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PRIMARY RESEARCH PAPER

Twenty year contrast of non-native parrotfeather distribution and abundance in an unregulated river

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Abstract Efficient management of invasive species benefits from understanding patterns of persistence and change over time. In this study, we compare distribution and abundance of the invasive macrophyte parrotfeather (*Myriophyllum aquaticum*) in an unregulated river system between the time near its presumed introduction and 20 years later. Initial surveys were conducted in 1996–1997, and were repeated in 2015–2016 using similar methodology. Moderate increases in the proportion of river kilometers with parrotfeather between the two periods were observed, but the distribution of sites with low, medium, and high abundance remained consistent, with small numbers of sites in either period having well-established extents of parrotfeather. The distributional extent has moved downstream, with the most upstream and downstream presences shifted by 17 and 28 river kilometers, respectively; however, parrotfeather remains sparse in the lower reaches below the historical downstream extent. Sites with high abundance and stable presence over time are in the intermediate segment of the river, indicating longitudinal and hydrologic controls on distribution. In contemporary sites, area of parrotfeather cover was associated with larger, deeper habitats, whereas dominance of parrotfeather occurred in smaller sites having uniformly shallow depth and low bank slopes. Sites where both abundance and dominance were low had dense canopy cover. Our results demonstrate that landscape and site-level characteristics restrict establishment and persistence of parrotfeather, and that hydrologic alterations to stabilize flow regimes and land use changes should be considered for their potential to increase presence of parrotfeather and other invasive aquatic plants in dynamic floodplain habitats.

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Introduction

Parrotfeather [*Myriophyllum aquaticum* (Vell.) Verdc.] is a native macrophyte to South America, which gained popularity in the aquarium trade over a century ago and has since become a problematic invader in waterways worldwide (Sutton, 1985; Moreira et al., 1999; Hussner et al., 2017). Parrotfeather establishes and can become abundant in lotic and slow-moving lentic systems (Hussner & Champion, 2012), and its distribution is likely to be influenced by changes or stabilizing of the hydrologic regime from water regulation (Aguiar et al., 2001; Wersal & Madsen, 2011; Zhang et al., 2021). The ecological impacts of parrotfeather can be wide ranging, including causing reductions in dissolved oxygen, changes in invertebrate communities, and significant modifications to availability and complexity of fish habitat (Hussner, 2009; Kuehne et al., 2016). Parrotfeather infestations can also interfere with built infrastructure such as drainage ditches and irrigation canals by impeding water flow (Guillarmod, 1979; Moreira et al., 1999). Parrotfeather is notoriously difficult to control using herbicides or biocontrols (Catarino et al., 1997; Armellina et al., 1999; Hofstra et al., 2006; Garner et al., 2013; Kuehne et al., 2018), and has been shown to be highly tolerant of cold and periods of extended water drawdown (Moreira et al., 1989, 1999; Wersal & Madsen, 2013; Hussner et al., 2017). These attributes underlie studies demonstrating that management and eradication of parrotfeather requires long-term and persistent effort over many years (e.g., Hofstra et al., 2006), which may unduly tax limited resources of public and private entities tasked with control (Pluess et al., 2012).

Management efforts for parrotfeather and other aquatic invasive species can benefit from understanding how environmental features at landscape or local levels may promote or constrain populations (i.e., environmental filtering) (e.g., Vander Zanden & Olden, 2008). Such knowledge can make management efforts more efficient by tailoring resources based on likelihood of success over shorter or longer time periods in different areas, and provide important context to evaluate the success of containment and treatment. Evaluating the ecological impact of non-native species requires not only an understanding of per-capita effects at different spatial and organizational scales (Cucherousset & Olden, 2011; Kuehne et al., 2016), but also understanding change in abundance and distribution over time (Strayer et al., 2006; Blackburn et al., 2014). Furthermore, understanding the role of environmental filtering is critical to evaluate how distributions of invasive species may be impacted by changes in land use, hydrologic alteration, and anthropogenic climate change (Radinger et al., 2019; Li & Shen, 2021). However, knowledge of the temporal dynamics of invasions is very limited, in part because the timing of introduction is often unknown or poorly documented (Strayer et al., 2006) and surveys may not be conducted until invaders have become prevalent (Costello & Solow, 2003; Solow & Costello, 2004).

We had the opportunity to assess changes in the distribution and abundance of non-native parrotfeather between a 20-year period in the Chehalis River Basin, Washington (USA), by comparing a present day and historical survey that was conducted shortly after parrotfeather was introduced. Furthermore, the Chehalis River offers a unique opportunity to evaluate spatial and temporal shifts in an unregulated and relatively undeveloped river system, which can help extend previous research on how hydrology and land use may influence establishment and persistence of parrotfeather and other invasive macrophytes (Aguiar et al., 2001; Demars & Harper, 2005; Ot'ahel'ová et al., 2007; O'Hare et al., 2011; Demars et al., 2014). Experimental work has demonstrated that parrotfeather biomass increases with stable water levels, warmer temperatures, and light (Wersal et al., 2011; Wersal & Madsen, 2011, 2013; Zhang et al., 2021). Field studies have shown that parrotfeather establishment and abundance is associated with areas of low discharge, shallow depth, and high availability of light; when these factors are all present parrotfeather can become dominant or monotypic (Moreira et al., 1989). These environmental determinants of establishment and growth suggest that parrotfeather populations may be limited by or respond to larger landscape-scale factors such as floodplain extent and channel morphology, which often vary longitudinally (O'Hare et al., 2011). Site-level characteristics that could constrain or promote parrotfeather include riparian canopy and shading, water depth, and shoreline length (Hussner, 2009, 2014; Xie et al., 2013). Both landscape and site-level features may also interact with flood regime (Aguiar et al., 2001; Hussner & Lösch, 2005; O'Hare et al., 2011); for example, the Chehalis River is a rain-dominated system that is subject to large fall and spring floods, increasing the likelihood of dramatic water level fluctuations and winter scouring flows (Reidy Liermann et al., 2012).

