percent change in total biomass collected for individual species between 2013 and 2014 is 'Change (%)'. Not shown in the table are species where <10 g of dry weight biomass was collected: yellow pond-lily (*Nuphar lutea*: Nymphaeaceae), blunt-leaved pondweed (*Potamogeton obtusifolius*), fern-leaf pondweed (*P. robbinsii*: Potamogetonaceae), hardstem bulrush (*Scirpus acutus*: Cyperaceae), bladderwort (*Utricularia vulgaris*: Lentibulariaceae), and non-native water celery (*Vallisneria spiralis*: Hydrocharitaceae). Additional species that were recorded only in visual observations were pond water-starwort (*Callitriche stagnalis*: Callitricaceae), lesser duckweed (*Lemna minor*: Lemnaceae), grass-leaved pondweed (*P. gramineus*), and giant duckweed (*Spirodela polyrrhiza*: Lemnaceae).

Family name	Scientific name	Common name	Non-native	Depth in m (mean \pm SD)	Obs (%)	Biomass (g dry wt)		Change (%)
						2013	2014	
Ceratophyllaceae	<i>Ceratophyllum demersum</i>	Hornwort		0.66 \pm 0.49	20	507	2384	370
Haloragaceae	<i>Myriophyllum aquaticum</i>	Parrotfeather	x	0.47 \pm 0.25	9	814	1165	43
Hydrocharitaceae	<i>Egeria densa</i>	Brazilian elodea	x	0.47 \pm 0.32	0.5	0	27	–
	<i>Elodea canadensis</i>	Common waterweed		0.50 \pm 0.29	25	687	1833	167
Poaceae	<i>Phalaris arundinacea</i>	Reed canary-grass	x	0.48 \pm 0.24	3	22	23	5
Polygonaceae	<i>Persicaria hydropiperoides</i>	Mild waterpepper		0.46 \pm 0.21	5	277	1039	276
Potamogetonaceae	<i>Potamogeton foliosus</i>	Leafy pondweed		0.42 \pm 0.21	3	39	139	256
	<i>Potamogeton crispus</i>	Curlyleaf pondweed	x	0.55 \pm 0.39	5	51	30	–41
	<i>Potamogeton richardsonii</i>	Richardson's pondweed		0.55 \pm 0.34	9	160	38	–76
	<i>Potamogeton natans</i>	Floating-leaved pondweed		0.62 \pm 0.27	9	175	418	139
Typhaceae	<i>Sparganium angustifolium</i>	Narrow leaf bur-reed		0.42 \pm 0.18	10	98	102	4

sampling years were considered. Rock bass (*Ambloplites rupestris*) and pumpkinseed sunfish (*Lepomis gibbosus*: Centrarchidae) were the most commonly encountered non-native species, occurring in 77 and 59% of sites, respectively.

Fish community composition differed with respect to parrotfeather presence in both years, with shift in community structure along the first NMDS axis (Fig. 6); this pattern is more pronounced in 2014 than 2013. In both years, a consistent suite of native species – speckled dace (*Rhinichthys osculus*: Cyprinidae), reticulate sculpin (*Cottus perplexus*: Cottidae), and juvenile coho salmon (*Oncorhynchus kisutch*) – occurred in sites with little to no non-native parrotfeather. Native northern pikeminnow, three-spined stickleback, and the catostomid large-scale sucker (*Catostomus macrocheilus*: Catostomidae) were found in sites both with and without parrotfeather in 2013, although association with non-parrotfeather sites is more apparent in 2014. The state 'Sensitive' Olympic mudminnow had low association with parrotfeather sites, but was not a significant driver of community variation in either year. In both years, parrotfeather sites are distinguished by higher relative abundance of non-native species. Although species loadings in ordination space vary in significance (vector length) between years, non-native centrarchids – pumpkinseed sunfish, smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*) and warmouth (*Lepomis gulosus*) – and common carp (*Cyprinus carpio*: Cyprinidae) are

strong determinants of variation in community composition in both years.

Plant and fish diversity and abundance along the parrotfeather gradient

The PCA on the five site attributes (variables) characterising parrotfeather abundance and extent resulted in highly similar patterns between years, with the first principal component (PC1) describing a large majority of the variation (79% in both years). All five variables had highly similar eigenvector loadings on PC1 (range = 0.41–0.48 across both years), indicating similar contributions of each variable to describing the gradient of increasing parrotfeather abundance. The second principal component explained considerably less (14–15%) of the variation in both years.

Diversity of native and non-native macrophytes was both positively correlated with the parrotfeather gradient (i.e., PC1 scores) ($0.24 \geq R \geq 0.69$, Fig. 7a) in both sampling years, although the relationship was significant only for native diversity in 2014 ($P = 0.01$). Diversity of non-native plants is uniformly low in this system, with a majority of sites exhibiting a non-native H' of zero (Fig. 7a). In both years, biomass of all plants (native and non-native combined, excepting parrotfeather) was positively correlated with the parrotfeather gradient ($R = 0.79$ and 0.43 in 2013 and 2014), although this relationship was significant in 2013 only ($P < 0.01$).

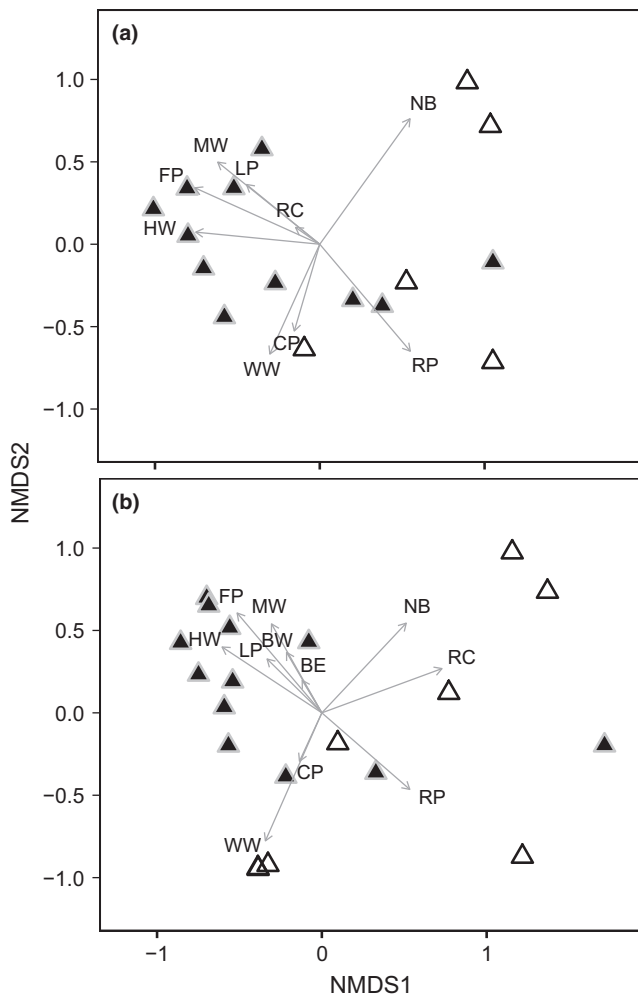


Fig. 5 Ordination of sites using non-metric multidimensional scaling (Bray Curtis distance matrix) based on relative abundances of plant species' biomass collected in (a) 2013 ($stress = 0.10$) and (b) 2014 ($stress = 0.11$). Species that occurred in only one site were excluded from analysis for that year. Sites are designated as parrotfeather present (▲) or absent (△), and vectors showing species' loadings are labelled using an abbreviation of the common name. Native species: HW = hornwort, WW = waterweed, RP = Richardson's pondweed, NB = narrow leaf bur-reed, BW = bladderwort, LP = leafy pondweed, FP = floating leaved pondweed, and MW = mild waterpepper. Non-native species: RC = reed canary-grass, CP = curly-leaf pondweed, and BE = Brazilian elodea.