We hypothesized that the contemporary distribution of parrotfeather would show evidence of downstream dispersal since the initial survey in 1996–1997, with an overall greater number of river kilometers being occupied, and previously unoccupied downstream areas now containing large (i.e., established) extents of parrotfeather. Because only female plants are present in North America, dispersal is via fragmentation only (Aiken, 1981); we anticipated that the annual flood events that occur in the Chehalis River would create consistent propagule pressure to downstream reaches (Honnay et al., 2001), where the floodplain is widest and there is ample off-channel wetland habitat (Chehalis Basin Strategy, 2019). Within sites, we expected that abundance (i.e., extent or area of plant cover) and dominance of parrotfeather (i.e., the proportion of the site that was covered) could be predicted by physical and chemical site characteristics. Shoreline length, shallow nearshore depth, and reduced canopy cover were expected to promote abundance, whereas dominance was expected in sites with uniformly shallow water and reduced canopy cover. Both abundance and dominance were expected to be associated with warmer temperatures and lower dissolved oxygen. Abundance was distinguished from dominance due to differences in ecological impacts that can occur across a gradient of parrotfeather infestation (Kuehne et al., 2016), as well as the potential need for differing management and restoration approaches in areas where parrotfeather may be abundant but not dominant and vice versa.

Efforts to control parrotfeather along the Chehalis River have been sporadic and in limited areas (Kuehne et al., 2016, 2018, 2020). This is in contrast to more systematic efforts to eradicate Brazilian elodea (*Egeria densa* Planch.) and purple loosestrife (*Lythrum salicaria* L., Lythraceae) (Simon & Peoples, 2006). However, management efforts for these other species have not included comprehensive and systematic mapping such as exists for parrotfeather, making the historical survey a unique opportunity to contrast differences in distribution and abundance between time periods. Contrasting the two survey periods and identifying environmental features that promote or constrain parrotfeather should help guide future survey and management by state and county agencies and private landowners, which are mandated to control invasive plants within and between their jurisdictions (Simon & Peoples, 2006).

In this study, we compared the occurrence and abundance of parrotfeather along ca. 100 km of the Chehalis River, and quantified changes over a 20-year period. Importantly, we evaluate the degree to which longitudinal position along the river is associated with establishment and persistence over time, and factors within sites that are associated with parrotfeather abundance and dominance. In addition to casting light on rarely studied temporal dynamics of species invasions, we also demonstrate how understanding these spatial and temporal trends can be translated into concrete management recommendations to support basin-wide planning for aquatic species.

Methods

Study area

The Chehalis River is a low-gradient, rain-dominated system that flows 200 km and drains a 2700-km^2 watershed in southwestern Washington State. Parrotfeather has persisted here since 1994 when it was first discovered by the Lewis County Noxious Weed Board growing in backwater areas near Centralia (Wamsley & Hupp, 1997). The Chehalis River is Washington's second largest basin, and is currently unregulated with the exception of a single headwater dam; it is typified by many semi- and partially connected habitats (oxbow lakes, seasonal wetlands). Land cover in the watershed is predominantly forested, with smaller percentages of developed, wetland, and agricultural areas (Chehalis Basin Strategy, 2019). As part of comprehensive planning for aquatic restoration and flood control, ecological regions with distinct geologic and hydrologic processes have been identified (Chehalis Basin Strategy, 2019). This study was conducted in the three ecological regions that encompass the mainstem river (upstream to downstream): Middle Chehalis River, Lower Chehalis River, and Chehalis River Tidal. The Middle Chehalis region is characterized by a deeply incised channel and disconnected off-channel habitat, whereas the Lower Chehalis has a more extensive and connected floodplain; the Chehalis River Tidal region is very low gradient alluvial valley, but with substantial tidal influence.