Native fish diversity was not significantly correlated with parrotfeather abundance in both years ($R = -0.19$ and 0.00 in 2013 and 2014, $P > 0.56$; Fig. 7b). By contrast, non-native fish diversity was positively related to parrotfeather abundance in both years ($R = 0.22$ and 0.77), although this relationship was significant only in 2014 ($P < 0.01$; Fig. 7b). Density of all fish (native and non-native combined) was negatively correlated with parrotfeather abundance in both years ($R = -0.36$ in 2013 and -0.27 in 2014, both $P > 0.25$).

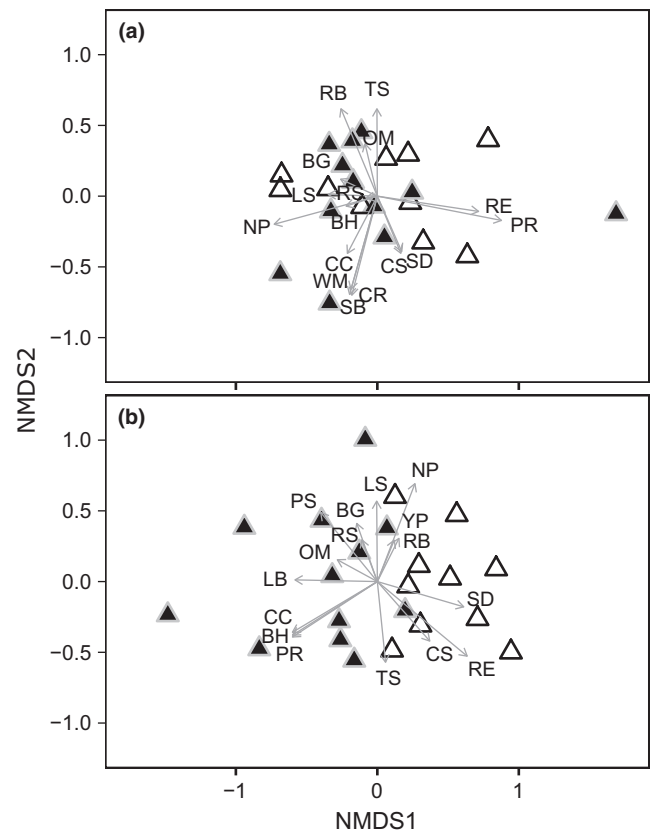


Fig. 6 Ordination of sites using non-metric multidimensional scaling (Bray Curtis distance matrix) based on relative abundance of fish in (a) 2013 ($stress = 0.16$) and (b) 2014 ($stress = 0.18$). Species that occurred in only one site were excluded from analysis for that year. Sites are designated as parrotfeather present (▲) or absent (△), and vectors showing species' loadings are labelled using an abbreviation of the common name. Native species: PR = prickly sculpin (*Cottus asper*: Cottidae), RE = reticulate sculpin, LS = largescale sucker, TS = three-spined stickleback, NP = northern pikeminnow, OM = Olympic mudminnow, RS = reidside shiner (*Richardsonius balteatus*: Cyprinidae), SD = speckled dace, and CS = coho salmon. Non-native species: BH = brown bullhead (*Ameiurus nebulosus*: Ictaluridae), RB = rock bass, CC = common carp, PS = pumpkinseed sunfish, WM = warmouth, BG = bluegill, SB = smallmouth bass, LB = largemouth bass, YP = yellow perch (*Perca flavescens*: Percidae), and CR = black crappie (*Pomoxis nigromaculatus*: Centrarchidae).

Discussion

Prior research on aquatic invasive species has tended to focus on single or small numbers of responses to non-native species, but approaches that evaluate multiple levels of biological organisation are recommended to move towards more balanced and unbiased assessments of ecological impact (Ehrenfeld, 2010; Cucherousset & Olden, 2011). By examining a diverse suite of abiotic and biotic (community) indicators, we were able to