Historical longitudinal survey

Shortly after the initial detection of non-native parrotfeather in the Chehalis River, a comprehensive survey was conducted by Lewis County in 1996–1997 to establish the early extent and impact (Wamsley & Hupp, 1997; Wamsley, 1998). We reconstructed these longitudinal surveys to compare distribution and prevalence (i.e., sites with low, medium, and high abundance of parrotfeather) with the contemporary period. The initial survey of 105 river kilometers (RKM) between Chehalis (RKM 125) and Montesano (RKM 21) occurred in June–July 1996. The upstream half of the survey (from Chehalis to Oakville) was conducted by canoe, and downstream areas (below Oakville) were done using an airboat. Locations with parrotfeather were georeferenced, and the extent of parrotfeather in sites was estimated using either a 3-category area estimate (< 100 ft^2; 100 ft^2-1 acre; > 1 acre) or a density rating (1–4) that described extent and likelihood of persistence in the site (Resource Management, Inc., 1997; Wamsley & Hupp, 1997). The following year, a large majority of the same river extent was resurveyed in the first week of July, with remaining sections surveyed in August–September. Only four new locations with parrotfeather (some very small) were identified in 1997 that were not noted in 1996. Not all of the locations reported from the combined 1996–1997 surveys were identifiable based on the GPS coordinates, maps, or site descriptions. However, these exceptions were few, with only 5 of 47 historical survey records excluded due to lack of confidence in georeferencing.

Contemporary longitudinal survey

To establish the contemporary distribution for contrast with the historical survey, we mapped presence and abundance of non-native parrotfeather along the mainstem Chehalis River in July of 2015 and 2016. The 2015 survey started at Centralia (RKM 108); in 2016 the survey began in Chehalis (RKM 125) to match the historical survey. The downstream extent in both years was in Montesano (RKM 21). In both years, the river was surveyed by canoe, and observers used binoculars to identify and map even small or isolated plants as well as patches and large extents of parrotfeather. Surveyors inspected all incoming creeks and tributaries, backwaters, and groundwater sloughs; at each of these points, surveyors inspected the area by walking a distance of 50 m from the mainstem river along the incoming waterway.

In both 2015 and 2016, the location and area of parrotfeather patches were mapped using a handheld GPS (Garmin GPSMAP 64sc, accuracy 3 m). Parrotfeather patches that were larger than 3 m^2 were mapped by walking or wading the perimeter (or paddling a float tube in deeper sites) with the GPS to create a tracklog (1 waypoint $second^{-1}$). Tracklogs were subsequently imported into ArcGIS and converted to polygons to calculate the area (m^2). The area of patches that were smaller than 3 m^2 were visually estimated; the majority of these small patches consisted of single plants approximately 1 m^2 in area. The area of patches from polygons and waypoints with visually estimated areas formed a combined georeferenced dataset that was then summarized by river kilometer or site.

Environmental and site characteristics associated with parrotfeather abundance and dominance

To evaluate how environmental features at the site level promote or constrain parrotfeather abundance and dominance, in the contemporary survey we measured characteristics of stable sites along the river where parrotfeather was present in both years of the contemporary survey. Parrotfeather was patchily distributed along the river, and found in greatest abundance and densities in semi- or fully enclosed areas such as well-defined backwaters, sloughs, and beaver-dammed areas. During the first contemporary survey in 2015, we identified 24 of these sites with parrotfeather patches that were likely to persist and/or expand in the following year (i.e., "fixed sites"), allowing comparison of parrotfeather extent and environmental characteristics in both years. [Note: approximately half of these sites were treated partially or wholly with herbicides in 2015, but change in parrotfeather biomass between the 2 years due to herbicide treatment was negligible (Kuehne et al., 2018, 2020)].

Within these fixed sites, environmental data were collected at cross-sectional transects every 10 m to evaluate the role of site-level characteristics in predicting abundance (i.e., total area) and dominance (i.e., proportional area of cover) of parrotfeather. Metrics were selected to reflect and characterize physical site characteristics expected to promote or hinder establishment of parrotfeather (i.e., water depth, shading, potential for scouring flows). At each transect, the following physical metrics were measured or visually estimated: bankfull width (m), mid-channel depth (m), half-channel (i.e., nearshore) depth (m), density of the canopy cover (0–100%) and the bank slope (0°–90°). Water quality parameters can also promote (or be influenced by) presence or prevalence of aquatic macrophytes; abundance and dominance of parrotfeather might be expected to correspond with warmer temperatures (Wersal et al., 2011) and lower dissolved oxygen (Hussner, 2009; Kuehne et al., 2016). Temperature (°C), dissolved oxygen (mg L^{-1}), and conductivity (S m^{-1}) were measured at every transect having sufficient depth ($\geq$ 20 cm) using a handheld YSI meter (Model Pro 2030).

Data summary and analysis

All data summaries and statistical analyses were conducted in the R Statistical Programming Environment (R Core Team, 2019). Parrotfeather occupancy in historical and contemporary periods was compared for the 105 river kilometers between Chehalis and Montesano. Historical and contemporary parrotfeather points were snapped to the mainstem Chehalis River flowline according to the U.S. National Hydrography Dataset (U.S. Geological Survey, 2019), and distance calculated from the mouth of the river. Occurrence data were binned to create historical and contemporary datasets of occupied and unoccupied RKM. Occupancy and longitudinal abundance in the two contemporary years (2015 and 2016) was compared; however, the historical period was contrasted with contemporary data from 2016 only, as this was the year where the upstream survey extent matched that of the historical period. The number of occupied and unoccupied RKM in historical and contemporary surveys was contrasted using a Chi-squared test for paired samples, and occupied RKM in each period were plotted to evaluate changes in the longitudinal distribution of parrotfeather over time.

To compare the proportion of sites between historical and contemporary periods having low to high parrotfeather abundance, we first aggregated the waypoints and tracklogs from the contemporary survey into discrete sites. Twenty-four fixed sites were identified in the field (see above); for dispersed parrotfeather points outside of these areas (i.e., individual waypoints or tracklogs along the river), we used a threshold of 100 m to consolidate points that were close to one another, using the central point as the site location. The total area of parrotfeather cover (m^2) was summed for each site, which were then categorized into density ratings (1–4) using the criteria from the historical survey protocol (Resource Management, Inc., 1997). To statistically contrast the distribution of sites with low (density rating = 1) to high (density rating = 4) abundance of parrotfeather, we used a test of equal densities implemented in the sm package (Bowman & Azzalini, 2018) on the distributions of parrotfeather ratings for sites in each period.

To relate patterns of parrotfeather abundance and dominance with physical and chemical characteristics in the 24 fixed sites, we used non-metric multidimensional scaling (NMDS) to first establish multivariate relationships among the environmental variables. The variables included the following derived from transect data: shoreline length (i.e., mean bankfull width x site length), the standard deviation of mid-channel depths, mean half-channel depth, mean percent canopy, mean bank slope, mean temperature, mean conductivity, and mean dissolved oxygen. We also included a variable for year to account for inter-annual differences in environmental variables. The NMDS was performed on the $\ln(x + 1)$ transformed variables with Bray–Curtis distance, and data were initially tested for univariate and multivariate normality (MVN package, web version 1.6).

The ability of the ordination to explain parrotfeather abundance and dominance was evaluated by fitting separate Generalized Additive Models (GAMs) to the first two NMDS axes using the ordisurf function in R. GAMs allow identification and testing of non-linear relationships, and create fitted contours between the ordination of environmental variables and response metrics. Parrotfeather abundance was the summed area of parrotfeather cover for the site, and parrotfeather dominance was calculated as the proportion of the total site area with parrotfeather cover present; both metrics were log-transformed prior to analysis. The NMDS and ordisurf GAMs were implemented and the significance and model fit assessed using the vegan and mgcv packages in R (Wood et al., 2016; Oksanen et al., 2019).

Results

The longitudinal distribution of parrotfeather shifted downstream between the historical and contemporary periods (Fig. 1), while the proportion of RKM occupied by parrotfeather increased between the two periods, demonstrating marginal significance, χ^2 (1, N = 105) = 3.4, P = 0.07. Parrotfeather was present in 24 of the 105 RKM (23%) surveyed in the historical period, and 36 of the RKM (34%) in the contemporary period, representing a doubling of river kilometers where parrotfeather was documented (Fig. 2). Although the percentage of occupied RKM was higher, parrotfeather recorded in the upstream reaches of the river (> RKM 100) during historical surveys was rarely detected in contemporary surveys, and the uppermost contemporary occurrence was 17 RKM downstream from that of the historical period (Figs. 1–2). The opposite trend was observed in lower reaches, where parrotfeather was undetected in historical surveys but was present in contemporary surveys, and the furthest downstream occurrence was 28 RKM below that of the historical period. Nine of the 10 RKM where parrotfeather was detected in both historical and contemporary surveys were in the intermediate segment of the river (between RKMs 57 and 75). Longitudinal abundance or total area of parrotfeather cover in 2016 corresponded with areas of persistence, where RKM with highest abundance were the same or highly proximate to those where parrotfeather was detected in both periods (Fig. 2). In the two contemporary survey years, the number of RKM with parrotfeather was greater in 2016 than in 2015; area of parrotfeather cover by RKM was strongly correlated between the 2 years (Pearson's r = 0.95, P < 0.001) and was more abundant in the 2nd year.

The proportion of sites having low, medium, and high abundance density ratings did not change significantly between the two time periods (P = 0.59) (Fig. 3). More than half of the sites in both periods (57–58%) had the lowest density rating of 1 (< 100 ft^2). Sites with density ratings of 3 (> 1000 ft^2 and < 1 acre) and 4 (> 1 acre) comprised the smallest proportion of sites in both survey periods.