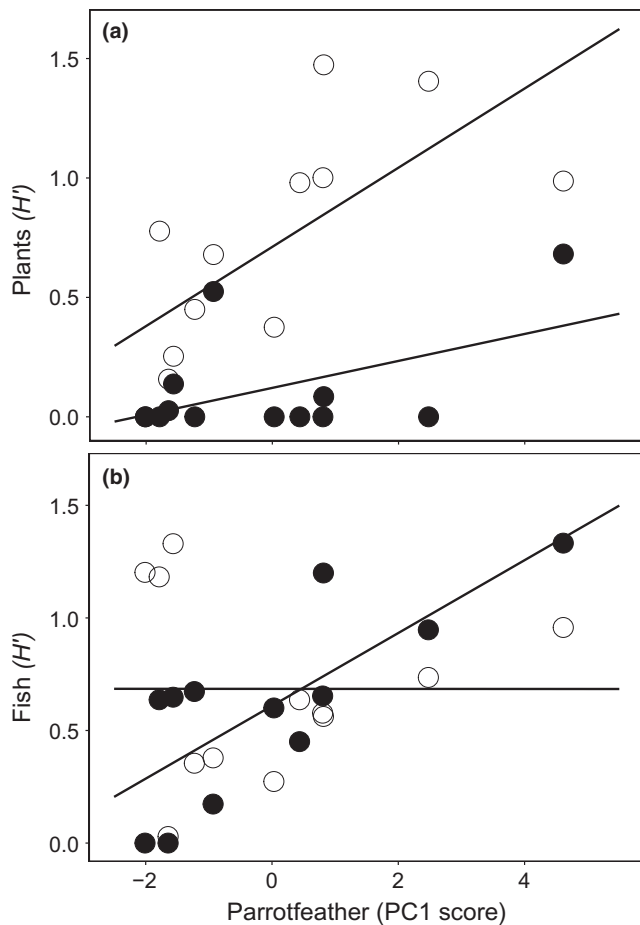


Fig. 7 Diversity described by the Shannon–Wiener diversity index (H') of (a) macrophytes and (b) fish across a gradient of increasing parrotfeather abundance (PC1 score); correlations are shown separately for native (○) and nonnative (●) species groups. Results are shown for 2014 only but exhibited similar trends in 2013 (see text). Parrotfeather was excluded from calculation of non-native macrophyte diversity.

demonstrate multi-trophic impacts of non-native parrotfeather through the mechanisms of oxygen depletion, altered invertebrate communities, and habitat that favours non-native fishes.

We found that the abundance of parrotfeather has consequences for slow-flowing riverine habitats in ways that are distinctive from the effects of native plants. The first of these is dramatic reductions in DO when parrotfeather is dominant, producing oxygen concentrations approaching hypoxic conditions ($<3 \text{ mg O}_2 \text{ L}^{-1}$). Our results are corroborated by other field-based and laboratory reports wherein DO concentrations associated with parrotfeather ranged from *c.* $2.6 \text{ mg O}_2 \text{ L}^{-1}$ (Oborn & Hem, 1962; Wamsley, 1998) to $<1 \text{ mg O}_2 \text{ L}^{-1}$ (Hussner, 2009). Our findings of persistently low DO concentrations are also consistent with the emergent growth form

of parrotfeather. Although low DO can occur in submersed vegetation at night, emergent and floating vegetation is more likely to be associated with these events due to mats that reduce exchange with atmospheric oxygen, shade-induced reductions in photosynthesis, and oxygen being vented to the atmosphere rather than the water column (Pokorný *et al.*, 1984; Cattaneo *et al.*, 1998; Caraco & Cole, 2002).

We also demonstrated distinct differences in the physical structure of parrotfeather compared to the native plant community. Of the suite of plants measured, parrotfeather complexity (as measured by fractal D) is surpassed by only one native species, narrow-leaf bur-reed (an emergent shoreline plant). When additional metrics of volume and dry weight biomass are considered, the potential for parrotfeather to disrupt typical patterns of habitat complexity through addition of dense biomass is apparent. Although Brazilian elodea was not abundant enough to be a focal organism, we were able to collect samples for characterising physical structure (and invertebrate assemblages). It is worth noting that Brazilian elodea has a similarly distinctive physical structure (higher fractal D , volume, and dry weight) compared to the native community, which may result in cascading effects on abiotic and biotic features in areas where Brazilian elodea becomes dominant.

The relatively high diversity of epiphytic invertebrates associated with parrotfeather (and Brazilian elodea) are consistent with greater physical complexity. In laboratory and field studies, invertebrate diversity and density are frequently correlated with macrophyte biomass and higher fractal D (e.g., Kelly & Hawes, 2005; Warfe & Barmuta, 2006). This phenomenon is thought to result from a combination of more surface area, corresponding increases in epiphyton, and greater refuge from fish predation (Warfe & Barmuta, 2006; Warfe *et al.*, 2008). Although the number of invertebrates associated with some invasive macrophytes may be higher, the net result can be reduced foraging efficiencies for fish predators (Crowder & Cooper, 1982; Valley & Bremigan, 2002).

Greater diversity of invertebrates also may not be of particular benefit to fish predators if the supported species are not part of the preferred prey complex (Toft *et al.*, 2003). We saw substantial differences in the invertebrate communities associated with native and non-native macrophytes, with higher relative abundance of cladocerans, chironomids, and gastropods in the native vegetation shifting towards dominance by amphipods in both parrotfeather and Brazilian elodea. We also found lower relative abundance of taxa from the Odonata, Ephemeroptera, and Hemiptera orders (class Insecta)

associated with these non-native plants. Selectivity of macroinvertebrate and zooplankton prey by fish can be highly species- and even context-specific; focused diet and prey selectivity analyses could help determine whether the observed differences in invertebrate communities are likely to have negative, beneficial, or negligible consequences for fish predators in the Chehalis River. In the absence of these studies, however, we can note that the invertebrate community associated with native vegetation – particularly cladocerans (*Daphnia* spp.) and chironomids – appear prominently in fish diets of Pacific Northwest fishes (Tabor, Luecke & Wurtsbaugh, 1996; Francis & Schindler, 2009), including Olympic mudminnow (Tabor *et al.*, 2014). Amphipods are also often considered a lower quality prey option in bioenergetics modelling (Cordell *et al.*, 2010; Tiffan, Erhardt & St. John, 2014), suggesting that amphipod-dominated communities could present a less hospitable foraging environment.

The native fishes that we observed in association with parrotfeather are those that are more tolerant of a range of environmental conditions. The three native species consistently not found in parrotfeather sites (coho salmon, speckled dace, and reticulate sculpin) are not vegetation specialists, and are all classified as 'Intolerant' or 'Sensitive' based on declines in response to various types of habitat degradation (Zaroban *et al.*, 1999). Native species that were more flexibly associated with parrotfeather – northern pikeminnow, three-spined stickleback, and large scale sucker – are all classified as 'Tolerant', and it is worth noting that northern pikeminnow and largescale sucker are also considered tolerant of poor water quality including low DO (Hughes & Gammon, 1987; Cech, Castleberry & Hopkins, 1994).

One of the more striking findings is the positive correlation of non-native fish species with increasing degree of parrotfeather abundance. Ours is not the first study to demonstrate higher abundance of non-native fish in connection with a novel macrophyte; Houston & Duivenvoorden (2003) found that 79% of fish in sites with introduced West Indian marsh grass (*Hymenachne amplexicaulis*) were non-native compared to 3% in areas without West Indian marsh grass. Other studies have documented shifts in both composition and size structure of native or naturalised assemblages in relation to invasive macrophytes (Keast, 1984; Parsons, Marx & Divens, 2011). In the Chehalis River, the non-native fish community is comprised largely of centrarchids, a family of fishes that includes bluegill (*Lepomis macrochirus*), pumpkinseed, smallmouth and largemouth bass. All of these species are generalist predators that prefer well-

vegetated habitats; several are well known for foraging and behavioural plasticity (Cooke & Philipp, 2009). In the case of both smallmouth and largemouth bass, there are concerns regarding the potential ecological consequences due to the predatory tendencies of these fishes (Carey *et al.*, 2011). With very few exceptions, the non-native fish we found associated with parrotfeather sites are classified as 'Tolerant' among Pacific Northwest fishes (Hughes & Gammon, 1987; Zaroban *et al.*, 1999), and two (common carp and brown bullhead) are known for exceptional tolerance of low and fluctuating DO (Beamish, 1964; Davis, 1975).