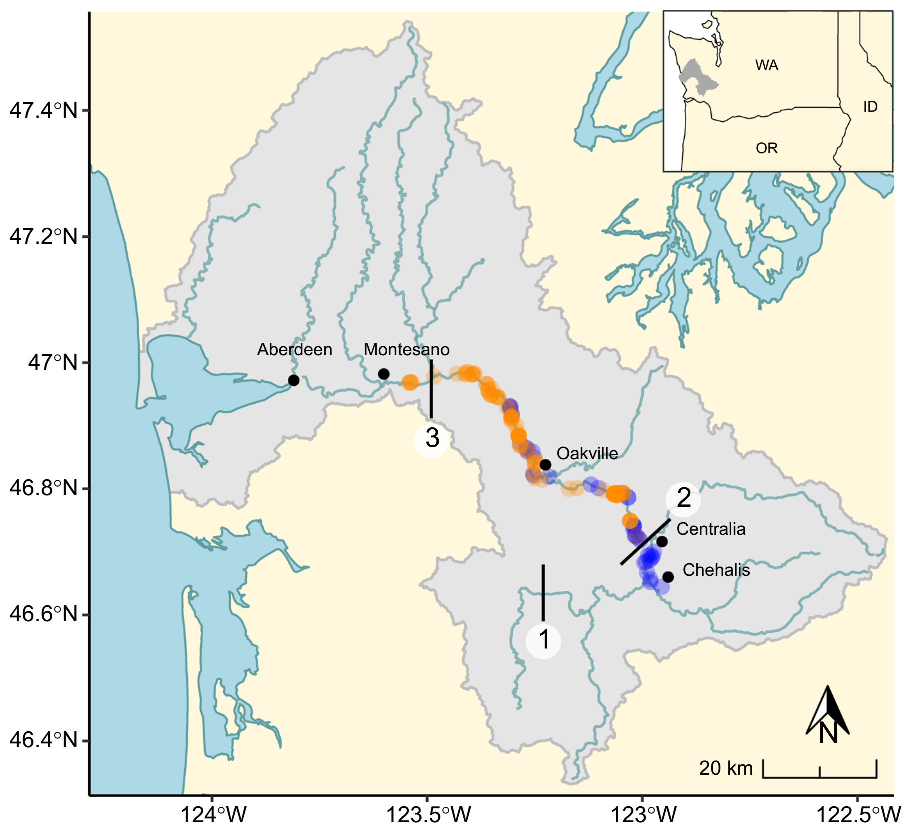

Fig. 1 Distribution of non-native parrotfeather along the mainstem Chehalis River between the cities of Chehalis (RKM = 125) and Montesano (RKM = 21) as documented during surveys in 1996–1997 (blue circles) and 2016 (orange circles). Numbered segments show the upstream points of the Middle Chehalis (1), Lower Chehalis (2), and Chehalis River Tidal (3) ecological regions, which were defined as part of basin-wide restoration planning (Chehalis Basin Strategy 2019). Inset shows the location of the Chehalis River watershed (grey shading) in southwestern Washington State, USA

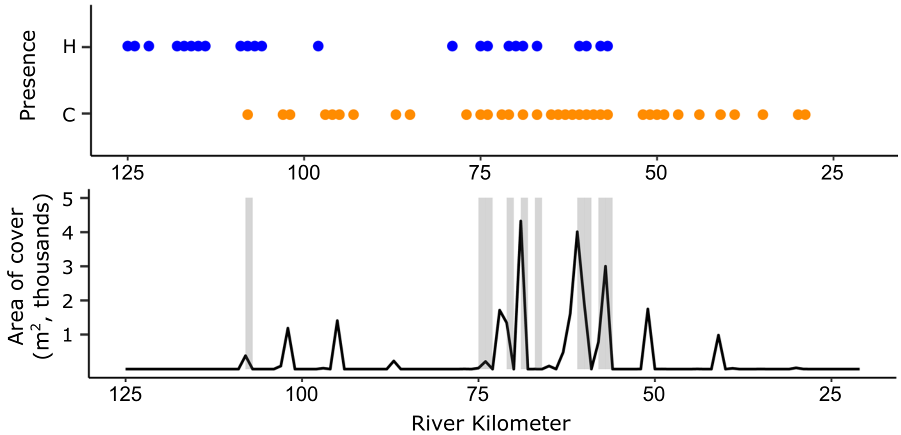

Fig. 2 River kilometers (RKM) between Chehalis (RKM = 125) and Montesano (RKM = 21) where parrotfeather was present in historical ("H", blue circles) and contemporary ("C", orange circles) surveys, and the summed area of parrotfeather cover (black solid line) as surveyed in 2016. Grey shading indicates RKM where parrotfeather was present in both periods

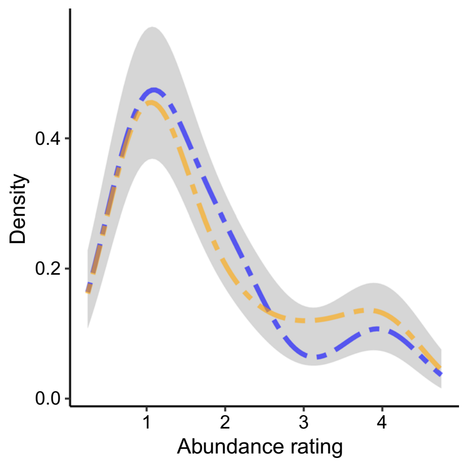

Fig. 3 Comparison of kernel density estimates of the distribution of parrotfeather ratings (1–4, lowest to highest abundance) at sites along the Chehalis River in historical (blue dashed line) and contemporary (orange dashed line) periods. 95% confidence intervals (grey shading) indicate that the distributions are statistically equal between the two periods

In the 24 fixed sites where environmental transect data were collected in 2015 and 2016, parrotfeather abundance and dominance were significantly correlated with each other ($R^2 = 0.71$, $P < 0.01$) but have different non-linear relationships with the ordination of environmental variables (Fig. 4). Six variables contributed strongly ($P < 0.05$) to the ordination: shoreline length, standard deviation of mid-channel depth, half-channel depth, bank slope, canopy, and dissolved oxygen. GAM fitting demonstrated that the gradient of parrotfeather abundance was strongly and significantly explained by the ordination (*Adj.* $R^2 = 0.61$, $P < 0.01$). Abundance was positively associated with greater shoreline length, nearshore depths, and variability in mid-channel depth, and was negatively associated with increased riparian canopy and dissolved oxygen (Fig. 4a). Dominance of parrotfeather was significantly but less strongly explained by the ordination (*Adj.* $R^2 = 0.32$, $P < 0.01$), and was associated with more intermediate environmental conditions than abundance. Dominance was associated with reduced shoreline length, nearshore depths, and depth variation; it was also more strongly associated with low riparian canopy cover, bank slopes, and dissolved oxygen than was abundance (Fig. 4b).