We did not find strong evidence that parrotfeather is outcompeting native plants, but this may reflect the fact that our community analysis was at a site rather than at a plot scale. Diversity and abundance of native and non-native plants were correlated with parrotfeather extent, suggesting that habitat characteristics that promote parrotfeather (e.g., increased light, shallow depth) also support a variety of native species. The native species that co-occurred with parrotfeather include hornwort (a submersed rootless macrophyte), and floating-leaved pondweed. Both prefer deeper water (>0.6 m) and are unlikely to be competitive with parrotfeather. Two common native species that were disassociated from parrotfeather sites were waterweed, a submersed species, and narrow leaf bur-reed, a shoreline plant. Both occur in the same depth zone and are among the more likely species to be in direct competition with parrotfeather. Given parrotfeather's emergent leaves, formation of dense mats, and capacity for rapid growth, as parrotfeather biomass increases at a plot level we would expect declines in native richness as has been previously documented with parrotfeather in ponds in Belgium (Stiers *et al.*, 2011). However, formation of monospecific stands might be true of some native macrophytes as well: experimental approaches combined with assessment of plant communities over time (e.g., Santos, Anderson & Ustin, 2011) may help better resolve whether parrotfeather can outcompete native species and which species would be most at risk.

A fundamental motivation of this research was to examine the multi-trophic consequences of parrotfeather in order to develop a comprehensive and mechanistic understanding of impact. Such approaches represent a much needed advance not only for non-native macrophytes, but aquatic invaders generally (Strayer, 2010; Cucherousset & Olden, 2011), particularly as we move towards a more nuanced outlook that accounts for the broader environmental context of invasions (Schlaepfer *et al.*, 2011). While the ultimate consequences for the

aquatic plant community in the Chehalis River remain uncertain, we found that parrotfeather has the potential for dramatic local impacts in areas that support fish populations: the primary mechanism appears to be the uniquely dense and emergent physical structure that drives changes in DO and invertebrate assemblages.

These changes, in turn, may facilitate occupancy by non-native fish, suggesting that parrotfeather is creating or enhancing a novel habitat niche. That non-native fish diversity, but not density, increased along the parrotfeather gradient suggests that sites with parrotfeather may support more diverse non-native assemblages but may not provide particularly high quality habitat for these species. The potential for parrotfeather to promote changes in physical habitat complexity that supports novel species compositions is underscored by the fact that in addition to increased prevalence of non-native fish, we captured tadpoles of invasive American bullfrog (*Rana catesbeiana*) only in sites with parrotfeather. Furthermore, the proportion of traps containing tadpoles was strongly and significantly correlated with the increasing parrotfeather gradient (results not shown).

Additional research opportunities exist that would further illuminate the degree to which parrotfeather may impact freshwater ecosystems. Changes in the overall invertebrate community were strongly indicated, but were based on small sample sizes and low taxonomic resolution. Our findings of increased epiphytic invertebrate diversity associated with parrotfeather is an intriguing contrast with other research documenting reduced diversity of benthic invertebrates in patches of non-native macrophytes including parrotfeather (Stiers *et al.*, 2011). Future research could focus on underlying mechanisms of divergent invertebrate assemblages (e.g., DO tolerance or increased refuge) as well as consequences for higher trophic predators. An assessment of the distributional extent of parrotfeather and rates of spread in the Chehalis River has not been done recently, but is an important component in characterising the impact of parrotfeather at larger scales. These uncertainties notwithstanding, our research suggests that parrotfeather can be a highly impactful invader in slow-water habitats, justifying the attention of natural resource agencies worldwide towards management and prevention of further spread.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supplemental methods.

Figure S1. Diel DO concentrations within native waterweed (dark grey dotted) and parrotfeather (black

dashed) and open water (light grey solid). Measurements were made using an unattended sonde over consecutive 24-h periods (instrument sensor depth = 0.4 m). Measurements were corrected for drift and the 24-h periods aligned temporally for comparison.

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