Discussion

This study documented change in the distribution of an invasive aquatic plant in a large unregulated river system with a 20-year interval between survey periods. Importantly, the initial survey is likely to have occurred within a relatively short period (i.e., within 5–10 years) following introduction and detection, meaning that we are able to document differences between early and more mature stages of the invasion process (Strayer et al., 2006). Previous work on spatio-temporal changes in the distribution and abundance of invasive species in rivers has largely focused on fish and invertebrates, which differ in mobility and

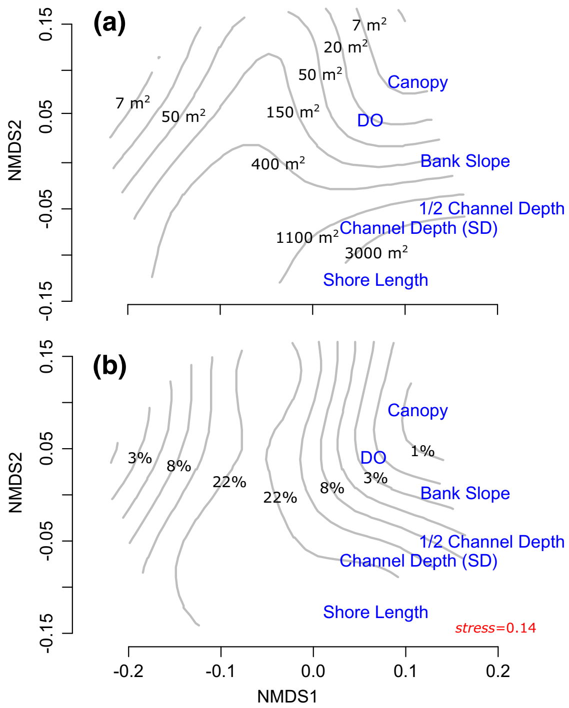

Fig. 4 Nonmetric multidimensional scaling ordination with Bray–Curtis distance and fitted GAMs representing the relationship of total and proportional areas of parrotfeather cover with physical and chemical characteristics measured at 24 fixed sites in 2015 and 2016. Contour lines show the gradient fit computed by ordisurf GAM of **a** parrotfeather abundance and **b** parrotfeather dominance and overlaid on the ordination of environmental variables. The position of the six variables that contributed strongly ($P < 0.05$) to the ordination are shown in blue text: shore length = site shoreline length, channel depth (SD) = standard deviation of mid-channel depth, 1/2 channel depth = mean half-channel depth, bank slope = mean bank slope, DO = mean dissolved oxygen, canopy = mean riparian cover

mechanisms of dispersal. When plants have been studied, the focus has been on riparian areas and species (Tickner et al., 2001; Renöfält et al., 2005; Catford et al., 2014). Furthermore, the opportunity to survey invasion dynamics in an unregulated river system is increasingly rare, but one of the best opportunities to understand how longitudinal position, hydrology and other abiotic conditions relate to establishment and persistence of aquatic plants (Nilsson & Jansson, 1995; Demars & Harper, 2005; Ot'ahel'ová et al., 2007; O'Hare et al., 2011).

In line with our hypotheses, the proportion of river kilometers where parrotfeather is present has increased since the initial survey in the mid-1990s; however, the increase was only marginally significant. Because of methodological differences between the two time periods, we believe that these results are in fact conservative (i.e., the increase may be slightly overestimated). In the contemporary surveys, every plant or patch encountered was documented, whereas historical survey points were more likely to be collected as an aggregated site point. This process would tend to overestimate contemporary occupied RKM compared to historical surveys. Due to uncertainty in coordinates or site descriptions a small number of historical locations could not be georeferenced with confidence, which additions may have increased the number of unique sites. Lastly, surveyors noted that the winter of 1996 (pre-survey) had record flooding, and suggested that smaller plant populations in the mainstem river may have been scoured out (Resource Management, Inc., 1997). Corresponding with the relatively small increase in occupied RKM, we found that the proportion of sites with low to high parrotfeather abundance or density has not changed significantly since the historical survey period. The majority of locations with parrotfeather during both time periods were small (< 100 ft^2) infestations, with low numbers of sites supporting extensive areas of parrotfeather. Collectively, the historical-contemporary contrast indicates that parrotfeather is slowly expanding its distribution along the river, but that it becomes abundant and/or dominant in a minority of newly established sites.

River conditions seemed to favor parrotfeather establishment and growth between 2015 and 2016, a further indication that 2016 provided a conservative year for comparison with the historical survey. Previous studies have shown that annual species turnover for macrophytes in lowland rivers can be substantial over 1–5 years (Demars et al., 2014), and the measurable increase in occupancy and abundance between the contemporary years raises the question as to how well surveys conducted over short periods (i.e., 2 years) can capture variability that ultimately underlie long-term invasion dynamics. We believe that climate and hydrologic conditions during the contemporary survey period were likely to promote parrotfeather and other emergent macrophytes that benefit from reduced or moderate flow conditions (O'Hare et al., 2011). In 2015 there was a severe drought, with warmer temperatures and reduced summer flows relative to historical conditions and to 2016, and both years had relatively stable winter flows (Thurston County, 2017). An alternative or complementary explanation could reside in more stable spring (i.e., May) flows in 2016 compared with 2015, which may also have helped parrotfeather establish or expand. Notably, the Chehalis River is subject to very large winter floods that may periodically suppress populations, and a study that encompasses more years and a broader range of hydrologic conditions could help determine relationships between interannual variation in parrotfeather abundance and streamflows (Demars et al., 2014).

Also consistent with our hypotheses, we found evidence for downstream dispersal and establishment of parrotfeather, with a 28 RKM downstream shift from the historical period. Downstream dispersal and colonization of plant fragments can be expected in river ecosystems, particularly when frequent flooding and lack of natural or manmade barriers allows transport of propagules in a consistent way (Honnay et al., 2001). Less expected was that presence and abundance were relatively sparse in these lowest river reaches, with few well-established (i.e., large) parrotfeather sites below the historical downstream extent (RKM 57); this supports the conclusion that landscape or environmental features are limiting establishment or persistence in that segment of the river. During the historical surveys, surveyors noted the unexpected and complete absence of parrotfeather in lower river reaches (below the Satsop River, RKM 32) despite an abundance of apparently suitable wetland habitat, and suggested that tidal influence may have restricted establishment (Resource Management, Inc., 1997). Based on experimental work, it is plausible that parrotfeather would be limited in areas that are tidally influenced due to increased salinity of water and soil (Haller et al., 1974; Thouvenot et al., 2012) and consistent fluctuations in water level (Cao et al., 2012; Hussner & Champion, 2012; Zhang et al., 2021). We also find support for the observed sparseness in downstream reaches in work by O'Hare et al. 2011, which found reliable patterns of macrophyte distribution along a longitudinal gradient that was represented most strongly by specific stream power and associated factors of altitude, bed slope, bankfull width, and flood discharge. Furthermore, these relationships differed with plant morphology, with 'linear emergent' and 'branched emergent' species (i.e., the most likely classifications of parrotfeather) associated primarily with intermediate specific stream power, and diminishing downstream with high flood discharge and large bankfull width.

Consequently, the observed reduction of parrotfeather from upstream river reaches (which must be due to natural extirpation over time or control efforts) corresponds with the same longitudinal gradient, where emergent species were also diminished in upstream areas associated with altitude and increased bed slopes (O'Hare et al., 2011). The river segment where we observed parrotfeather was strongly reduced (from the urban centers of Chehalis to just downstream of Centralia) is closely aligned with the Middle Chehalis River ecological region (Fig. 1), which is characterized by an incised channel, resulting in low connectivity with the floodplain and stronger instream flows (Chehalis Basin Strategy, 2019). Bank stabilization practices have further reduced channel migration and creation of new wetlands in this area. We speculate that the initial introduction of parrotfeather occurred in this segment, near the town of Chehalis, but that populations disappeared over time due to winter scouring floods, channel migration and movement, or wetland succession, and that colonization of new suitable areas was minimal. Although control efforts were implemented between 1995 and 1997 (Wamsley & Hupp, 1997), we do not believe they contributed substantially to the observed contemporary distribution; parrotfeather requires many years to successfully eradicate and is likely to rebound in suitable areas (Moreira et al., 1999; Hussner et al., 2017). However, though our information is anecdotal, we suggest that the role of wetland succession in the disappearance of parrotfeather populations should not be discounted, and potentially warrants further study. As river channels migrate and riverine wetlands fill and shift toward riparian plant communities (Shankman, 1993), parrotfeather will disappear from those areas; if colonization of new areas nearby does not occur (or they are managed or extirpated rapidly), this could result in large-scale disappearance over time.

In contrast with low abundance and reductions in the Chehalis River Tidal and Middle Chehalis River regions (respectively), parrotfeather persisted over time and had the greatest contemporary abundance in the intermediate Lower Chehalis River ecological region. Persistence in this river segment, which is distinguished by an extensive floodplain and "diverse off-channel habitats" (Chehalis Basin Strategy, 2019), accords with the site-level characteristics that were observed to promote abundance and dominance of parrotfeather. We found that abundance or total area of parrotfeather cover was reliably associated with length of site shoreline, deeper water, and more variable water depth, all of which are characteristics of larger sites. However, dominance of parrotfeather—meaning the tendency to become monotypic and invade the entire water column—occurred in habitats with more uniformly shallow depths, and low bank slopes; these features were more prevalent in smaller sites with less shoreline length. Both abundance and dominance were limited in sites with denser riparian canopy cover. Our results agree with experimental and field studies where dominance and persistence of parrotfeather are associated with areas of shallow (< 0.8 m) water (Moreira et al., 1989; Sytsma & Anderson, 1993; Wersal & Madsen, 2011) and availability of light (Hussner, 2009; Xie et al., 2013). It should be noted that steep bank slopes reduce availability of light, but could also indicate areas with stronger winter (i.e., scouring) flows, which would also be expected to limit growth of parrotfeather (Moreira et al., 1999; Hussner & Lösch, 2005). Finally, we found that parrotfeather dominance was associated with low dissolved oxygen. Although we must consider that oxygen levels can be influenced by flow conditions and diurnal variation, previous testing has demonstrated that dissolved oxygen was reduced in quadrats where parrotfeather was dominant (Kuehne et al., 2016), and the current study supports that this is also observable at the site level.

Our work has multiple implications for management and control of parrotfeather, including illustrating value in understanding how environmental filtering can promote or constrain invasive aquatic plant populations. These results demonstrate that parrotfeather abundance and persistence is longitudinally associated with intermediate river reaches with extensive off-channel habitats, but seems less likely to establish or persist in areas where the channel is constrained and has higher water velocities (upstream) or where water depths and fluctuations become more extreme (downstream). The contemporary pattern of low occurrence and abundance of parrotfeather in the upper and lower segments of the river (above RKM 75 and below RKM 57) suggests that control efforts are more likely to be successful here, with less chance of new successful establishments and recolonizations. Conversely, containment may be the most feasible strategy in the intermediate segment, where parrotfeather has persisted over time and remains abundant. Management in this segment of the river could focus on stopping establishment in new areas, with an emphasis on early eradication in sites having features associated with parrotfeather dominance (shallow depth, low bank slope, and sparse canopy). In our own work surveying and experimentally treating parrotfeather over multiple years, we have seen large changes in abundance (both increases and dramatic reductions, including disappearance) that seem to result from regular processes of channel migration and wetland succession. A strategy that includes monitoring natural progression, stopping establishment in new areas, and focusing treatment in high-priority sites is likely to represent the most efficient use of management resources and the best likelihood of reducing occurrence over time.

Our results also demonstrate that parrotfeather distribution and abundance are related to landscape characteristics and site-level features that can be influenced by humans, namely through hydrologic alteration and land use practices; this includes restoration activities such as increasing riparian shading and restoring connectivity of off-channel areas. Although our methods and dataset did not allow evaluation of flow conditions, the strong association of parrotfeather with an extensive floodplain and areas of low flow such as backwaters, channels, and sloughs in this and other studies is consistent with minimal tolerance of high flow conditions (Moreira et al., 1989, 1999; Hussner & Lösch, 2005; Hussner, 2014). Areas where parrotfeather is prevalent and persistent are likely to be ongoing sources of secondary spread downstream as well as through lateral movement via flooding and transport by wildlife (i.e., nutria, beaver, birds). Consequently, we recommend that hydrologic alteration that stabilizes the natural flood regime and reduces winter scouring flows, such as those associated with new dam construction, should be carefully considered for its potential to increase distribution of parrotfeather, Brazilian elodea (*Egeria densa*) and other invasive macrophytes as has been found across diverse riverine systems (Ot'ahel'ová et al., 2007; Aguiar & Ferreira, 2013; Martins et al., 2013; Demars et al., 2014; Vivian et al., 2014). Our results are also consistent with other studies showing that parrotfeather is sensitive to shading (Wersal & Madsen,

2013) and that reducing canopy cover in riparian areas can promote establishment and persistence of parrotfeather (Xie et al., 2013).

We note that this analysis was only possible because mapping and surveys for parrotfeather existed for more than one time period; other non-native plants present in the basin have been the focus of consistent control efforts (i.e., *E. densa*), but without similar systematic surveys that allow examination of longitudinal or landscape patterns. Evaluation of invasive plant management and control efforts are the exception rather than the norm, and understandable given that resources to control non-native plants invariably outstrip demand (Pluess et al., 2012). However, there is then little guidance as to whether current control methods are a good investment of resources, and how environmental filtering could enhance or optimize management. We hope that this study helps incentivize systematic surveys and analysis of landscape and hydrologic factors to inform management of invasive plants, which can result in ecological damage to aquatic habitats (Thomaz & Cunha, 2010) and high management costs (Hussner et al., 2017). Understanding the environmental factors that facilitate and promote establishment and growth of parrotfeather and other invasive macrophytes should also be a critical feature in planning large and small-scale restoration of aquatic habitats (Chehalis Basin Strategy, 2019), including the preservation and restoration of natural hydrologic regimes (Tonkin et al., 2018).

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Author contributions LMK and JDO designed and procured funding to conduct the 2015–2016 survey, and LMK led the field component of this survey. BW designed, procured funding for, and implemented the 1996–1997 survey. LMK, BW, and MH designed and implemented the contrast between the two survey periods. LMK and MH synthesized survey and spatial data for the two periods, and conducted the data analysis. All authors contributed to writing and editing the final manuscript.

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Availability of data and material The datasets generated during and/or analyzed during the current study are not publicly available due to some locations being on private land, but are available from the corresponding author on reasonable request.

Code availability These analyses do not rely on specialized software or custom code; however, code used in analysis or development of figures is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest or competing interests to report.

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